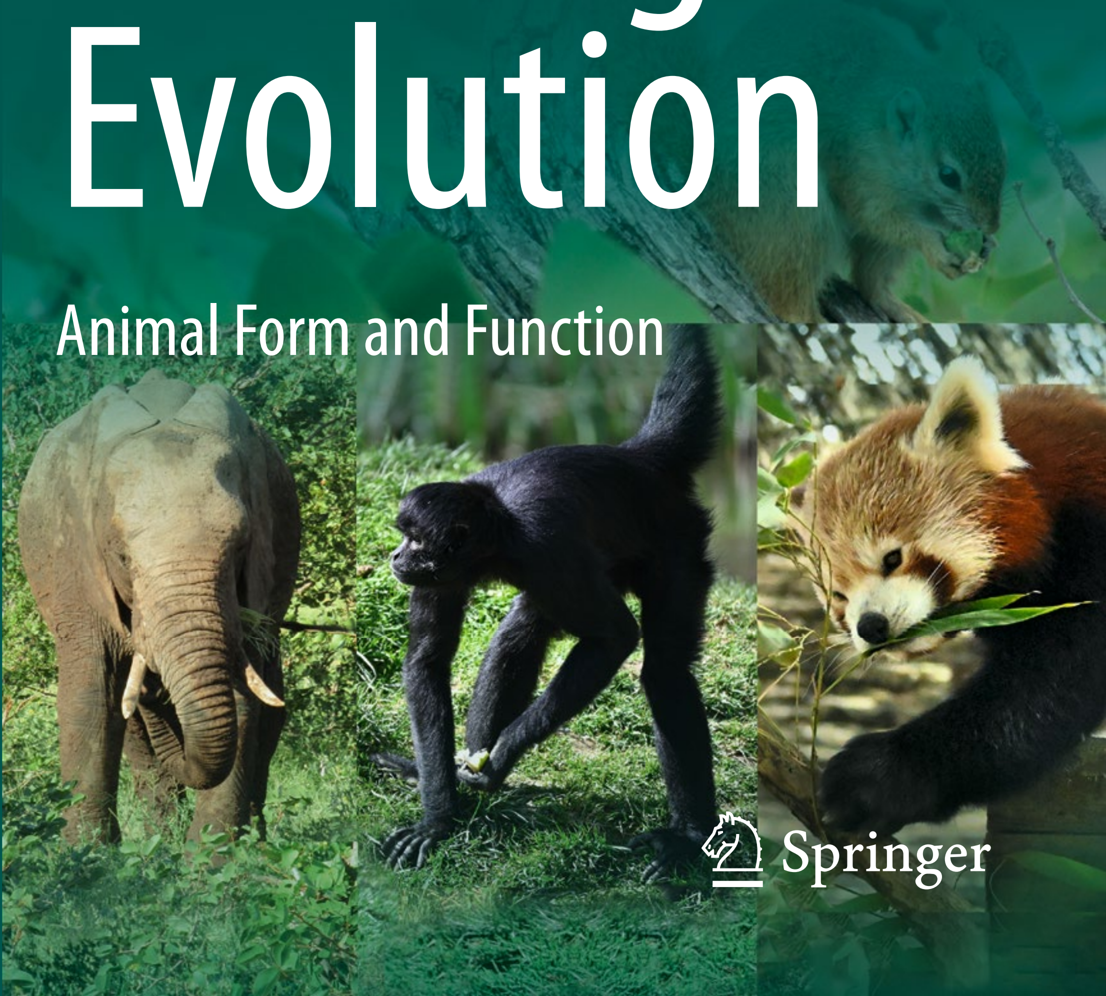
Fascinating Life Sciences

Vincent L. Bels
Anthony P. Russell *Editors*

Convergent Evolution

Animal Form and Function



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Editors

Convergent Evolution

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ISSN 2509-6745 ISSN 2509-6753 (electronic)
Fascinating Life Sciences
ISBN 978-3-031-11440-3 ISBN 978-3-031-11441-0 (eBook)
https://doi.org/10.1007/978-3-031-11441-0

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The editors wish to dedicate this volume to the memory of Professor David Wake (July 8, 1936–April 29, 2021) who was a source of inspiration in initiating this volume on convergent evolution.

Preface

Convergence is a concept of paramount importance for explaining similarities, across all length scales (from macroscopic to the nanometer level) between organisms whose similarities cannot be attributed to the sharing of features due to common ancestry. The investigation of evolutionary convergence is conducted in a variety of ways and employs various methodological, technical, and conceptual approaches.

The idea for this book, which focuses on convergence of functional approaches to environmental challenges, was spurred by the plethora of studies that explore this phenomenon from the perspective of pattern, process, or both. Our aim is not to provide a catalogue of the thousands of examples of biological convergence but to provide thoroughly considered examples at several levels within the taxonomic hierarchy of animals, both extant and extinct. Since the 1980s, functional convergence has been a major focus of investigators seeking to understand how organisms respond to their invasion of new habitats or to changing environmental conditions over evolutionarily long spans of time.

We are extremely grateful to the many authors who have contributed to this volume. They have provided fascinating insights into the extent of convergence between distantly related organisms and the role that phylogenetic history plays in the structural responses to major challenges imposed by the environment. We are also greatly appreciative of the selfless contributions made by reviewers of each chapter who devoted their time and energy to improving the chapters. We are particularly grateful to P. Aerts, A. Bauer, Ch. Boehmer, C. D'Août, Ph. Cox, P. Flammang, P. Gignac, S. Gorb, E. Heiss, O. Lambert, D. Schmitt, M. Segal, R. Tague, C. Turcotte, S. Van Wassenberg, and A. Werth.

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Chapter 1
The Concept of Convergent Evolution and Its Relationship to the Understanding of Form and Function

Vincent L. Bels and Anthony P. Russell

Within the field of evolutionary biology, divergence and convergence are two major phenomena that have helped shape the diversity and disparity of the Earth's biota throughout the history of life. Exploration of them has contributed to the interpretation of dissimilarities (divergence) and similarities (convergence) in organismic form, function and behaviour at various hierarchical levels and how they favour, in some fashion, the emergence of optimal traits via natural and/or sexual selection across the full spectrum of occupied environments.

