Eric Thomas Brazil Francis and the Evolutionary Morphology of Salamanders

Introduction to the Reprint of *The Anatomy of the Salamander*

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NO HIGHER COMPLIMENT CAN BE PAID TO A REFERENCE BOOK THAN WHEN IT IS DEEMED WORTHY of reprinting many years following its initial publication. Such is the case with E. T. B. Francis's *The Anatomy of the Salamander*, which first appeared in 1934. Very simply, Francis (as the book is commonly called) remains the starting place for virtually any rigorous study of salamander comparative or functional anatomy and is an indispensable reference for studies of urodele developmental anatomy, endocrinology, and physiology.

To fully appreciate the book, one must view it in the context of its time. In Francis's day, monographic treatments represented the benchmark of intellectual accomplishment in the study of vertebrate anatomy, especially in the United Kingdom and Europe. Chronologically, for example, his book lies almost exactly between Edwin Goodrich's (1930) *Studies on the Structure and Development of Vertebrates*, on the one hand, and P. D. F. Murray's (1936) *Bones* and Gavin de Beer's (1937) *The Development of the Vertebrate Skull*, on the other.

Interestingly, all three latter works have themselves been reprinted in the last few years, in response to continuing demand for them as essential reference material in the study of vertebrate biology and anatomy (Hall 1985; Hall and Hanken 1985; Thomson 1986). Indeed, one would be hard-pressed to name another decade from the 20th Century that has left as impressive an intellectual legacy for vertebrate biology as the 1930s. Francis himself was well aware of the prevailing standards of his time, although, as stated in the Preface, his specific goal was to produce an anatomical reference work for salamanders that was comparable to the classic treatments of anuran anatomy by two great 19th Century German morphologists, Alexander Ecker and Ernst Gaupp (1896–1904).

Francis's treatment emerges from his professional identity as a bedrock empiricist. It also presages his later research career, which yielded a series of thorough and detailed studies of vertebrate cardiovascular anatomy and histology (Gans 1998). He certainly is not one to explicitly include idle chitchat regarding underlying assumptions, guiding philosophy, or theoretical underpinnings. Indeed, his Preface is barely two pages long, whereas the lengthy Historical Introduction, which outlines "the history of . . . relevant anatomical and physiological literature" (p. xiii) is authored—not by Francis—but by his "Tutor" at the University of Reading, the distinguished anatomist and historian of science, Francis J. Cole. Similarly, Francis provides no overall summary or general conclusions. Instead, the text ends with a sober account of the glands of the nasal capsule. One needs to look carefully elsewhere for underlying motives that guided and justified the work.

Why is Francis (1934) still relevant today? The most obvious reason, of course, is the anatomical accounts themselves. The bulk of the book comprises a series of 11 chapters that treat the anatomy of adult urodeles, organ system by organ system, beginning with the skeleton and ending with the skin and sense organs. Many of the accounts provide extremely worthwhile summaries of individual components. In "The Nervous System," the account of cranial nerve V (the trigeminal) is six pages long, and the description of nerve X (the vagus) identifies no fewer than 32 separately named nerves

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and associated rami. In "The Muscles," each muscle is described in terms of anatomy, innervation, synonymy, function, and homology. To be sure, biases in Francis's knowledge and interests are evident; a few organ systems receive short shrift. Accounts for the alimentary tract and respiratory system, for example, total nine and six pages, respectively. And while Francis's accounts of cranial anatomy and diversity, especially concerning hyobranchial components, do not rival the wonderfully detailed treatments by Drüner (1901, 1904), Wiedersheim (1875, 1877), Parker (1877, 1882a, 1882b) and others, most contemporary readers find his accounts more accessible than these earlier works. Use of a standard format across chapters further enhances the book's value as a reference work for organismal anatomy.

