Chapter 1
Feeding, a Tool to Understand Vertebrate Evolution Introduction to “Feeding in Vertebrates”

Vincent Bels and Anthony Herrel

A major problem of evolution addressed by Darwin, in his *Origin of Species* (Darwin 1859) is the evolutionary relationship between complex structures and their function, colloquially referred to as *form-function* relationships. Many of the insights that Darwin contributed to our conceptual framework of evolution are based on careful observations of traits in diverse fossil and extant vertebrates. The morphology and ecology of organisms revealed by subsequent experimental work and detailed study of behavior have added to Darwin’s observations to shape our understanding of the evolutionary relations between form and function (Stauffer 1957; Schulter and Grant 1984; Liem 1990). Following this biological tradition, the present volume describes the *trophic system*, the body parts of animals, and their associated behaviors that are central to feeding. According to Dullemejier concluding the book *Biomechanics of feeding in vertebrates* (Bels et al. 1994), this book reports on “…*the astonishing diversity of ways in which organisms cope with the problem of obtaining food…*”.

The structures and behaviors, and the mechanisms leading to form–function relationships under natural and sexual selection have been described in previous works (i.e., Thomson 1917, 1988; Dullemejer 1974; Gans 1974; Gould 1971; Lauder 1985; Hanken and Hall 1993; Reilly and Wainwright 1994; Wainwright 1994, 2007; Lauder and Thomason 1995; McGowan 1999; Dutta and Munshi 2001; Irschick and Higham 2016; Schwenk 2000; Alfaro et al. 2004; Cooke and Terhuve 2015; Mcnulty and Vinyard 2015; Saxena and Saxane 2015; Abzhanov 2017; Barnet 2017). In addition, over the last 50 years, many studies have addressed the interactions between phenotypic

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traits and the function of the trophic system in vertebrates (i.e., Bels et al. 1994, 2003; Schwenk 2000; Bhullar et al. 2012, 2015). Schwenk (2000) provides a guide to the problem addressed in this volume "*…Despite extreme variation in form and function, tetrapod feeding systems are amenable to comparative analysis because they represent modifications of the same basic apparatus comprising, for the most part, a set of unequivocally homologous parts…*". He goes on to emphasize "*…the relative functionality of the feeding system has, without a doubt, a large impact on individual survival and hence lifetime reproductive success…*" as Gans (1994) highlights "*The study of feeding types and ingestion patterns … consequently offers great opportunities for understanding evolutionary patterns*".

The skull has been described in a plethora of studies documenting its relation to environmental, historical, development constraints acting on its morphology, and its biomechanics and function (i.e., Lauder and Shaffer 1993; Dial et al. 2015; Tseng and Flynn 2015; Wilga and Ferry 2015; Ledogar et al. 2016; Olsen and Westneat 2016; Abzhanov 2017; Fish 2017; Pestoni et al. 2018). Smith (1993) identifies a number of constraints that explain the characteristics of the form of the skull in vertebrates including: (i) physical constraints due to the basic physical (mechanical) processes, (ii) selective or compromise constraints that are produced by competing demands on the interdependent elements of the structure, (iii) phylogenetic constraints due to evolutionary modifications in lineages with a common ancestor, and (iv) developmental constraints produced by morphogenetic processes. To these constraints must be added epigenetic constraints (Smith 1993). Epigenetic constraints show that distinct morphs can be selected through regulating developmental and cellular differentiation processes within the bounds of the phylogenetic plasticity of the structure.

The present volume describes the functional evolution of feeding in chordates and vertebrates in aquatic, terrestrial, and interface habitats. In the introduction to the volume "*Biomechanics of Feeding in Vertebrates*" edited by Bels et al. (1994) in the series *Advances in comparative Environmental Physiology* (Volume 18, Springer-Verlag), Gans (1994) wrote: "*Feeding involves the development of hunger, the identification and positioning of the predator relative to the prey, and the acquisition of the entire or part of the prey*" and emphasized "*Finally it seems useful to remember why the magnitude of adaptation is of interest. The role is that functional aspect of the phenotype that enhances the survival or evolutionary fitness of the individuals*" *and "…analysis of adaptation always depends on a detailed characterization of suites of interactions…*".

The present book "*Feeding in Vertebrates*" integrates the complex morphological, functional, and behavioral interactions of cranial and postcranial systems in the phylogenetic and ecological contexts of food exploitation. This endeavor involves linking various disciplines as emphasized by Ashley-Ross and Gillis (2002): "*…those interested in animal form and function have recently begun branching out to incorporate approaches from experimental biomechanics and other disciplines (see accompanying symposium papers), and functional morphology now stands at the threshold of becoming a truly integrative, central field in organismal biology*". Obviously, this book raises empirical questions concerning the adaptive radiation of chordates and vertebrates derived from interactions in which the anatomical (and physiological) properties of the structures play a key role "…*the morphological diversification that is functionally related to the utilization of different types of resources following the expansion into a variety of unoccupied ecological niches*" (Tokita et al. 2017).