Convergent evolution is one of the most commonly invoked evolutionary processes in macro- and micro-evolutionary studies for explaining the repeated appearance of organismic forms and traits. Agrawal (2017) emphasizes that "*The search for convergent evolution and its causes is one way to make sense of the wonderfully bewildering biological diversity on our planet*". Various definitions of convergence have been advanced, but all attempt to explain the resemblance between traits resulting from the influence of proximal and ultimate factors impinging upon organisms in their habitats. Stated most concisely, convergence is "*the evolution of the same or very similar traits independently in different lineages of organisms*" (McGhee, 2011). At the organismal level this results in phenotypic similarity (Mahler et al., 2017) either in particular suites of features or in whole body form (Arbuckle & Speed, 2016; Arbuckle et al., 2014; Almeida et al., 2021). Historically this similarity, initially established with regard to the form of organisms, became further refined through the description of anatomical traits that related morphological

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V. L. Bels, A. P. Russell (eds.), *Convergent Evolution*, Fascinating Life Sciences,
https://doi.org/10.1007/978-3-031-11441-0_1

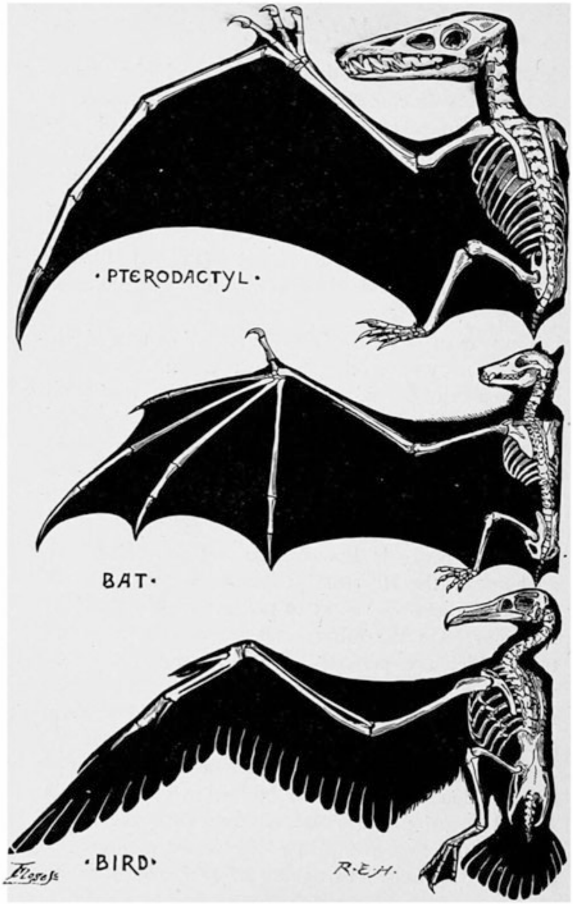

Fig. 1.1 A classical historical view of how homologous morphological traits of the forelimbs of distantly related vertebrates have evolved in a similar fashion in response to similar functional demands (powered flight) acting as selective forces. (**a**) Pterosaur, (**b**) Bat, (**c**) Bird (source: Wikipedia.org/wiki/Convergent_evolution#/media/File:Homology.jpg)

form to function in different groups of organisms, a classical case in point being modifications relating to powered flight (Fig. 1.1). The literature is rich in such examples of evolutionary convergence (and parallelism) that are based upon comparative studies at different scales of the classificatory hierarchy.

In this volume we explore the idea of convergent evolution across a broad range of phylogenetic scales, focusing upon the ways in which environmental challenges drive organisms towards similar outcomes through the evolution of complex form-function systemic adaptations (e.g., Shadwick, 2005; Quinn, 2020; Ballell et al., 2019; Gómez & Lois-Milevicich, 2021; Higham et al., 2021). The contemporary study of convergent evolution, as it relates to form and function, employs a variety of approaches, allowing form to be investigated at various levels, from the overall shape of the structures to their constituent elements. The application of novel technological imaging approaches (such as 2D and 3D geometric morphometrics and digital measurement; 3D tomography; surface scanning; digital reconstruction; finite element analysis) has become increasingly prevalent (Brainerd & Camp, 2019; Rayfield, 2019). These investigative tools have become important for addressing "*big evolutionary questions*" (Agrawal, 2017) and have enabled demonstration of the complexity of the traits involved in the realization of perceived function.

1.1 Recognition of the Phenomenon of Convergent Evolution

What ultimately became recognized as convergent evolution had its beginnings in the investigation and interpretation of morphology. Although no longer restricted to morphology, the issues raised during the initial investigation of what came to be recognized as convergent pathways in the history of life still influence the understanding and discussion of this concept.

The study of morphology experienced fundamental changes throughout the nineteenth century, in parallel with the emergence of biology as a unified discipline devoted to the scholarly exploration of life. Three major phases of research on animal morphology occurred throughout the nineteenth century (Russell, 1916). In the early years, during which Wolfgang Goethe characterized the study of organismal form as morphology (Nyhart, 1995; Singer, 1959), a transcendental approach was carried over from the previous century. In the second half of the nineteenth century this gradually gave way to an evolutionary approach (led by scholars such as Ernst Haeckel and Carl Gegenbaur), which emphasized phylogenetic trees and employed the methods of comparative anatomy to try to explain form (Nyhart, 1995). This, in turn, was superseded in the latter part of the century by a causal approach to morphology that integrated experimental embryology (as practiced by Wilhelm Roux). Collectively these changes characterized a transition from "structural" to "functional" morphology as the century progressed (Singer, 1959).

