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Ludwig Edinger: The Vertebrate Series and Comparative Neuroanatomy

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Ludwig Edinger: The Vertebrate Series and Comparative Neuroanatomy

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At the end of the nineteenth century, Ludwig Edinger completed the first comparative survey of the microscopic anatomy of vertebrate brains. He is regarded as the founder of the field of comparative neuroanatomy. Modern commentators have misunderstood him to have espoused an anti-Darwinian linear view of brain evolution, harkening to the metaphysics of the scala naturae. *This understanding arises, in part, from an increasingly contested view of nineteenth-century morphology in Germany. Edinger did espouse a progressionist, though not strictly linear, view of forebrain evolution, but his work also provided carefully documented evidence that brain stem structures vary in complexity independently from one another and across species in a manner that is not compatible with linear progress. This led Edinger to reject progressionism for all brain structures other than the forebrain roof, based on reasoning not too dissimilar from those his successors used to dismiss it for the forebrain roof.*

Keywords Ludwig Edinger, evolutionary morphology, comparative neuroanatomy, vertebrate series, German Romanticism, Carl Gegenbaur, Ernst Haeckel

Introduction

In 1896, German neuroanatomist Ludwig Edinger published the first comprehensive account of the comparative microstructural anatomy of the vertebrate nervous system. Modern comparative neuroanatomists show conflicted attitudes towards Edinger and his achievement. On the one hand, they revere him as the founder of their field. His comparative work is held in high esteem today, as it was in his own time (Herrick, 1908; Glees, 1952; Northcutt, 2001; Kreft, 2003; Striedter, 2005; Stahnisch, 2008). On the other hand, they criticize his method of anatomical comparison as tainted by linear thinking about evolution and the pre-Darwinian metaphysics of the *scala naturae*. In 2002, they repudiated the nomenclature he established for the structures of the avian forebrain (Reiner et al., 2004; Jarvis et al., 2005; Reiner, 2005).

Most modern secondary historical literature available about Edinger is written by comparative neuroanatomists whose work played a major role in supplanting his views of forebrain evolution with their own alternatives (Northcutt, 2001; Butler & Hodos, 2005; Jarvis et al., 2005; Reiner, 2005; Striedter, 2005; Reiner, 2009; though see also Kreft, 1996, 1997, 2003). Edinger put forward an influential progressionist interpretation of forebrain evolution, in which the forebrain roof steadily grew larger and more elaborate with the appearance of successive vertebrate classes. Drawing on a vast compendium of new studies in comparative vertebrate neuroanatomy and new tools for reconstructing phylogenies,

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modern investigators instead concluded that an elaborate forebrain roof evolved from simpler precursors in multiple separate instances across the vertebrates and rejected any global trend towards increasing forebrain roof complexity and size (Northcutt, 1981, 1984, 1995).

In their assessments of Edinger, modern comparative neuroanatomists emphasize what they suppose are the lingering influences of the medieval *scala naturae* and linear thinking in their forbearer's work. Glenn Northcutt (2001), a comparative neuroanatomist whose work was central to establishing the new view of forebrain evolution, charged Edinger with adopting "an erroneous pre-Darwinian context based on *scala naturae*" (Northcutt, 2001, p. 663). Jarvis et al. (2005), in a review announcing a replacement for Edinger's terminology for the avian forebrain, wrote that "Edinger and other early comparative neurobiologists combined Darwin's concept of 'evolution' with the nineteenth-century version of Aristotle's '*scala naturae*' which resulted in the view that evolution was progressive and unilinear—from fish, to amphibians, to reptiles, to birds and mammals, to primates, and finally humans—ascending from lower to higher intelligence in a chronological series" (Jarvis et al., 2005, p. 151). In the principle modern textbook of comparative neuroanatomy, Ann Butler and William Hodos (2005) write that "a notion that has misguided comparative studies has been the concept of the phylogenetic scale or evolutionary scale, which is derived from the medieval notion of the *scala naturae*" (Butler & Hodos, 2005, p. 95). In discussing the genesis of Edinger's views in a textbook on brain evolution, Georg Striedter (2005) states that "most of Darwin's contemporaries were quite ready to recast Aristotle's *scala naturae* as a phylogenetic scale" (Striedter, 2005, pp. 26, 29). Anton Reiner (2005), a specialist in the evolution of the basal ganglia, offers a more nuanced view of Edinger, noting his acknowledgement of branching evolution in the case of birds.[1]