The approach in this book is integrative and based on studies of the links between form and function in the tradition of functional morphology and evolutionary biology (i.e., Bock and Wahlert 1965; Dullemejer 1980, 1994; Lauder 1981, 1983; Bramble and Wake 1985; Reilly and Lauder 1990; Hiiemae and Crompton 1985; Hildebrand et al. 1985; Liem et al. 2001; Bout 2003; Homberger 2003; Kardong 2015; Wake 2015). In all of the chapters in this volume, the term "*function*" refers to the "*biological role*" of the morphological traits (Irschick and Higham 2016) in the broadest sense. "*Biological role*", is defined by Irschick and Higham (2016) as "*the action that natural selection has previously favored*". Thus, the biological role is viewed through the behavior (i.e., feeding, drinking, displaying, and chemical collection) that vertebrates use in order to respond to environmental stimuli. This is accomplished through the action of the various hard (e.g., skull, hyoid apparatus) and soft (e.g., musculature) elements of the trophic system. These responses are complex and involve not only the tropic system per se but also the whole body of the animal, and are governed by a complex physiological process such as satiation (Fig. 1.1). In the case of feeding "*function*", the diversity of properties of the nutritious substances (i.e., living prey, meat, plants and fruits, nectar) selected by chordates and vertebrates have acted as one of the key selective pressures in the evolution of chordate and vertebrate lineages resulting in the evolution of the trophic system.

The trophic system includes the tongue, head and skull, the teeth, as well as the rest of the body for all lineages considered in this book. The functional output of the trophic system can be quantified by its performance. For Wainwright (2007), performance is the ability of individuals to do the tasks that fill their lives. Feeding performance traits have a complex underlying basis in the size, shape, and various properties of the components of the trophic system (Bels et al. 1994; Schwenk 2000; Liem et al. 2001; Aerts et al. 2002; Dial et al. 2015), and the interactions between per-

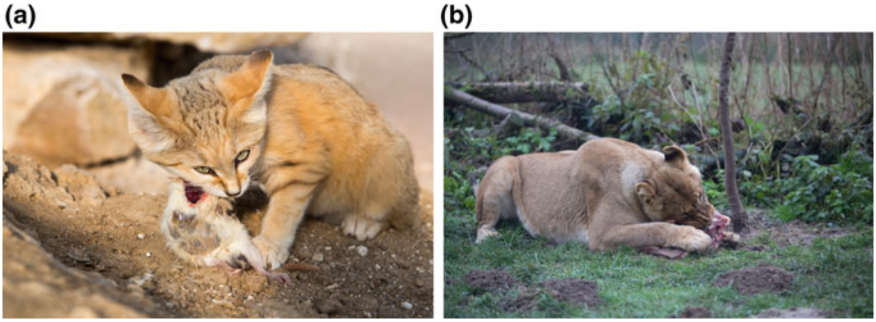

Fig. 1.1 Typical feeding posture in vertebrates using cranial and postcranial systems during feeding behavior. The small felid uses only the jaw apparatus (**a**) while large felids use their forelimbs to manipulate carcasses and meat (**b**)

formance and its underlying anatomical elements reveal a large number of complex evolutionary dynamics. The chapters in this book summarize the functional diversity of the trophic system from anatomy to performance and behavior (sensu, Wainwright 2007) and depict and interpret the complexity of this functional diversity in chordate and vertebrate lineages through empirical case studies.

The role of feeding in evolutionary processes is evident at all levels, from individuals to communities, and in all lineages that, at different geological times, successfully occupied a diversity of aquatic and terrestrial ecosystems. Feeding, and especially predation, has had a major structuring effect on animal communities since the Cambrian (Bengton 2002; Marshall 2006; Vannier 2009). A large number of studies on cranial and postcranial musculoskeletal systems in vertebrates demonstrate that feeding behavior has played a key role in the theories of evolutionary biology. This is best illustrated by the biological diversity of the beak and feeding (behavioral ecology) of Galapagos finches noticed by Darwin. The form–function interaction exemplified through a "*form-function complex*" as suggested by Williams (Chap. 18) can be viewed as a trait with implications for our understanding of the evolution of these animals.

All of the chapters in this book relate to one or more of the five levels of analysis (e.g., behavior, peripheral morphology or anatomy of the musculoskeletal system, motor pattern, central nervous system structure, and circuit), needed to study the relationships between trophic form function as suggested by Lauder (1991). These levels are approached in different ways in each of the chapters in the biological context of the relationships of form and function demonstrated for all lineages of chordates and vertebrates (Chaps. 7–21). These chapters refer to the "*function*", "*biological role*" or "*role-associated aspects*" of the structure (Bock and Wahlert 1965; Gans 1994) as stated by Bock and Van Wahlert (1965): … *Its function is its action or simply how the feature works, as stemming from the physical and chemical properties of the form; a feature may have several functions that operate simultaneously or at different times. A faculty is defined as the combination of a form and a function of a feature; it is what the feature is capable of doing in the life of the organism. The biological role is the action or the use of the faculty by the organism in the course of its life history. A biological role can be ascertained only by observation of the organism living naturally in its normal environment.*