These shifts in the study of animal form resulted in the replacement of the idea that purpose was sufficient for explaining both organic structure and the succession of life through geological time (commonly held by morphologists at the beginning of the nineteenth century; Ospovat, 1978) by a nascent non-teleological interpretation of form by its end. Even so, morphology as a whole was not particularly successful in the assimilation of evolutionary ideas into its *modus operandi* (Ghiselin, 1980). This was so because the evolutionary approach to morphology, embarked upon as Darwinian reasoning gained increasing acceptance, brought with it fundamental questions about structural resemblances as indicators of evolutionary relationship (Bowler, 1996). Morphology played a prominent role in attempts to reconstruct patterns of historical connectivity (Bowler, 1996). Such investigations soon revealed that structural resemblances could not be universally explained as resulting from common descent and were thus not always reliable indicators of phylogenetic affinity. Instead, it became increasingly evident that structural resemblances could be independently acquired on different branches of the emerging tree of life. For morphologists the possibility of the same structure evolving independently in more than one group became problematic because, if evolution was to be a guide to classification, then shared characteristics should be a consequence of common ancestry (Bowler, 1996). It gradually became realized that when two or more originally very distinct forms came to occupy the same general environment they could, independently, acquire similar structural characteristics (Fig. 1.1). As a result, what became recognized as convergent evolution was identified as a topic worthy of investigation in its own right.

In the 1840s Richard Owen advanced the concepts of homology and analogy for, respectively, structural similarities fundamental to idealistic archetypes and superficial adaptive modifications (Bowler, 1996). Darwin, however, intimated that adaptive specialization was an inextricable consequence of natural selection and that, therefore, homology and analogy had to be assessed in a genealogical, rather than idealistic, framework. Lankester (1870) addressed the multiple origins of seemingly shared characteristics from a Darwinian perspective and coined the term homoplasy for adaptive analogies that were not due to common descent. Osborn (1902) subsequently advocated that convergence was the result of similar adaptation to particular environmental conditions.

Even so, morphologists were generally reluctant to acknowledge convergence as a major feature of evolution. Indeed, Willey (1911) regarded it as being essentially a hindrance to the identification of “genuine” homologies and a detraction from the reconstruction of the tree of life, which he saw as the primary goal of evolutionary morphology. Morphologists of the time lacked techniques that were able to unequivocally distinguish homologies from homoplasies (Bowler, 1996). Ultimately, they had to grapple with the competing ideas of whether evolution was driven by functional adaptation or by formal constraints dependent upon developmental attributes innate to the organism. By the 1940s, however, “The Modern Synthesis” (Huxley, 1942) enabled accommodation of the demands of both form and function. Interpretations of convergence were thus able to be framed within this unifying philosophy, with common descent implying that evolutionary novelties have arisen only once and that convergence results when putative evolutionary novelties are interpreted to have had more than one origin, reflecting similar adaptive responses to particular environmental challenges. Increasingly detailed morphological analyses have shown that seemingly identical structures often exhibit lineage-specific characteristics that confirm their homoplastic nature (e.g. Bergmann & Morinaga, 2018).

1.2 Approaches to the Study of Convergent Evolution in Contemporary Biology

Various terms have been employed in attempts to define and explain convergent evolution. Prominent among these are homology and homoplasy (see above), which Ochoa and Rasskin-Gutman (2015) regard, along with homogeny and parallelism, as evolutionary developmental (evo-devo) mechanisms acting along an evolutionary continuum. Hall (2007) and Wake (2013) conceptualize these various mechanisms as those relating to deep or more recent shared ancestry and that are based upon shared cellular mechanisms, processes, genes, and genetic pathways and networks.

Arendt and Reznick (2008) opine that distinguishing between evolutionary convergence and parallelism is problematic because these terms infer mechanisms that are seemingly dependent on the phylogenetic level at which the comparison is undertaken, as well as upon underlying genetic mechanisms that largely remain uninvestigated. They suggest that convergence be invoked for all evolutionary hypotheses that relate the independent acquisition of phenotypic form: "*Biologists often distinguish 'convergent' from 'parallel' evolution. This distinction usually assumes that when a given phenotype evolves, the underlying genetic mechanisms are different in distantly related species (convergent) but similar in closely related species (parallel). However, several examples show that the same phenotype might evolve among populations within a species by changes in different genes. Conversely, similar phenotypes might evolve in distantly related species by changes in the same gene. We thus argue that the distinction between 'convergent' and 'parallel' evolution is a false dichotomy, at best representing ends of a continuum. We can simplify our vocabulary; all instances of the independent evolution of a given phenotype can be described with a single term - convergent.*" Contrastingly De Lisle and Bolnick (2020) retain the two terms that Arendt and Reznick (2008) regard as representing a false dichotomy and argue that "*...conserved directional selection across lineages could result in parallelism without convergence. Alternatively, adaptation towards a shared optimum by lineages with unique evolutionary histories, and thus unique ancestral positions in trait space, could result in convergence without parallelism. Yet, parallel evolutionary processes can lead to divergence if, for example, one lineage evolves faster along a shared trajectory. Thus, separating parallelism and convergence may often be necessary to link evolutionary pattern and process*".

McGhee (2018), seemingly in at least partial agreement with Arendt and Reznick (2008), provides another viewpoint on the employment of terminology for distinguishing between the outcomes of evo-devo processes that operate along an evolutionary continuum. He suggests broadening the scope of the term "convergence" by recognizing three categories: allo-convergent evolution to account for the independent evolution of the same or very similar traits from different precursors in different lineages (= the conventional representation of convergence); iso-convergent evolution to account for the independent evolution of the same or very similar traits from the same precursor in different lineages (= the classical view of parallelism—see, for example, Riedel et al., 2021); and retro-convergent evolution to account for the independent re-evolution of the same or very similar ancestral trait in different lineages (= the classical view of reversal). Whether such revised terminology will become more universally applied in future remains to be seen. Based upon developmental processes, Hall (2013) regards homology and parallelism as concepts associated with features that arise from similar developmental processes (thus incorporating iso-convergent evolution as proposed by McGhee, 2018); reversals as potentially, but not necessarily arising from different developmental processes (thus incorporating [depending upon the developmental evidence that applies] retro-convergent, iso-convergent or allo-convergent evolution as proposed by McGhee, 2018); and convergence being dependent upon features arising from different developmental processes and characterized by homoplasies [thus incorporating allo-convergent evolution as proposed by McGhee (2018)].