These views echo earlier criticisms of the use of phylogenetic scales in comparative psychology and neurobiology, first aired in the 1960s by Hodos and Campbell (1969; Campbell & Hodos, 1991). These commentators make no specific mention of Edinger, and their principle concern was not historical. They sought rather to decry the use of phylogenetic scales by their contemporaries to draw inappropriate evolutionary conclusions. These authors equated phylogenetic scales to the medieval *scala naturae* in which organisms (and sometimes also entities posited by Christian theology, such as angels and God) were ranked along a linear scale by some criterion of "perfection" or complexity (Aristotle, 350 BC/1994; Lovejoy, 1964; Ruse, 1996). As applied historically to Edinger, the *scala naturae* charge reflects misconceptions about nineteenth-century morphology, particularly in Germany, and a simplified caricature of Edinger's ideas.

The misconceptions are fostered, in part, by older historiographical understandings that have been challenged in recent decades. These older views derived from

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[1] Striedter cites Bowler's *The Eclipse of Darwinism* (Bowler, 1983), which documents the widespread skepticism about Darwin's mechanism of natural selection and the advocacy of neo-Lamarckianism and orthogenesis in the post-Darwinian period. Bowler's focus on the inner progressive trends posited by such theories, together with a lack of any extensive discussion of evolutionary genealogy, can leave readers with the erroneous impression that these theories envisioned a linear genealogy. Striedter does not cite Bowler's later *Life's Splendid Drama* (Bowler, 1996), a history of evolutionary morphology that makes Darwinian genealogy a central focus of concern. This volume provides a corrective to the false impression left by his earlier work, documenting the acceptance of Darwin's divergently branching genealogy, and the extensive late-nineteenth-century debates concerning its implications and meaning engaged in by the proponents of the various evolutionary mechanisms. Reiner's more cautiously nuanced view of Edinger may derive from his reading of Bowler (1996), which he cites as a reference.

the pioneering historical work of zoologist Edward S. Russell (1887–1954; Russell, 1916/1982). A Scotsman, Russell wrote at the height of anti-German feelings during World War I. He was a proponent of a common sense approach to biology that eschewed unnecessary theorizing and was a strong opponent of materialism (Roll-Hansen, 1984). Accordingly, he was skeptical of both Darwinism and comparative morphology. As seen through his eyes, pre-Darwinian German morphology was uniformly dominated by a speculative idealist metaphysics that saw biological forms as expressions of archetypes that had no material existence but occupied a separate Platonic realm or the mind of God. Transcendental types were arranged on an idealized scale of nature harkening to the medieval *scala naturae* (Gliboff, 2008; Richards, 2008).

The introduction of Darwinism in the middle-nineteenth century was said to have changed this perspective only minimally. Russell's judgment of the prominent German evolutionary morphologist Ernst Haeckel (1834–1919), an avowed monist materialist, was especially harsh. He denounced Haeckel's work as a garbled "medley of dogmatic materialism, idealistic morphology, and evolutionary theory" (Russell, 1916/1982 as cited in Richards, 2008, p. 440). This assessment set the context for historical work on nineteenth-century German evolutionary morphology for decades to come, resulting in it being seen as a kind of aberrant romantic evolutionism dominated by linear scales with minimal accommodation to Darwin. Such views were re-enforced after World War II, when Gasman (1971) sought the roots of Nazi racist ideology in nineteenth-century German morphology. His ideas were endorsed in Gould's (1977) widely read *Ontogeny and Phylogeny* and also influenced Bowler's (1983) *Eclipse of Darwinism*, a major work concerning this period (Gliboff, 2008; Richards, 2008).

More recently, historians have shown that this older framework is deeply flawed and have sought a more balanced and nuanced understanding of German biology. They have argued that the role of transcendentalist metaphysics in nineteenth-century morphology has been greatly exaggerated (Lenoir, 1982; Rehbock, 1990; Gliboff, 2008; Richards, 2008). Although the late-nineteenth century was marked by lively debate concerning the mechanisms of evolution, and the nature and existence of evolutionary progress, in Germany and elsewhere (Bowler, 1983; Ruse, 1996), investigators were nonetheless largely united in their acceptance of Darwin's theory of common descent, with its divergently branching genealogies (Bowler, 1996). While some investigators did rank organisms along linear scales, they typically did so as part of a struggle to grasp the complex relationship between changes in morphological complexity and Darwinian genealogy, and the nature of the relationship between modern forms and ancestral forms, rather than as a harkening back to earlier metaphysics.