A second benefit is derived from Francis's explicit efforts to organize the relevant literature for each organ system. He thus provides an effective means to investigate individual topics in greater depth. He lists synonymous terms, assesses homology between structures in *Salamandra* and those in both other urodeles and other vertebrates, and provides complete citations to published works. Where appropriate, he corrects earlier errors, e.g., Parker's (1882a) report of a septomaxillary bone (p. 29). Many sections within each chapter begin with a focused historical account of earlier literature, which supplement the more general narrative offered by Cole in the Historical Introduction.

Within the anatomical accounts themselves, the numerous assessments of homology were done as much to offer insights into evolutionary transformations as to standardize a very confused and widely scattered literature. Some specific features were, in the 1930s, extremely controversial and difficult to resolve, such as the homology of the vomer bone between mammals and other vertebrates (pp. 30–31). In such instances, Francis impressively resists the temptation to impose a Procrustean solution and simply declare a homology assessment by fiat, and instead offers a balanced and reasonable explanation of the nature and basis of the disagreement. Similarly, he identifies areas where the knowledge base simply is inadequate to resolve a controversy, as in the discussion of investing membranes of the brain and spinal cord (pp. 123–125). Several homologies that were unresolved in Francis's day continued to be discussed decades after he addressed them and are still relevant today. Two examples are the hyobranchial skeleton (pp. 34–36; Deban and Wake 2000; Reilly and Lauder 1988; Wake and Deban 2000) and the vomer (pp. 30–31; Moore 1981; Presley 1993).

One must also remember that many of the accounts report the results of original empirical research by Francis, which were published in *The Anatomy of the Salamander* for the first time. The description of the nervous system is based "almost entirely" on his own dissections, which were supplemented by examination of serial sections (p. 134). His account of the anatomy of the cardiac outflow tract was based on a three-dimensional, wax-plate reconstruction of this region, as well as examination of the corresponding serial sections and additional gross dissection. The venous and lymphatic systems were described from whole-mounts made by injecting specimens with Prussian blue, a precursor of the latex- and resin-based methods used today. (The technique is described in considerable detail on p. 250.) Indeed, the anonymous reviewer for *The Quarterly Review of Biology* reserved special praise for this treatment of "the lymphatics—that mysterious system so frequently referred to by comparative anatomists but so infrequently and inadequately dealt with" (1935a, p. 234). Perhaps most impressive, the text is illustrated with 25 plates containing 84 figures, nearly all of which are original.

Finally, while ostensibly describing the anatomy of a single species, Francis's treatment actually is much more. In the course of offering a standardized anatomical terminology, assessing homologies between *Salamandra* and other urodeles, and reviewing interspecific variation concerning specific features, the volume offers a synthesis of comparative morphology of an entire clade, at least as it was understood in Francis's day. Accounts of specific features are also used as opportunities to address more general topics in vertebrate anatomy and evolution.

One can gain additional appreciation for *The Anatomy of the Salamander* by asking what might have motivated Francis to invest the tremendous amount of physical effort, time, and mental energy that undoubtedly went into writing it. Why, in the 1930s, was there a "market" for an exhaustive treatment of salamander anatomy? Who besides salamander specialists would be interested in it? Answers to these questions provide insights into Francis's underlying motives and rationale. They also provide a convenient opportunity to discuss how much contemporary views of tetrapod origins and evolution differ from those that prevailed in Francis's day, and to indicate why several of Francis's claims—however appropriate they seemed at the time—must be qualified today.

As now, one of the central debates in animal biology and evolution during the early part of the 20th Century concerned the origin of terrestrial vertebrates: Who were the immediate piscine ancestors of the earliest tetrapods? When, where, and under what ecological circumstances did successful colonization of the terrestrial environment occur? And, perhaps most important, what anatomical and physiological changes characterized this evolutionary transition, both from fish to archaic amphibian and from amphibian to "higher" tetrapods, e.g., mammals? It is both logical and appropriate that data from living amphibians would be brought to bear on this problem. They share many features that likely were present in the earliest tetrapods, such as a well-developed posterior branchial-arch skeleton bearing gills (typically, in larvae). They also were classified with the (extinct) archaic tetrapods and apart from other living tetrapods, the amniotes. Moreover, many of them "recapitulate" the water-to-land transition during ontogeny in the form of the discrete metamorphosis from aquatic larva to terrestrial adult, thereby offering at least an analogous situation to the one that occurred hundreds of millions of years ago.