It is evident from the foregoing that different authors regard convergence in various ways, leading to inconsistency and potential confusion in the application of the concept and the sorts of phenomena to which the term "convergence" should be applied. In this volume we deal essentially with what McGhee (2018) regards as "allo-convergent evolution" and use "convergence" in this sense, as advocated by Hall (2013) and Ochoa and Rasskin-Gutman (2015). Convergence, regarded this way, can result from the operation of various evolutionary processes (adaptation, constraint, development) or from purely stochastic events (Losos, 2011; Stayton, 2015a; Agrawal, 2017; Speed & Arbuckle, 2017) and appears to be widespread throughout the history of life. Two approaches have been taken to analyse the occurrence of the repetition of similar phenotypic traits of organisms at all levels: "pattern-based" and "process-based" (Stayton, 2015a). Pattern-based explanations rely upon the estimation of convergent evolution by comparing "terminal" traits without invoking any particular underlying evolutionary process, the observed pattern potentially resulting from shared or different evolutionary processes or simply from stochastic events. Process-based explanations, in contrast, incorporate adaptive and developmental factors (Stayton, 2015a), with convergence regarded as having arisen through shared evolutionary processes, such as natural selection, in response to similar internal or external environmental challenges. Interpretations of the convergence of form and function are almost exclusively process-based.

Recently, increasingly quantitative explorations of various traits, assessed in a phylogenetic context, have been employed to identify convergent patterns at various levels within the hierarchy of organismic structure and behaviour (for example Morris et al., 2018; De Lisle & Bolnick, 2020). In such instances convergence is viewed as a deterministic process that drives patterns that can be quantified and compared (De Lisle & Bolnick, 2020), in contrast to contingency that underpins less predictable, and thus less repeatable, outcomes. The potential for convergence in quantifiable traits, however, is dependent upon their own evolutionary history that is itself subject, at any time, to some degree of contingency (Blount et al., 2018; Powell, 2020).

During the last 20 years conceptual and methodological (such as the application of phylogenetic algorithms) analyses have enabled the interpretation of whether traits recorded in various lineages are attributable to the operation of selective pressures or simply the result of stochastic events (whereby random evolutionary changes result in descendant species becoming more similar to one another than were their ancestors) (Losos, 2011). Wake (2013) indicated that studying convergent evolution may provide insights into both the proximate and ultimate mechanisms that generate diversity and can be informative concerning the extent to which the evolutionary process is both repeatable and predictable (Mahler et al., 2013). Employment of robust phylogenetic hypotheses coupled with more stringent analyses of morphological data (Assis et al., 2011), together with the application of molecular, genomic and developmental techniques, will enable a more integrated investigation of the mechanisms through which similarity arises (Wake et al., 2011; Hall, 2013). Sackton and Clark (2019) note that widespread gene sequencing fosters the investigation of how convergence evolves at the molecular level and indicates that there is increasing evidence of correlation between morphological and genetic information with regard to trait convergence. Changes in regulatory genes, such as homeobox (Hox) genes, that govern the expression of traits make it likely that some traits will appear repeatedly in closely- as well as distantly-related taxa, resulting in convergence. Speed and Arbuckle (2017) and Lamichhaney et al. (2019) suggest that new genomic data sets will enable detailed and tractable analysis of the genetic underpinnings of convergent phenotypes. The examination of genomic data relating to morphological, behavioural, physiological and developmental traits holds great potential for revealing a mechanistic understanding of convergent phenotypes, especially if taxa expressing intermediary conditions along evolutionary continua are incorporated (rather than comparing only binary endpoints) (Lamichhaney et al., 2019).

The phylogenetic history and relationships of particular organismic groups influence the actual expression of their adaptive complexes, so in this volume we also examine the potential constraints that lead to differences in morphological expression in the face of similar environmental challenges. In recent years comparative phylogenetic analyses of sets of structural traits have led to the recognition of what has been called “imperfect convergence” (Bergmann & Morinaga, 2018) or “incomplete convergence” (Grossnickle et al., 2020). For example, Bergmann and Morinaga (2018) considered the convergence upon snake-like body form in six squamate clades and noted that each lineage has, from its different structural starting point, evolved a slightly different expression of it, accompanied by convergent changes in associated anatomical systems. Bergmann and Morinaga (2018) emphasized the important role that historical contingency plays in the attainment of a particular morphological form (Dolezal & Lipps, 2019). Such so-called imperfect or incomplete convergence is what might be expected, because lineages may be anticipated to differ in their phenotypic responses to similar selective demands (Collar et al., 2014) due to constraints imposed by the ancestral forms from which the convergent pathways begin. Different approaches, leading to different morphological combinations that generate essentially the same functional outcomes (Thompson et al., 2017; Russell & Gamble, 2019), are underpinned by genetic (Hu et al., 2017), developmental (Gutierrez et al., 2019; Tokita et al., 2012), phylogenetic, morphological and physical factors that affect the modularity of the convergent structures (Fernández et al., 2020; Grossnickle et al., 2020; Quinn, 2020).

Stayton (2015b) notes that although pattern-based and process-based definitions can both legitimately be applied to biological phenomena, most measures of convergence that are based upon the quantification of patterns do not demonstrate the action of any particular process. Furthermore, he notes that when the distinction between modalities for interpreting convergence is not explicitly stated, assumptions about the potential underlying process are often made, thereby obfuscating alternative explanations. As Mahler et al. (2017) state, convergence itself is not indicative of any particular evolutionary process and only through careful analysis can a particular process be invoked. Indeed, Powell and Mariscal (2015) note that it is difficult to demonstrate non-convergence because many of the statements advocating it as being responsible for observed pattern are too vague. Accordingly, it is advocated that robust evidence be presented for cases to qualify as "true" cases of convergence.