As described throughout this book, the tentative correlation between form and function of the trophic system must be considered as hypothetical until functional principles are established to demonstrate that the observed "*form*" properties necessarily respond to one or several environmental constraints. This is a difficult approach. Before postulating an established relationship between the properties of a structure and its "*function*" or its biological role, it is necessary to determine the involvement of the structure studied in all behaviors, not only feeding, used by an organism to interact with its environment. In this context, two chapters (Brainerd and Camp, Chap. 2; Rayfield, Chap. 3) deal specifically with questions of structural complexity and the relationships between the properties (e.g., anatomical, mechanical) of the trophic musculoskeletal system in diverse vertebrates and the complexity of the performance traits and behaviors in which they are involved. Defining all of the performance traits involved in behaviors thus remains a central point. According to Schwenk (2000), "*form and function, experiment and description, qualitative and quantitative data must be held as equally important, complementary, and ideally, "reciprocally illuminating" elements…*".

All of the chapters in this book place the integrated form-function properties of trophic (and sometimes non-trophic) features into the evolutionary and ecological contexts to explain how chordate (Clark et al., Chap. 7) and vertebrate (all other chapters) organisms are able to feed and thus assure their survival and reproductive fitness. For this reason, this book can be viewed as continuing the work of Arnold (1983), modified by Garland and Losos (1994) and more recently by Irschick and Higham (2016), exemplifying the relationship between structures and individual fitness (Fig. 1.2). This paradigm makes it possible to situate studies related to the adaptive nature of feeding behavior by providing information on how factors ("stressors" after Arnold 1983) relate to behavior (i.e., prey/food availability and properties) to influence fitness.

Garland and Losos (1994) refined the paradigm by associating two factors (environment and genotype) influencing morphological traits and by indicating that intra- and interspecific interactions can influence behavior. Similarly, they propose that the environment ("habitat") can directly influence performance and the resulting behaviors. Finally, they suggest that morphological traits can directly impact fitness through their effect on performance as emphasized by Johnson et al. (2008): "*The*

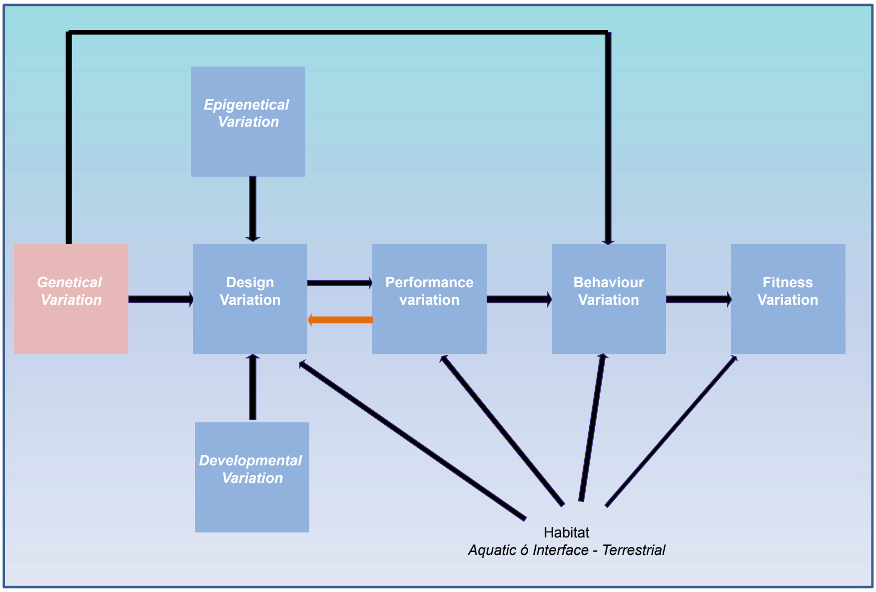

Fig. 1.2 Oversimplified heuristic diagram showing factors influencing the relationships between morphology, performance, and fitness through feeding behavior in chordates and vertebrates (modified from Arnold 1983; Irschick and Higham 2016)

outcome of species interactions (competition, predation, etc.*) is determined not by traits directly but how traits affect performance in the whole organism* (Arnold 1983). *Performance, when integrated as a function of a trait's contribution to fitness, can clarify how selection operates. In addition, unmeasured aspects of performance may be inferred by including direct pathways to fitness*". To understand how the complete evolutionary context of natural and sexual selection (e.g., the hyoid apparatus in Squamates) drive the evolution of the trophic system, an integrative view of the interaction between environment and development and how this influences morphology, performance, and fitness is essential. Therefore, all of the chapters of this book can be integrated into the paradigms determined by Arnold (1983), and modified by Garland and Losos (1994) and more recently by Irshick and Higham (2016).