Perhaps most important, there already was an accepted precedent for looking to the development and anatomy of Recent amphibians for significant insights regarding the origin and evolution of tetrapods. Nearly 20 years before the release of *The Anatomy of the Salamander*, for example, the Russian morphologist I. I. Schmalhausen had completed his doctoral dissertation at Moscow University. Entitled "The Development of Appendages in Amphibia and Their Significance in the Problem of the Origin of Terrestrial Vertebrates" (Gans 1968), Schmalhausen's study included extensive accounts of limb development in the (extant) hynobiid salamander genus *Ranodon*. (Although this and related works by both Schmalhausen and his mentor, A. N. Severtsov, were not widely appreciated by English readers until much later, largely through the publication of Schmalhausen's *The Origin of Terrestrial Vertebrates* [1968], Francis includes several of them in his extensive bibliography [citation numbers 659–661, 697, and 698].)

Yet living amphibians, but especially salamanders, were regarded by Francis and his contemporaries as more than just a surrogate for an early tetrapod for the purposes of scientific study: they were offered as a truly intermediate form between sharks—then viewed as an almost archetypal primitive jawed fish—and amniotes. Knowledge of salamanders thus bore *directly* on the problem of tetrapod origins and the evolution of terrestriality. Salamanders were favored over frogs and especially caecilians in this regard, because the latter groups are so obviously specialized anatomically vis-à-vis the presumed ancestral tetrapod condition. This belief is revealed early on, in regards to body and limb proportions: "mechanically, as in many other ways, the Salamander is truly intermediate between the piscine structure . . . and that of the typical land vertebrate" (p. 11). A similar sentiment is expressed much later, in the description of the sympathetic nervous system: "it is evident that Salamandra forms a truly intermediate type between this [the pattern of innervation found in sharks and their relatives] and the more regular and definite arrangement found in the Frog" (p. 181).

Relations between salamanders and early tetrapods now are viewed much differently than they were in Francis's day. These differing views must be kept in mind when reading the various anatomical accounts contained in *The Anatomy of the Salamander*, or at least the corresponding interpretations regarding specific homologies and the anatomical transitions that accompanied the evolution of terrestriality. Thus, while the evolutionary origin of modern salamanders has been pushed back much closer to the origin of tetrapods than was ever imagined in Francis's day (Gao and Shubin 2001), salamander anatomy can no longer be automatically assumed to represent a retained primitive, early tetrapod condition. Many features of brain and sense organ anatomy in salamanders, for example, are simplified relative to their organization in most other vertebrates, including many fishes (Roth et al. 1993, 1997). This simple organization was once regarded as paradoxical in light of the phylogenetic position of salamanders vis-à-vis both fishes and other tetrapods. Today, instead of being primitive, it is regarded as a highly specialized configuration that has been derived secondarily from a more complex ancestral state. Indeed, it represents only one of many instances of secondary simplification and loss that have accompanied the pervasive trend towards paedomorphosis, which dominates the evolution of urodele morphology (Hanken 1989).

Another feature that forces us to qualify many of Francis's claims is the extensive interspecific morphological variation among salamanders that has been revealed since 1934. Despite his recognition of variation in some traits among some species, Francis employs a largely typological approach to urodele anatomy: "the Salamander, considered as a whole, is one of the best examples of Urodele organization, towards which other types may be regarded as leading, or from which they may be derived" (p. 21). Later, he compares "The brain of the Salamander . . . with that of the Frog" (p. 131). Yet, far from asserting anything new or controversial, Francis here simply reflects the typological approach to teaching and research in comparative animal morphology and zoology that prevailed in Great Britain throughout much of the 20th Century (e.g., Parker and Haswell 1940; Saunders and Manton 1931).