1.3 Convergence of Form and Function

Formally, the concept of convergence is based upon analogous traits in relation to their adaptive value, wherein analogy relates to similarity of function in structures with different origins. In many instances analogous structures tend to become similar in appearance, which leads to the invocation of the concept of convergence of form. In similar fashion, analogous convergence may also occur for physiological processes (for example, Schott et al., 2019) and behaviour. Extension of the concept of convergence into studies in the realm of the "-omics" has assisted in our understanding of the underlying processes that drive convergence. Waters and McCulloch (2021) note that genomic analyses have led to the recognition of convergence as the major driver of repetitive evolution above the species level, whereas repeated sorting of standing variation is the main impetus for repeated shifts within species. The latter is exemplified by the alternation of direction of change in Darwin's finches on the Galapagos Islands, as documented by Grant et al. (2004). Over a period of several decades they noted that species lacking postmating barriers to gene exchange can alternate between what manifests as convergence and divergence as environmental conditions oscillate.

Many papers that deal with convergence, whether focusing on pattern or process, allude to function and thus address functional convergence, with function playing a key role in explanations of the similarity of phenotypic traits (Ochoa & Rasskin-Gutman, 2015). Indeed, Powell and Mariscal (2015) and Kuhn et al. (2020) define convergence as being an evolutionary phenomenon that results in the independent origin of both form and function. The incorporation of function into the concept of convergence, as applied to comparative studies, has fostered the generation of hypotheses about how organisms may respond similarly to selective pressures when under the influence of potential constraints (Casinos & Gasc, 2002).

Investigations of functional convergence generally focus on aspects of form that relate to recurrent "everyday behaviour" (e.g., foraging, feeding, ventilation, locomotion, adhesion) that influences the survival of the organisms through the maintenance of homeostasis, and on aspects of social behaviour (e.g., communication) that involve intra- and interspecific interactions between individuals (e.g., territoriality, social systems). Various examples that attempt to assess convergence in different disciplines show that the concept of function is, however, complex because it encapsulates various factors that might drive evolutionary convergence. Thus, the assessment of "functional convergence" may be conducted to explain similarities of any phenotypic traits across the organizational and structural spectrum from molecules to behaviour. All such behaviours are under complex sensory-motor control governed by neuro-hormonal mechanisms. With regard to this, Fischer et al. (2019) state: "*A major strength of evolutionary comparisons is the ability to determine whether shared genomic and/or neural mechanisms are associated with similar behaviours across species or if there are many alternative mechanistic 'solutions' that can produce similar behaviours.*".

Regardless of whether or not any particular evolutionary process is invoked to account for the convergence advocated, the literature is replete with accounts of similarity attributed to convergence. For almost all animal lineages quantitative analyses of phenotypic traits, particularly those relating to morphology, reveal multiple instances of convergence (Fig. 1.2).

Powell and Mariscal (2015) note that the strongest examples of convergence are those representing adaptive complexes that perform the same function and that incorporate several hierarchical layers of underlying form (Speed & Arbuckle, 2017). Such assessments stem from the recognition that certain design "problems" are pervasive in the history of life and can only be "solved" by a limited number of structurally specific outcomes. These may be regarded as being ecomechanical challenges (Higham et al., 2021) that are based upon "simple" physical laws and are perceived to play a key role in impacting performance. Such challenges are seen to be agents of selection but are modulated in different lineages by the internal constraints imposed by phylogenetic history.

Given that when colonizing new environments organisms are challenged to adapt, both morphologically and behaviourally, to survive and thrive (Kowalko et al., 2013), it is evident that such challenges initiate responses governed by physical and mechanical demands (Higham et al., 2021). These demands potentially drive morphological systems (and the behaviours responsible for their operation) toward similar endpoints. Such responses lead to ecomorphological patterns (*sensu* Norton & Brainerd, 1993) related to those environmental challenges (Toussaint et al., 2019).

Comparative studies related to such challenges tend to reveal that a relatively limited number of morphological attributes account for the similarities between organisms. For example, many recent studies of birds, fishes and marine vertebrates, at various taxonomic levels, tend to confirm the notion that form-function associations will reflect convergence towards predictable trait combinations, suggesting that

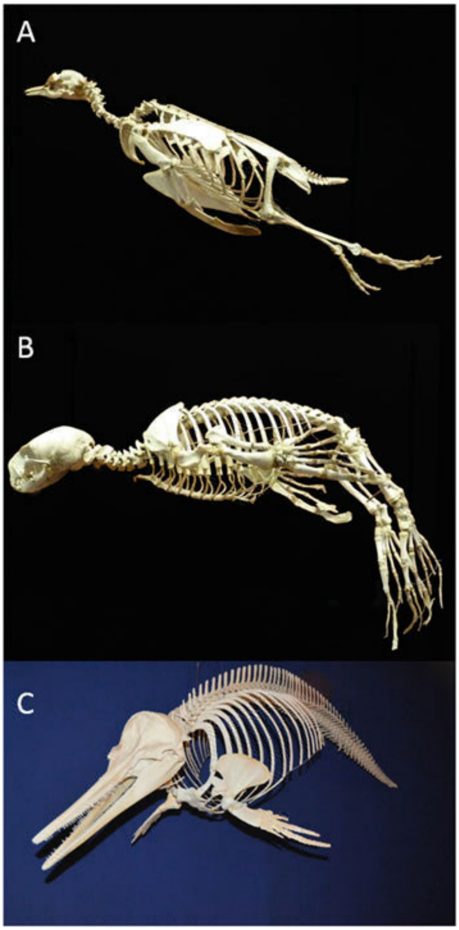

Fig. 1.2 Examples of convergent morphology in two distantly related vertebrate classes (birds and mammals) in relation to modifications for swimming in the marine environment. (**a**) penguin, (**b**) pinniped, (**c**) whale (Photographs courtesy of Eric Pellé, Muséum national d'Histoire naturelle, Paris, France)

morphological variation is channeled into a limited set of possibilities (Pigot et al., 2020) that lead to similar structural adaptations (Donley et al., 2004; Shadwick, 2005). Repeated adaptive radiations within the same group frequently produce convergent forms (Mahler et al., 2013). Although these are often encountered in geographic isolation, it is becoming evident that such convergent patterns may also occur in sympatry in different clades within radiations (Muschick et al., 2012; Llaurens et al., 2021). This occurs when the number of species exceeds the number of available niches. In such instances, sister taxa tend to deviate from one another in morphospace (Muschick et al., 2012) and come to resemble species in other lineages.