Conceptually all of the chapters of this book illustrate, at various levels, the effect of selection through the influences of environment, genetics, epigenetics, and development, and so help to clarify the selective forces in chordate and vertebrate lineages (Fig. 1.3). Epigenetic and developmental approaches are currently being developed with several models that link functional morphology, phylogeny, and the evolution of the relations indicated in this paradigm. For example, recent work done on the beaks of birds (Abzhanov et al. 2006, 2007; Bhullar et al. 2012, 2015; Abzhanov 2017) combines the diversity of form function (sensu Lauder 1996) with genetic control during development.

Approaching questions pertaining to form-function diversification and evolution in the radiation of chordate and vertebrate lineages requires an integrated approach. Gans (1994) stated, "*It has become common to start functional and biomechanical comparisons by mapping their states on phylogenetic diagrams*". Integrated studies are needed at several time scales, as demonstrated in the majority of the lineages studied (see Chaps. 7–21). Paleontology, comparative and functional anatomical studies, behavioral ecology studies, and comparative studies of trophic systems have all provided evidence that evolutionary changes in the feeding system have defined the success of every vertebrate lineage. Recent evidence that changes can occur very rapidly and be observed on a timescale "*commensurate with ecological processes*"

Fig. 1.3 The demands of feeding on various types of foods with different trophic designs are highly variable as demonstrated in many chordate and vertebrate lineages. **a** A whole fruit is transported without any kind of manipulation in *Rhyticeros undulatus* (*Aceros undulates*). **b** Crushing a snail in *Dracaena guianensis* requires the development of high bite forces and the control of a complex jaw musculature. **c** *Lialis burtonis* has to deal with large prey items

as suggested by Stroud and Losos (2016) also shows that rapid changes in trophic systems and behavior result from the adaptive responses to environmental changes that can be extremely “brutal”. This volume shows how various forces (historical and environmental) drive this complex system. By using empirical and experimental approaches to establish functional micro- and macroevolutionary scenarios of the evolution of food acquisition in chordates and vertebrates, significant insights into the drivers of phenotypic diversity are gained.

Lauder (1991) raised two important questions about the complexity of form—function relationships that depend on ecological constraints: (i) At what level of integration do complex systems exist in an organism? (ii) Does the change of a component of a complex system affect (necessarily or not) the other elements of the same system? These questions summarize the complexity of the integration of the different elements that make up the trophic system. Trying to understand the evolution of feeding through a view of the trophic system only is too restricted. Classically, the trophic system is viewed as the major unit associated with feeding (and drinking) with the postcranial structures being the secondary unit (Kardong 2015; Ken and Carr 2019). Although noting the need for integration, many previous reviews focusing on feeding behavior have not attempted to document the involvement of other body elements (Bels et al. 1994; Schwenk 2000) that Dullemeijer (1994) insisted on by stating “*Therefore, one should bear in mind that not only the head, but also many other regions of the animal body, cooperate in the feeding mechanism*”. Higham (2007) (in aquatic habitats) and Bels et al. (2019) (in terrestrial habitats), focus on the major functional and integrated role of locomotor and trophic designs in predator–prey interactions. For the predator, capturing and killing prey involves the postcranial musculoskeletal system as shown in several chapters of this volume. The biological role of the postcranial elements and their association in feeding is therefore not negligible (Marshal and Goldbogen 2015; Hocking et al. 2017). Efficient feeding requires the combined movements of cranial and postcranial elements. The use of the forelimbs and hands for feeding in many vertebrate species as described by Montuelle and Kane (Chap. 4) and Wishaw and Karl (Chap. 6) plays a key role in the success of feeding. For example, feeding behavior in carnivorous mammals (Fig. 1.1) is related to the involvement of two distinct modules: a cranial module and a limb module (Gatesy and Dial 1996, Meachen-Samuels and Van Valkenburgh 2009). Clark et al. (Chap. 7) also demonstrate that jawless hagfishes use their flexible bodies to create rigid structural support for their everted tooth plates to create an efficient prey capture. These authors demonstrate the hierarchy in movements to reach, grasp, and bring food to the mouth within their own phylogenetic history as explained for vertebrates by Whishaw and Karl (Chap. 6).