Salamanders are now known to be far more diverse morphologically and functionally than was ever appreciated by Francis and his contemporaries. This includes repeated instances of homoplasy, both among urodele taxa and between urodeles and other vertebrates (Larson 1991; Parra-Olea and Wake 2001; D. Wake 1991; D. Wake and Larson 1987). Thus, members of the Plethodontidae have been found to possess a true spinal accessory nerve (cranial nerve XI), which previously was regarded as unique to amniotes among living vertebrates (Roth et al. 1984). This pattern of innervation has been incorporated into a unique, ballistic tongue-projection system for terrestrial prey capture in plethodontids (Deban and Dicke 1999; Deban et al. 1997; Lombard and Wake 1986; D. Wake et al. 1993), although it may also exist in other urodeles. Francis's brief account of tongue functional anatomy (pp. 61–62) does not even hint at this tremendous functional and anatomical diversity. It is based largely on the classic work of Drüner (1901), who ignored plethodontids entirely. At present, this single family comprises nearly 70% of the world's salamander species (Frost 2000).

Do these recent insights mean that salamanders can no longer appropriately serve as surrogates for studying the anatomy of early tetrapods? Definitely not. Clearly, salamanders do display many primitive tetrapod features, such as the presence and general anatomy of the limbs, a tail present in both larvae and adults, and basic locomotor mechanics. However, these insights do preclude the assumption that each organ system represents a perfect transitional state between fishes and amniotes. Rather, each system has had a long evolutionary history, and the specific configurations observed today represent particular solutions to a series of developmental, functional, and ecological constraints and opportunities. Assessments regarding the relative degree of primitiveness or specialization require careful analyses that incorporate data from comparative anatomy, developmental biology, functional morphology, and paleontology, as well as ecology and life history. The anatomy of

living salamanders constitutes a mosaic of primitive and derived traits, which vary in their ability to inform the debate regarding the origin of tetrapods and terrestriality.

It is worth noting one additional reason why a tome on salamander anatomy might have received more than the usual amount of attention in Great Britain and Europe of the 1930s. What we now recognize as the established science of evolutionary biology was a very different beast in the early part of the 20th Century. The "evolutionary synthesis," which signaled a broad consensus regarding the basic tenets of evolutionary pattern and process, was still years away (Mayr and Provine 1980). One particularly bitter controversy concerned the validity of Lamarckism, or the inheritance of acquired characters (Mayr 1980). Among the theory's most sensational proponents was the German biologist Paul Kammerer, who championed Lamarckism on both theoretical and empirical grounds in a long series of articles and books that spanned more than 25 years beginning at around the turn of the century (Kammerer 1924).

Kammerer is perhaps best known for his purportedly fraudulent studies of the midwife toad, *Alytes obstetricans* (Koestler 1971). Indeed, the revelation that his toad specimens had been "doctored" is believed to have precipitated his tragic death by suicide in 1926 (Burkhardt 1980). Yet, before his work with *Alytes*, Kammerer had initiated an extensive series of experiments on the development of external coloration in *Salamandra* (e.g., Kammerer 1913a). He offered this work as key support for his early claims of Lamarckism (Kammerer 1913b) and confessed on more than one occasion that, next to the midwife toad, his research with the "Salamander . . . has become my favorite" (Kammerer 1924, p. 88). "Kammerer's Celebrated Salamander Experiments" (Kammerer 1924, p. 13) brought dubious notoriety to salamanders—and especially *Salamandra*—which thus became more widely known among both the general scientific community and the lay public than they otherwise might have been.