The way in which any particular functional response under investigation is related to convergent evolution is dependent upon the discipline or domain within which comparative studies are conducted. Behavioural traits have been the focus of study for many interested in responses to functional demands that lead to convergence.

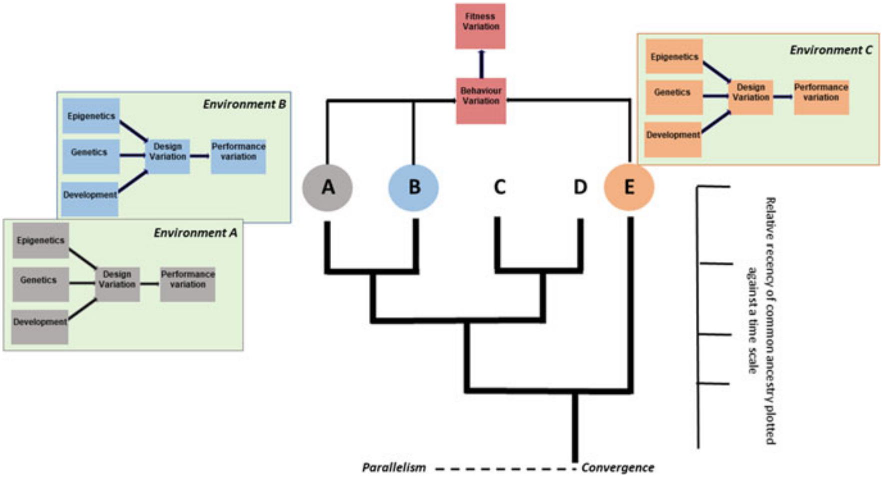

Fig. 1.3 Theoretical framework based on Arnold's (1983) paradigm of support for evolutionary convergence. Each highlighted species A, B, E, is exposed to similar environmental challenges and responds to them. At one level the different environments impose, overall, essentially similar challenges (e.g., aquatic environment), but at other levels may have more particular properties (e.g., surface of the substrate, narrow branches in the arboreal habitat). These responses constitute the links between organismal properties (e.g., design variation and performance variation) resulting from genetic, epigenetic, and/or developmental processes, or from stochastic events (Losos, 2011). These links result in similar responses (behavioural or functional variation) that enhance their fitness in the environment. A, B, phylogenetically closely-related species, E, phylogenetically distantly-related species relative to A and B

Arnold's (1983) paradigm (Fig. 1.3) has been adopted by many when assessing anatomical and functional morphological (including paleontological) approaches to questions relating to design (*sensu* Lauder, 1996) and fitness (e.g., Garland Jr & Losos, 1994; Reilly & Wainwright, 1994; Johnson et al., 2008; Lailvaux & Husak, 2014; Irschick & Higham, 2016; Binning et al., 2017). Within this framework particular behaviours or functions (constituting "performance") are viewed as resulting from one or several traits being used by an individual throughout its life in response to environmental challenges. Characterization of such performances is employed to determine the potential for convergence in distantly-related organisms. Such performances are defined as "*. . .the ability of an animal to conduct a key task. . .*" (Irschick & Higham, 2016). Many approaches to the study of functional convergence in the domains of ethology (including neuroethology) and behavioural ecology have focused on the mechanisms of neuro-motor and physiological (e.g., hormonal) control of morphological structures and the manner in which these influence various responses, including actions/movements, complex sensory-motor coordination and control, cognition and memory, and thus performance. For example, several studies have demonstrated that convergence has probably played a major role in the evolution of the anatomy and functioning of the nervous system and the behaviours that it controls. Consideration of convergence has also focused upon the expression of increasingly complex behaviours or abilities (such as, social behaviour, parental behaviour, nest-building), as illustrated by many studies devoted to the association of cognitive abilities, brain structure, and behaviour. Some of these studies have explored the convergent evolution of complex neurological traits ("mental capacities", *sensu* Roth, 2015) such as "high intelligence", and raise questions about the convergent evolution of advanced cognition (for example, in corvid birds, apes and cetaceans) under shared selective environmental pressures (Seed et al., 2009). Some approaches to convergence in ethology have drilled down to the genomic level, investigating the recurrent evolution of gene sequences related to echolocation patterns in different lineages of bats (Jones & Holderied, 2007), or more broadly between bats and cetaceans (Parker et al., 2013).

1.4 The Objectives and Structure of this Volume

McGhee (2011) notes that, in reality, convergent evolution (except in cases in which resemblance in form results from purely stochastic processes) is grounded in the interplay between form and function, a recognition that is well-supported by the literature in general. Indeed, an understanding of the interplay between form, performance(s), and behaviour(s) in the context of determining function is essential for understanding how organisms survive, persist in their ecological environment, and reproduce (Lauder, 1996). In this book we provide examples of how functional considerations are necessary for understanding the integrative evolution of complex adaptations (*sensu* Frazzetta, 1975) in organisms faced with similar environmental challenges. The physical challenges imposed by the environment and the ecological factors that drive convergence (Donley et al., 2004; Shadwick, 2005; Higham et al., 2021) are emphasized in each chapter.