Trophic form–function interactions need to investigate properties of a set of skeletal (including teeth as demonstrated by Ungar and Sue, Chap. 11) and muscular (Bels et al. 1994; Schwenk 2000; Kardong 2015; Abzhanov 2017; Diogo et al. 2018) organs under neuronal control (Filosa et al. 2016). Experimental methods such as electromyography, strain gauges, high-speed cinematography, can be used for describing feeding. Our knowledge of form–function relationships and the biological role of the structure are increased by methodological, technical, and conceptual advances. These allow the investigation of the properties of the anatomical structures while simultaneously describing and quantifying feeding. In part I of this book "*From structure to behavior*", two chapters emphasize how several new methods such as X-ray Reconstruction of Moving Morphology (XROMM) and fluoromicrometry use images for revealing 3D form–function relationships of cranial and cervical musculoskeletal structures (Brainerd and Camp, Chap. 2) and deductions based on Finite Element (FE) analysis (Rayfield, Chap. 3). These approaches show promise in revealing the morphological and functional properties of the trophic systems in relationship to historical and environmental constraints. As demonstrated by Brainerd and Camp (Chap. 2), questions related to the biomechanics of the trophic system in aquatic and terrestrial environments such as cranial kinesis in squamates, jaw mechanics and tooth occlusion in mammalian mastication, and pharyngeal jaw mechanics in fishes can all be understood using these novel approaches. Combined with fluoromicrometry to measure activity in muscles with complex architectures in association with experimental devices gives one the opportunity to understand the intrinsic functioning of the trophic system within its adaptive and evolutionary contexts.

How feeding and other behavioral activities take place, and the nature of form—function interactions of the trophic system, are reviewed in all of the chapters of part II "*Feeding in vertebrate lineages*" of this book. The new findings presented in these chapters emphasize the contribution of empirical, experimental, and field studies to integrating functional morphology and biomechanics with disciplines such as behavioral ecology, physiology, and biomimetics. The relationships between structure and fitness revealed by performance and behavior take place in specific environments, thus constituting the ecological context that impacts each of the relationships (Fig. 1.2). Three environmental constraints are summarized in the chapters of this part of the book: (i) aquatic habitats (Chaps. 7–9, 10, 12, and 19), (ii) the interface between aquatic and terrestrial habitats (Chap. 5), and (iii) the terrestrial habitat (Chaps. 10–18 and 20–21).

The question of feeding in water (Fig. 1.4) is documented in chordates (Clark and Uyeno) and a series of vertebrate lineages as documented by Huber et al. (Chap. 8), Gidmark et al. (Chap. 9), Herrel et al. (Chap. 12), Gignac et al. (Chap. 15), Lemell et al. (Chap. 16), and Marshall and Pyenson (Chap. 19). These chapters show that understanding feeding in an aquatic habitat by the different vertebrate lineages provides examples of the form–function complex shaped by the physical constraints of feeding in water (Fig. 1.4). Clark et al. (Chap. 7) explain how hagfishes and lampreys, who have no jaws, use their dentation to feed by biting and causing damage to the tissue of large marine animals. They present the jawless feeding mechanism of these animals as a way to understand the evolution of chordate feeding behavior, and the evolutionary origins of jaw-driven feeding. Based on a comprehensive integrative review of the morphology, biomechanics, and performance, these chapters also show the complexity of the feeding behavior related to the diversity of chordates and conclude, "*Because the jawless condition represents the primitive feeding apparatus for vertebrate animals, the biomechanics and functional morphology of jawless feeding in hagfishes can bear some insight into the selective and functional advantages of jaws…*".

Fig. 1.4 Feeding in whale (*Courtesy* Amy Knowlton, New England Aquarium, NOAA Permit Number 15415)

Huber et al. (Chap. 8) provide a novel holistic approach of feeding in elasmobranchs or cartilaginous fishes, and develop an integrative synthesis of the relationship between structure, performance, and behavior. They bring an analysis of these relationships within a phylogenetic and ecological framework that permits them to emphasize that "…*we are now beginning to understand the manner in which sensory perception guides the movements of the jaws, and how the biochemical composition of those jaws affects their mechanical performance. Developing this synthesis has also helped identify knowledge gaps that will hopefully be rectified as research on feeding in cartilaginous fishes continues into the 21st century*".

Gidmark et al. (Chap. 9) describe the feeding of fishes and demonstrates the extensive progress made in describing their morphology, development, and feeding behavior within evolutionary and ecological frameworks. The authors propose integrative ways to understand the diversity of feeding mechanisms and to understand how animals respond to the constraints on feeding behavior: "*The integration of musculoskeletal biomechanics with research approaches in neurobiology, such as neurophysiology and brain to behavior approaches, could potentially produce important insights and make fish feeding an important model system for neuromechanics*". Moreover, they confirm that an integrative approach of experimental biomechanics in fish model systems such as zebrafish or medakas within a phylogenetic context can bring new insights to the form–function complex of vertebrates in aquatic habitats. This a key point to understand how natural selection acts on form function. They emphasize that "... *using phylogenetic frameworks to make informed choices* *for species selection in feeding studies is important in order to get maximal value out of often difficult to obtain biomechanical data. As our database on feeding traits and integrative form-function insights grows, this will empower a new generation of research on the diversity and evolution of fish feeding mechanisms*".