Francis was well aware of Kammerer's work and lists seven publications by him in the Bibliography (which is more literature citations than were included for nearly any other individual author). However, Francis early on completely sidesteps the controversy over Lamarckism and its possible role in shaping the biology of *Salamandra* by declaring in chapter two, "This question is one of experimental zoology rather than of anatomy, and it is not proposed to discuss the matter here" (p. 12).

The Anatomy of the Salamander is a treasured member of a long series of classical studies in comparative vertebrate anatomy, whose intellectual descendants are the contemporary school of evolutionary vertebrate morphology (M. Wake 1992). Yet, it is a far different treatment than would be the case if Francis were writing it today, with our current emphasis on rigorous functional, developmental, and phylogenetic analyses as a means of divining the "logic" of adult anatomy (D. Wake 2001). Thus, we now have a much greater understanding of terrestrial locomotion in urodeles and its relation to limb posture and anatomy than the relatively crude account offered by Francis (p. 12; Ashley-Ross 1995; Delvolve et al. 1997). Similarly, in Francis's account of the physiology of amphibian respiration (pp. 274–276) we can see only the beginnings of what has become a vast field of inquiry into the functional morphology and mechanics of aerial respiration in urodeles (e.g., Meban 1979; Shoemaker et al. 1992; Sheafor et al. 2000; Simons et al. 2000).

One must resist the temptation to view these differences as errors or mistakes on Francis's part. His work betrays the assumptions, beliefs, and biases that prevailed in his day. Moreover, by so excellently and thoroughly collating and synthesizing the "facts" as they were then known, he tremendously facilitated subsequent research. Most of his claims have been validated by subsequent work, a few have been shown to be incomplete or even false, but all have enriched our understanding of the anatomy and evolution of a critical group of vertebrates. It is, indeed, a "very competent and thorough piece of work" (Anonymous 1935a, p. 234).

Taxonomy of *Salamandra*

An important consideration when using Francis (1934) as a reference work is knowledge of exactly which "salamander" he is describing. The taxonomy of the genus *Salamandra*—indeed, the classification of salamanders in general—has changed dramatically since the works of E. G. Boulenger (1911) and Noble (1931) on which Francis based his accounts.[1] There are now, for example, nearly twice as many genera in the family Salamandridae than those listed by Francis (15 vs. 8; Frost 1985, 2000; Duellman 1993). Moreover, recent taxonomy assigns six species to *Salamandra* (Veith 1994; Veith et al. 1998; Steinfartz et al. 2000), only two of which are discussed by Francis under their current names.[2] Fortunately, one of these two species, *S. salamandra*, is the principal subject of his text. Even here, however, the situation is both more complicated and vastly different than portrayed by Francis.

According to Francis, *S. salamandra* comprised three discrete "varieties"; these are beautifully illustrated in his color frontispiece, which is reproduced in this reprint. These varieties recognized known color variants, which "are correlated, to a very large extent, with geographical distribution" (p. 13). There were problems with this taxonomy, however, even to Francis's contemporaries. The anonymous reviewer for *Nature* (1935b) declared "the taxonomic and zoogeographical chapters . . . disappointing," because they ignored the already formally described subspecies. They also did not explain the relation between these subspecies and the three named varieties, some of which were described as co-occurring in the same broad geographic region, e.g., the Iberian peninsula. Finally, the distribution map (Fig. 84) didn't always jibe with the corresponding accounts of geographic ranges provided in the text.