As noted above, and as argued by McGhee (2018), establishing the boundaries for what constitutes convergent evolution, as opposed to parallelism and reversal, is conceived of differently by different authors. The contributors to this volume (who report on taxa and aspects of functional morphology that fall within their areas of expertise) were invited to select and document cases of evolution of form and function that they perceived to be driven by environmental abiotic and/or biotic challenges and that have resulted in convergence. The chapters comprising this book show that examples have been selected across a broad phylogenetic spectrum, representing different levels in the classificatory hierarchy. At the least inclusive level purported convergence among lineages within a single order (Chaps. 2–4) form the basis for investigation. In contrast, at the most inclusive level convergence of structure and function are contemplated across entire Classes (Chaps. 11, 12, 14, and 15) or even Phyla (Chaps. 13 and 16).

The sequence of chapters in this book reflects the phylogenetic breadth of the taxa selected for study, from least to most inclusive, rather than the clustering of chapters by perceived similarity of the phenotypic features or biomechanical challenges being considered. All chapters stress the need for integrative approaches for the elucidation of both pattern and process as they relate to convergence. Employment of multipronged approaches to the study of convergence (Mahler et al., 2017) characterizes the included contributions. We adopt the tenet of Mahler et al. (2017) that evolutionary pattern and process cannot be decoupled in comparative studies of convergence, even though such a decoupling could, in theory, guard against adaptationist bias.

Chapter 17 focuses on how links between convergent evolution and bioinspiration can be forged. Such a chapter has been included because we believe that the study of convergence can be instrumental in refining approaches to biomimetic applications of biological knowledge.

In Chaps. 2–4, convergent patterns are explored at the ordinal level within the confines of a single taxon (from Insecta [Arthropoda] to Mammalia) in relation to eco-mechanical challenges (*sensu* Higham et al., 2021). Nel and Piney (Chap. 2) discuss the highly complex morphological structure of wing venation in representatives of the superorder Odonatoptera (Insecta), emphasizing convergence in both extant and extinct representatives. Gomes-Rodriguez et al. (Chap. 3) demonstrate for rodents (Mammalia) the impact of the fossorial habitat on digging abilities as they relate to behavioural, functional, and morphological convergence. Examination of traits related to the long-distance communication songs of mysticetes (baleen whales) by Park et al. (Chap. 4) exemplifies the difficulties associated with approaching the question of convergence of sensory function and discusses the problems related to the demonstration of potentially convergent patterns in the context of our limited understanding of hearing in the largest creatures in the oceans.

Chapters 5–10 explore the question of convergent evolution between more distantly-related taxa within groups of organisms with relatively similar “Bauplans”. Pallandre et al. (Chap. 5) address the question of convergence of the articulation between the hind limbs and the axial skeleton within the Carnivora and contrast this with the situation in ungulates (Mammalia). They compare the form and function of the sacroiliac joint in relation to forces generated during predatory bouts that are associated with different behaviours and strategies in felids and canids, thereby exploring the functional morphology of this arthrological complex beyond that related to routine locomotor associations.

Three chapters (Chaps. 6–8) investigate convergence of approaches to aquatic feeding within different Orders of vertebrates. A salient point of these chapters is the application of the comparative approach to what are considered homologous and convergent traits within these Orders. Heiss and Lemell (Chap. 6) approach the question of convergent evolution in extant lissamphibians, a group generally characterized by an aquatic larval stage. In many species, however, there is a secondarily reduced, free-living larval stage that undergoes direct development as an adaptation to terrestrial life. After metamorphosis, some lissamphibians become terrestrial, others adopt a semiterrestrial/semiaquatic lifestyle, and others remain fully aquatic. The authors summarize the form and function of the trophic structures in these vertebrates to reveal how morphological features have evolved independently in several lineages to increase the efficiency of suction feeding, one of the major modes of aquatic feeding strongly influenced by hydrodynamic constraints. Regarding the

Sauropsida, Heiss et al. (Chap. 7) compare the spectrum of convergently-evolved responses to aquatic feeding, again centring their arguments on the hydrodynamic constraints imposed by the physical properties of water. Werth and Marshall (Chap. 8) demonstrate the large number of instances of convergence of the trophic system in relation to secondarily aquatic feeding in mammals, exploring both form (e.g., jaws, dentition, musculature, overall shape of the head and mouth) and function (e.g., methods for separating food from water, neural and behavioural adaptations for locating and capturing prey).

Chapters 9 and 10 deal with the convergence of adhesive mechanisms in terrestrial habitats in two distantly related Orders. Russell and Garner (Chap. 9) examine convergence in the form and function of the adhesive system within the Squamata by comparing geckos and anoles. Subsequent to considering the purely physical aspects that govern the functioning of dry, fibrillar adhesive devices at the microscopic and nanoscopic levels, they examine the spectrum of morphological configurations of the adhesive system that have evolved within the Gekkota and assess which of these configurations most closely resembles that exhibited by anoles. Büscher and Gorb (Chap. 10) examine patterns of convergence of the adhesive system among insects. They document adaptive solutions at various scales from similar attachment organs in different lineages to different organ properties in the same lineage, drawing attention to the biomimetic potential that these diverse form-function mechanisms present. Both of these chapters demonstrate the complexity required for organisms to attach to and release from the substrata they exploit during locomotion and document the physical and organismic drivers of convergence of the design of fibrillar adhesive systems.

Chapters 11–16 explore functional convergence across even broader scales, comparing structural and functional patterns between Classes within a Phylum (Chaps. 11, 12, 14 and 15) and even across Phyla (Chaps. 13 and 16). Chapters 11–15 are concerned with aspects of locomotion whereas Chap. 16 examines attachment mechanisms in aquatic animals.