Marshal and Pyenson (Chap. 19) describe feeding in aquatic mammals and illustrate the diversity of feeding phenotypes in response to changing environmental conditions in lineages with highly different phylogenetic histories, with all of the extant species departing from ancestors feeding in a terrestrial environment. They show the diversity of behavioral responses of animals exploiting various food resources with specialized trophic systems evolving from their terrestrial ancestors and note that "*…. mechanisms and adopted novel ways of feeding are influenced by both phylogeny and ecology. Here we highlight feeding strategies as diverse as aquatic herbivory, raptorial biting, suction to filter feeding, each of which have evolved in numerous mammalian lineages*" and conclude "*Most aquatic mammals are multimodal trophic opportunists that have made substantial departures from the classic terrestrial process model of feeding. Major departures from the process model have focused on food acquisition, and for most, the loss of mastication and intraoral transport to teeth, homodonty and even the total loss of teeth in some lineages*". As for fishes, they make the case for an integrative knowledge of the neuromuscular and sensorimotor control of feeding behavior in a comparative context and emphasize that "*discoveries of new fossils and the development of new phylogenetic tools will allow scientists to further clarify functional transitions from land-to-sea and provide new perspectives on the evolution of mammalian feeding*".

The other chapters involving aquatic and terrestrial species include Gignac et al. (Chap. 15) and Lemell et al. (Chap. 16) who demonstrate the importance of comparing aquatic and terrestrial species in the context of the phylogeny of these lineages. In Crocodylians, Gignac et al. emphasize the need to understand the morphological and functional implications of food/prey selection on the trophic system: "*What factors directly caused the many shapes of the suchian jaw, allowing their snouts to have been so evolutionarily variable? Perhaps ongoing studies focused on fluid flow and sub-aquatic hydrodynamics of the snout*". Turtles are one of principal groups that allow us to understand the effect of the transition from aquatic to terrestrial habitats in vertebrates as concluded by the authors: "*As might be expected, the morphology of the turtle feeding apparatus is closely associated with feeding habitat. Aquatic species have flat skulls, a large ossified hyobranchial apparatus with a small tongue, whereas purely terrestrial species possess the opposite: a high skull, and a small cartilaginous hyolingual apparatus with a large muscular and movable tongue that allows active lingual transport of food objects from the environment to the esophagus. Since turtles are characterized by a very long evolutionary history within diverse habitats, they are one of the most suitable groups within vertebrates to present morphological and behavioral variations and adaptations related to feeding medium and food type*".

The transition between aquatic and terrestrial habitats is one of the key points in understanding the evolution of tetrapods, as illustrated by feeding in amphibious fishes living at the interface between water and land. Van Wassenbergh and colleagues (Chap. 5) explain the mechanical challenges and functional solutions required to successfully feed in an environment that is key to the terrestrial transition in vertebrate evolution. Through their extensive studies, they generate hypotheses on the evolutionary history of early tetrapods. Again, this review shows how the integration of the cranial and postcranial elements to maintain body posture is essential to allow the capture of food in the terrestrial environment, and how the trophic system works to capture and transport the food for efficient digestion in air. They note, "*When transitioning to a life on land, ancestrally aquatic organisms are faced with numerous challenges caused by the physical and chemical differences between water and air …Since air is about 800 times less dense and 50 times less viscous than water, buoyancy forces on an animal's body become negligibly small relative to the opposing gravitational forces, and both frictional resistance of the air and the work needed to overcome inertia strongly decrease. This has drastic effects on the mechanics of movement: transitioning to the terrestrial environment requires morphological changes to support the body and to generate propulsive forces…Not only biomechanical problems need to be coped with by the musculoskeletal system, many other organ systems are challenged as well - such as vision, hydration/desiccation,* CO_2 *retention and acidosis, and ion-balance regulation…*". Food/prey capture, reduction, transport, and swallowing need to be supported by integrative complex actions of the hard (skull including teeth, hyoid apparatus) and soft (muscles) tissues organized as coordinated trophic elements. Chapters 12–21 demonstrate these challenges in morphology, performance, and behavior in relation to the capture, transport, and digestion of food as soon as vertebrates were able to survive and reproduce in aerial conditions.

Three chapters explain the diversity of two key elements of the trophic system: tongue and teeth. Iwasaki et al. (Chap. 10) describe comparative studies of anatomical and biomechanical traits of the tongue in tetrapods. They state the tongue "*…plays a crucial role in many vital functions, such as food-uptake, mastication and swallowing. The morphological concept of the tongue is that of a voluntary muscle mass covered by a mucosal sheath. However, the tongues of amphibians, reptiles, birds and mammals have deviated in terms of general morphology and function*". Their review describes the diversity in "*form*" and "*function*" of the tetrapod tongue. The central role of this element of the trophic system is exemplified in chapters on amphibians, reptiles, birds, and mammals and demonstrated through examples such as the morphology and function of the tongues of specialized species such as frogs, chameleons among reptiles and nectar-feeding bats among mammals (part II of the book). Comprehensive studies of the lingual mechanism such as exemplified in amphibians (Herrel et al. Chap. 12) and lizards (Bels et al. Chap. 13) permits the modeling of tetrapod feeding and drinking functions. In a lot of tetrapods, "*The ability to catch a diverse array of prey puts special demands on the adhesive performance of frog tongues. The attachment to the prey must be at least strong enough to prevent the prey from escaping before it is grasped by the jaws*" as stated by Herrel et al. (Chap. 12) and highlighted for frogs, salamanders (Herrel et al., Chap. 12), and lizards (Bels et al., Chap. 13).