Francis explicitly identifies var. *taeniata,* originating from central Europe ("France, Spain, Portugal, south Holland, Germany, and Switzerland"), as the form "on which the present investigation has been carried out" (p. 14). The geographic range of this form as depicted on the distribution map (Fig. 84) closely matches that of what is currently recognized as *S. s. terrestris* (Eiselt 1958; Steinfartz et al. 2000; Thorn and Raffaëlli 2001), which thus is the most likely identity of the principal salamander species considered by him. This interpretation is consistent with Francis's description of *taeniata* as the "variety which is commonly imported into this country [England]" (p. 14). Boulenger, for example, alludes to large numbers of salamanders coming to the (London) Zoological Gardens from the Harz Mountains in Germany, which lies within the range of *S. s. terrestris* (1911, pp. 338, 342). A second subspecies, *S. s. fastuosa*, was also included in var. *taeniata* by Boulenger (1911; Eiselt 1958). This subspecies, however, occupies a relatively small geographic range along the northeastern edge of the Iberian Peninsula (Alcobendas et al. 1994, 1996; Dopazo et al. 1998). It is a much less likely source population for England than central Europe in Francis's day.

The systematic biology of *S. salamandra* remains under active investigation in several laboratories. Molecular phylogenetic analyses reveal a complex evolutionary history, which likely has involved repeated instances of range regression and subdivision followed by expansion and secondary contact in response to climatic and geologic events (Alcobendas et al. 1996; Dopazo et al. 1998). They also provide little if any support for current subspecies designations (Alcobendas et al. 1994; Steinfartz et al. 2000). These and related data from morphology and life history will likely mandate

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[1] Francis's Bibliography incorrectly attributes the former work—citation number 76—to Edward G. Boulenger's father, George Albert Boulenger. The correct citation is listed below.

[2] Several populations once regarded as *Salamandra salamandra* are now assigned to three different species: *S. algira, S. corsica,* and *S. infraimmaculata* (Thorn and Raffaëlli 2001). A fourth species, *S. lanzai*, recognizes salamanders from the southwestern Alps that were previously placed in *S. atra* (Nascetti et al. 1988; Veith 1996). Conversely, the former *S. semenovi* is today regarded as a subspecies of S. *infraimmaculata*, while the former *S. caucasica* is assigned to a different genus, *Mertensiella*.

a substantial overhaul of the taxonomy of this and related species in the near future (Alcobendas and Castanet 2000). Possible changes include elevation of one or more subspecies to species rank (García-París et al. 1998) and reassignment of some existing species between genera (Özeti 1967; Özeti and Wake 1969; Titus and Larson 1995; Veith et al. 1998).

About the Frontispiece

The charming frontispiece of Francis (1934) is virtually an exact reproduction of plate XV from E. G. Boulenger's (1911) taxonomic review of *Salamandra salamandra*; only the captions above and below the figure are altered slightly from the original. Boulenger's taxonomy gave especial weight to adult coloration, and this chromolithograph (color-printed lithograph) supplemented the many black-and-white drawings that illustrated his verbal accounts of extensive geographic variation both among and within known forms. Each of the three salamanders corresponds to a real specimen, and all appear to have been drawn from life. The artist and lithographer is identified on the original plate as "J. Green" (=John Green), who, according to Boulenger, initially made a sketch of the specimen of var. *molleri* for "the Hon. Walter Rothschild" (p. 336).

Befitting the son of a museum scientist, Boulenger included the geographic source of two of the three illustrated specimens. This, plus additional information provided elsewhere in the text, enables assignment of each specimen to current subspecies (Eiselt 1958; Joger and Steinfartz 1994; Steinfartz et al. 2000):

var. *tæniata* — "a male specimen from the Harz" (p. 338). The Harz Mountains, in north central Germany, lie within the range of *S. salamandra terrestris*.

var. *molleri* — "a female specimen . . . exhibited a few years ago in the [London] Zoological Gardens" (p. 336), and "from Portugal" (p. 347). Boulenger cited three Portuguese localities for var. *molleri*: Coimbra, Cintra [= Sintra], and "near Lisbon" (p. 327). All three localities correspond to *S. s. gallaica*.

forma *typica* — "a male from Lugano, Ticino, sent alive by M. A. Ghidini" (p. 333). Lugano is the largest town in Ticino canton, southern Switzerland, which lies near the border with Italy. Salamanders from this region are currently assigned to *S. s. salamandra*.[3]

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