In Chaps. 11 (Young) and 12 (Pouydebat et al.) the authors explore convergently-evolved responses to the biomechanical problems of moving on narrow supports, emphasizing both morphological traits (e.g., small body size, enhanced mobility of appendicular joints, grasping extremities, and long and mobile tails) and behaviourally-based functional attributes (such as speed reduction, modulation of the duty factor, a switch to gaits facilitating continuous contact with the substrate, exaggerated limb joint excursions during the support phase). In these chapters, comparative analyses of both form and function reveal convergences in relation to locomotion on narrow substrates. Young (Chap. 11) identifies widespread convergence of locomotor morphology and behaviour among arboreal lissamphibians, lizards, and metatherian/eutherian mammals that has arisen in response to a common set of physical challenges imposed by the complexity (such as compliance, narrow perch diameter, 3D orientation of the substrates) of these habitats. Animals living in such habitats must be able to stabilize their body and manipulate their substrate to move efficiently. This is particularly evident for narrow supports, as is also demonstrated in Chap. 12 (Pouydebat et al.)

In a complimentary contribution Khandelwal et al. (Chap. 13) discuss the evolutionary trajectories relating to morphology and behaviour leading to convergence of gliding abilities in animals, focusing upon selective pressures that have been brought to bear on morphological and behavioural traits that permit distantly-related taxa to generate aerodynamic forces to exploit and control glide paths and to land successfully at the termination of the flight. Much of this chapter concerns vertebrates that live in the complex arboreal habitats considered in Chaps. 11 and 12, but also includes consideration of those animals that glide in air at the air-water interface in marine situations. The latter extends beyond vertebrate examples to include cephalopd mollusks.

Druelle et al. (Chap. 14) approach the question of evolutionary convergence as it relates to bipedal locomotion in terrestrial vertebrates. By considering the various form and function relationships within the distantly-related vertebrate taxa that exhibit bipedal locomotion, whether this be employed occasionally, habitually or obligately, they argue that tetrapods practicing this kind of locomotor behaviour converge upon the same functional anatomical outcomes (such as cyclic limb loading being higher when compared with quadrupedal locomotion). For habitual and obligate bipeds, the evolutionary pathways taken to achieve these capabilities have resulted in structurally and functionally different ways of overcoming the physical challenges involved, the differences being attributable to the differences in anatomical configurations from which the trend to bipedalism began.

Chapters 15 and 16 explore convergent patterns relating to two quite different behaviours that favour survival in aquatic (marine) habitats. Fish (Chap. 15) examines convergence of morphological and physiological traits relating to the locomotor performance of three distantly-related taxa (sharks, ichthyosaurs, and dolphins), a comparative scenario recognized as "*the quintessential example of evolutionary convergence*". Convergence in these vertebrates has been governed by the physical parameters of the fluid in which they live, driving morphological (such as body surface attributes, form of the appendages), physiological (body temperature) mechanical (such as frequency of oscillation of the thrust-generating hydrofoil, development of lift-based thrust, enhancement of speed), and behavioural (stability, manoeuverability, swimming) traits. These have resulted in independent evolutionary trajectories leading to great similarity in form of these high-performance marine predators and a remarkable amount of homoplasy. Delroisse et al. (Chap. 16) discuss the attachment strategies (glue-like bioadhesive secretions and pressure-driven suction) adopted for attachment.to the substrate by aquatic animals. They highlight convergence in underwater attachment mechanisms across a huge array of Phyla, examining these mechanisms across a hierarchy of length-scales (organism, organ, microscopic and molecular), and provide a synthetic overview of how organisms attach to various substrata. This broadly comparative approach permits the authors to posit that, at the molecular level of adhesion, the global amino acid composition of bioadhesives shows homologous characteristics.

In Chap. 17 Broeckhoven and du Plessis highlight the central role that the concept of convergent evolution can play in the quest for using biodiversity as a key source of bioinspiration. They provide valuable insights into methodological and experimental studies of biological systems at various scales to obtain a comprehensive understanding of biological structures, performance, and behaviour. Such knowledge can be used to inspire future directions for seeking innovative solutions to problems associated with human activities. Multiple repetition of functional assemblages, although not identically constructed, should provide biomimeticists with insights about what is collectively necessary and sufficient to carry out identified tasks and about how phylogenetic constraints and contingency have led to variation superimposed upon the fundamental configurational/operational commonality.

Acknowledgments We are highly grateful to Alex Werth for his comments on this introduction.

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Chapter 2
Odonatopteran Approaches to the Challenges of Flight: Convergence of Responses Subject to a Common Set of Morphological Constraints

André Nel and Bertrand Piney

Abstract Effective flight capacity is a crucial survival attribute of volant animals. Several vertebrate clades have acquired gliding capabilities and at least three of them independently acquired powered flight. Contrastingly, wings were probably acquired only once by pterygotan insects. Despite this, insects have developed a great variety of structural approaches that have diversified their collective flight capacity. Flight was a key contributor to their diversification during the Late Carboniferous (at least 330 Ma), and flying insects have remained the most diverse animal clade since then. Among pterygotans, representatives of the superorder Odonatoptera, which includes the extant Odonata, have developed impressive performance associated with the highly complex morphological structure of their wing venation. Some venation patterns, such as the nodus, discoidal complex, and arculus, were acquired only once, whereas others have been convergently acquired several times. One example of a pattern acquired more than once is the sclerotized pterostigma, convergently appearing in the Permian Protanisoptera and its sister group, the Discoidalia, these comprising the modern Odonata. All odonatopterans with broad wings were confronted by a major problem, that of 'how to strengthen the basal third of the wing' to prevent it from breaking longitudinally. At least eight different convergent 'solutions' have been 'adopted' that have resulted in the incorporation of structures oriented perpendicular to the main axis of the wing. Additionally, several clades within the Odonatoptera have convergently developed petiolated wings, adapted for flying in cluttered environments. The width and length of the petiole can vary greatly, with the most impressive ones being those of the 'giant' Permian-Triassic Triadophlebiomorpha. This great morphological disparity represents 'variations on a theme' of the already complex wing venation established by the first Carboniferous odonatopterans. It is possible that some of the 'solutions'

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V. L. Bels, A. P. Russell (eds.), *Convergent Evolution*, Fascinating Life Sciences,
https://doi.org/10.1007/978-3-031-11441-0_2