As demonstrated by Ungar and Sues (Chap. 11), teeth play a key role in the success of tetrapods because, as stated by these authors: "*Teeth provide an excellent model* *system for understanding evolutionary change and how it has led to adaptive diversity across tetrapods. Their durability over geological time scales and their ubiquity in the fossil record make teeth unique and allow direct comparison of dental structure for both extant and extinct species*". Ungar and Sues demonstrate the diversity of teeth (i.e., size, shape, and structure) and their central role in the adaptive radiation of a lot of tetrapod lineages to emphasize that teeth are "*are the front line in Nature's struggle for existence*". Their survey of all the morphological traits into ontogenetic and phylogenetic contexts opens clearly a lot of questions on feeding evolution as approached in all of the chapters in tetrapods (Chaps. 12–15, 18–21).

The complex interaction form function of the whole trophic system in terrestrial habitat (and in some cases in comparison with aquatic habitat) is discussed in amphibians by Herrel et al. (Chap. 12), in reptiles including turtles by Lemell et al. (Chap. 16), crocodiles by Gignac et al. (Chap. 15), snakes by Moon et al. (Chap. 14), lizards by Bels et al. (Chap. 13), and in mammals by Williams (Chap. 18) and by Ross and Iriarte-Diaz (Chap. 20) and Vinyard et al. (Chap. 21). These chapters provide examples of the evolutionary trends of the trophic system to exploit food/prey from food identification (i.e., vomerolfaction as described by Moon et al. (Chap. 14) and Bels et al. (Chap. 13) to food transport. The salient point of all of these chapters is to reveal the complexity of feeding behavior and the need for integrative studies to discuss the form–function complex. In amphibians, Herrel et al. (Chap. 12) suggest that "*…Future studies quantifying feeding performance across a wide range of species are likely to provide critical insights into the selective pressures underlying the evolution of the staggering diversity in feeding form and function observed in amphibians*". Snakes "*characterized by a unique feeding system and other traits associated with elongation and limblessness*" are described by Moon et al. (Chap. 14) who emphasize that these "*gape-limited predators*" are a key example of differences in head morphology linked to differences in diet. In the meantime, such differences are nested within the adaptive nature of head shape revealing striking evolutionary convergences in some clades of these vertebrates. Constriction present in various 'basal' (Henophidia) and 'advanced' snakes (Caenophidia) relates mechanisms associating trophic and axial systems in the evolutionary success. These authors also show the complexity of responses of vertebrates with highly specialized tongues in the behavioral and functional changes to morphological modifications associated with one key sensory function and conclude "*The great diversity of snakes calls for many more studies of feeding biology, which are likely to lead to the discovery of new mechanisms, as recent research has shown. In addition, by further integrating robust phylogenies, detailed morphological data, functional mechanisms, and ecologically relevant performance measures in future research, we will surely gain important new insights into how feeding, locomotor, and other mechanisms may have driven evolution and diversification of snakes*".

The diversity of the trophic system and its effect on the feeding behavior, particularly associated to morphological and functional tongue modifications is emphasized in some examples provided by Iwasaki et al. (Chap. 10) and exemplified for lizards (Chap. 13, Bels et al.). Bels et al. discuss trophic elements in light of the "Modal-Action-Pattern" of feeding (sensu Barlow 1978). Their chapter evaluates the effect of trophic specialization on the modulation and mechanisms of feeding and drinking in lizards (e.g., prey adhesion in chameleons). Lizards represent a model of evolution of prey/food capture in all tetrapods because in this clade the two modes of prey/food capture (lingual vs jaw prehension) can be observed (i) across species along the squamate phylogeny and (ii) within a same species in response to proximal factors of the prey/food. Indeed, as demonstrated by all tetrapods (Chaps. 18, 20 and 21), in an aerial environment the capture of prey/food is related to the actions of the jaws (jaw prehension) and/or the tongue (lingual prehension) toward the food. Bels et al. also show that the mechanisms of water collection are not constrained by tongue specializations until a "level" of morphological transformations observed in some clades "specialized" in vomerolfaction (Teiidae and Varanidae).

Questions related to the complexity of morphological, functional, and behavioral responses also drive Lemell's et al. description of turtles (Chap. 16). They argue that turtles "*are one of the oldest known reptile orders, appearing about 240 million years ago. Within the vertebrates, they have evolved the most unusual body plan, with most of their body inside a protective box made of bone and keratin. This peculiar morphology has persisted since the late Triassic, but has allowed them to adapt to very diverse ecological habitats, ranging from marine and freshwater to purely terrestrial environments, from temperate to tropical regions of all continents except Antarctica*". These authors focus on the adaptive morphological, functional, and behavioral traits of these tetrapods which feed in water and in air. They demonstrate that the morphology of the turtle feeding apparatus is "*closely associated with feeding habitat*".

Crocodylians with a "*wide range of snout shapes, tooth forms, and diets*" are "*exceptional ambush predators in near-shore environments*". Gignac et al. (Chap. 15) synthetize new knowledge on their feeding behavior and describe how feeding performance has shaped their head and jaws. Gignac et al. demonstrate that an in-depth knowledge of the fossil record reveals how form–function complexes and the subsequent feeding behavior in these reptiles evolved. They emphasize that biomechanical and functional questions still remain including, "*What factors directly caused the many shapes of the suchian jaw, allowing their snouts to have been so evolutionarily variable?*".

Rico et al. (Chap. 17) provide a form-function description of the trophic system in birds. Based on morphological traits, these authors review biomechanical and functional characteristics of feeding behavior in a wide diversity of bird species from hummingbirds to ostriches. From a comparative point of view, they "*explore the vast diversity of bird feeding environments by grouping foraging (searching) and feeding (handling – consumption) mechanisms that birds use on land, air, and water*". They associate "*what birds eat*" and "*how they feed*" through an understanding of the convergences, radiations, trade-offs, etc., that have shaped the feeding apparatus. As in the chapters on snakes (Moon et al., Chap. 14) and lizards (Bels et al., Chap. 13) they explain the drinking mechanism which often involves different actions than the ones used to feed. Finally, Rico et al. raise new questions about the competing selective pressures on the beak and head form–function complex; i.e., morphological novelties like casques or the de novo origin of muscles. As can be observed in all of the chapters, they also emphasize how new insights can come from methodological and conceptual approaches explained by Brainer and Camp (Chaps. 2) and Rayfield (Chap. 3).

Three chapters explore the evolutionary and adaptive nature of the trophic form—function complex in terrestrial mammals. Williams (Chap. 18) synthetizes integrated morphological, functional, and behavioral traits of mammalian feeding, from ingestion to swallowing, from comparative point of view of the clade. Various examples explain the complex interactions of the trophic elements (e.g., tongue) and solid food eating versus liquid food drinking to show the ability of this organ to play with proximal properties of the food. Williams highlights our understanding of how the tongue, lips, cheeks, jaw, soft palate, and hyoid are involved in feeding behavior. As exemplified in several chapters of the book, this chapter shows that some aspects of the interactions of form and function (i.e., muscles of mastication) in some models (e.g., primates) are becoming well understood. The motor control of structures such as the tongue, which plays a critical role in bolus manipulation and formation during chewing, remains to be explored not only in model organisms but also in the wide diversity of mammals exploiting different food resources. All these potential studies based on methodological and conceptual advances (Chaps. 2 and 3) will show what is called by Williams "*…novel form-function links… expanding our understanding of functional diversity, but may also bring to the forefront unexpected constraints and limitations on function and behavior in mammalian feeding*".

Feeding in primates (Fig. 1.5) is probably one key evolutionary model to explain the links between morphology, performance, behavior, and fitness (Ross and Iriarte-Diaz, Chap. 20, and Vinyard et al., Chap. 21). Ross and Iriarte-Diaz (Chap. 20) describe the evolution of feeding in primates and explain "*several ways in which integration of results from new and improved methods for experimental study of primate feeding biomechanics will significantly enhance our understanding of the biomechanical determinants of primate feeding performance*". Integration of data on high-resolution jaw kinematics in these model animals with the investigation of properties and mechanics of jaws and dentition provides an understanding of the role of diet, grit, and feeding behavior in evolution of primates and identifies the drivers of their craniomandibular diversity that play a key role in their adaptive radiation. As suggested in all of the chapters in part II of the book, Ross and Iriarte-Diaz emphasize "*One of the most exciting areas for future work is the integration of data on wild primate feeding behavior with the geometric and material properties of the foods they exploit*".

In the suite of chapters on the diversity of form–function interactions in mammals, Vinyard et al. (Chap. 21) conclude, when considering feeding in humans, that feeding "*played key roles in human evolution*". These authors pose questions on the evolution of feeding in humans and discuss "*…the functional consequences of gracilization and functional relationships within the human masticatory apparatus using non-human primates for comparison*". They conclude "*…that any performance deficits in the human masticatory apparatus are primarily related to gracilization. Humans possess a relative masticatory apparatus configuration that compares similarly to many other primates suggesting the evolution of humans has not unraveled the basic*

Fig. 1.5 Feeding in primates is one of the major models to understand the complexity of form—function relationship in vertebrates (*Courtesy* Emmanuelle Pouydebat, Muséum national d'Histoire naturelle, UMR7197 CNRS/MNHN)

functional relationships within the masticatory apparatus that characterize most primates".

In summary, this book provides an exposé of feeding in chordates and vertebrates. Each chapter reveals the complexity of morphological, functional, and behavioral traits and their interactions, and as such provides a tutorial of how natural selection has acted and still acts on the trophic system.

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