I will here show that Edinger employed standard methods and assumptions of nineteenth-century morphology as practiced in Germany and elsewhere. Like many of his contemporaries, Edinger employed the linear framework of the vertebrate series, in which successive vertebrate classes ranked "higher" or "lower" in morphological complexity, as a means of interpreting his pioneering comparative neuroanatomical data. However, his empirical findings actually forced him to repudiate linear thinking about brain evolution for structures other than the forebrain. Edinger retained a progressionist though not entirely linear view only for the crucial case of the forebrain roof, a case of special concern to modern commentators. Rather than reflecting an anti-Darwinian adherence to *scala naturae* metaphysics, his partial progressionism was merely incompatible with the empirical neuroanatomical findings of the second half of the twentieth century.

Historical Background to Edinger's Research

Evolutionary Morphology

The comparative study of biological form, of which Edinger's comparative neuroanatomy is an example, has long seen scales and grades of organization, along with progress, as central issues. German poet, writer, and natural philosopher Johann Wolfgang von Goethe (1749–1832) founded the science of morphology more than half a century before Ludwig Edinger was born. He coined the term "morphology" as his name for the search for unity of form across the diversity of living things. On the basis of comparative anatomical and developmental studies, Goethe constructed the *Urpflanze* [prototype plant] and *Urtier* [prototype animal], ideal archetypes based on those commonalities of form that all plants and all animals, respectively, shared. Although he espoused a linear scale as a useful method of biological comparison, he sought to replace the *scala naturae's* vague notions of "perfection" with clear functional and morphological criteria for arranging forms along the scale, as did other researchers who followed him (Richards, 2002; Gliboff, 2008).

German philosopher Immanuel Kant (1724–1804) independently proposed the search for biological morphotypes in his *Kritik der Urteilskraft* [*Critique of Judgment*] (Kant, 1790/1914). Kant's works were a major influence on Goethe and subsequent morphological researchers (Lenoir, 1987). Kant (1790/1914) recognized that, to understand living things, teleological language, morphotypes, and scales were useful tools, but he also doubted that the value of these tools carried any necessary metaphysical implications (McLaughlin, 1990; Gliboff, 2008). As a Kantian, Goethe likewise rejected the metaphysics of the *scala naturae*. He accorded no objective reality to his archetypes and scales but again saw them as nothing more than useful conceptual tools (Rehbock, 1990; Gliboff, 2008).

At the beginning of the nineteenth century, French anatomist Georges Cuvier (1769–1832) sought to make taxonomy more rigorous by incorporating extensive data from comparative anatomy. Rather than Goethe's single animal archetype, he argued instead that all animal forms could be classified into one of four "embranchements": vertebrates, mollusks, articulates, and radiates. Since these four types were incommensurable with one another, there could be no single linear scale of complexity for the animal kingdom. Applied to more limited groups of animals deemed similar in form, however, linear scales of increasing biological complexity continued to hold appeal for many morphologists, though they now had to compete with other schemes that were branching or reticulate (Bowler, 1996; Gliboff, 2008).

Morphological ideas influenced many naturalists, in the German states and elsewhere. In addition to Kant and Goethe, Germans Johann Friedrich Blumenbach (1752–1840), Carl Frederick Kielmeyer (1765–1844), and Lorentz Oken (1779–1851) were also major contributors (Lenoir, 1981; Rehbock, 1990; Bowler, 1996; Richards, 2002; Gliboff, 2008). French anatomist Étienne Geoffroy Saint-Hilaire (1772–1844) formulated the concept of homology, defining homologous parts in different species as those that bear the same relationship to the ideal archetype. This notion was further developed by the British naturalist Richard Owen (1804–1892) in the 1840s. They typically made use of archetypes and scales of morphological complexity to find order amidst the complexity of biological form.

Although traditional historiography portrayed these morphologists uniformly as transcendental idealists committed to the reality of natural scales and/or archetypes existing objectively in a Platonic realm or the mind of a Creator God (Russell, 1916/1982), more recent work demonstrates that they held a diversity of views, with several distinct traditions of *Naturphilosophie*. Creationist design arguments, such as those of the British clergyman, philosopher, and Christian apologist William Paley (1743–1805; Paley, 1809) exerted little influence on pre-Darwinian biology outside the church-dominated academic community of England (Amundson, 1998; Gliboff, 2000). Kant's epistemic strictures exerted a significant restraining influence on many researchers' belief in the objective reality of scales, especially in the German states (Lenoir, 1981; Rehbock, 1990; Bowler, 1996; Gliboff, 2008). For example, Blumenbach wrote:

> All the beloved pictures of chains, ladders, nets etc. in nature certainly do have an unmistakable usefulness for methodology in the study of natural history, since they give the basis for a so called *natural system* according to which all creatures are ordered according to the most numerous and most evident similarities. . . . But it is a grave weakness to see in such pictures the Plan of creation. (*Handbuch der Naturgeschichte* [*Handbook of Natural History*] 1802 as cited in and translated by Lenoir, 1981, pp. 131–132)

There were some who accorded objective reality to archetypes but as natural phenomena. Étienne Geoffroy Saint-Hilaire, for example, was a materialist with strong sympathies for the evolutionary theory of French naturalist Jean Baptiste Lamarck (1744–1829; Lamarck, 1809/1963; Rehbock, 1990; Bowler, 1996; Amundson, 1998; Gliboff, 2000, 2008).

Some researchers perceived parallels between scales of morphological complexity and the process of embryonic development. Kielmeyer wrote:

> I consider the force by means of which the [phylogenetic] *series* of organized forms has been brought forth on the earth to be in its essence and the laws of its manifestation *identical* with the force by means of which the organized [ontogenetic] stages in each individual are produced, which are similar to those in the [phylogenetic] series of organized bodies. (Kielmeyer's letter to Windischmann, 1804, as cited and translated by Lenoir, 1981, p. 163, emphasis in original)

Kielmeyer and some of his colleagues supposed that an internal "force" or natural self-organizing principle of *Bildungstrieb* guided both embryonic development and the phylogenetic development of multiple series of increasingly complex organisms, a kind of evolutionary theory (Lenoir, 1981; Gliboff, 2000).

These new ideas flourished as the German states sought to reinvigorate their universities in the early-nineteenth century. Research was added to the faculty's traditional goal of teaching, placing an emphasis on the pursuit of *Wissenschaft* or "pure knowledge." The universities became the prime locus of scientific research in the German-speaking world, and the German states became world scientific leaders. The new field of morphology held a powerful appeal for those who, in the spirit of *Wissenschaft*, sought to create a theory-based philosophical zoology. Morphological research was typically conducted by anatomists, who were frequently involved in the teaching of medicine or with zoology (Nyhart, 1995; Gliboff, 2008).

When Ludwig Edinger was four years old, British gentleman naturalist Charles Darwin (1809–1882) published the *Origin of Species* (Darwin, 1859/2003). His theory of evolution by natural selection transformed the study of morphology. Darwin represented the relationships among living species as a divergently branching genealogical tree. He explained similar characters among related species as due to retention by inheritance of characters from common ancestral forms and differences between groups as due, in part, to the extinction of intermediate forms. Darwin's theory gave the archetypes and homologies of the morphologists a solid, naturalistic genealogical explanation as the legacy of ancestral forms (Bowler, 1996).

Darwin wrote that "it is notoriously not possible to represent in a series, on a flat surface, the affinities which we discover in nature amongst the beings of the same group . . . on the view which I hold, the natural system is genealogical in its arrangement, like a pedigree" (Darwin, 1859/2003, p. 422). At numerous points in the *Origin*, however, he nonetheless uses the terms "higher" and "lower" when referring not to genealogy but rather to degree of morphological complexity. His notebooks and correspondence indicate that he struggled with such concepts, eventually concluding that "highness" corresponded to internal differentiation, specialization, and division of labor (Ruse, 1996). Ruse (1996) attributes Darwin's beliefs on the matter to the influence of Germanic morphologists on his thinking. While Darwinian genealogy precludes a simple ladder-like ranking of animals by morphological complexity, it nevertheless requires the existence of a relationship between genealogy and morphological complexity, since it is necessarily the case that complex organisms must evolve from simpler ancestors. The nature of that relationship was to remain a matter of debate during the post-Darwinian period (Bowler, 1996; Ruse, 1996). With respect to brains, we will see that it can be regarded as the central conceptual issue of Ludwig Edinger's work.

The eminent German paleontologist Heinrich Georg Bronn (1800–1862) introduced evolutionary theory into Germany with his translation of the *Origin*, published in 1861 (Gliboff, 2008). The field of evolutionary morphology, which attempted to explain animal form in terms of Darwinian genealogical relationships, was founded by two Germans, Karl Gegenbaur (1826–1903), who was a professor of anatomy at the Universities of Jena and Heidelberg, and his prolific student Ernst Haeckel (1834–1919).

Gegenbaur's major work, *Grundzüge der vergleichenden Anatomie* [*Elements of Comparative Anatomy*], was originally published in 1859. Its revised Darwinian version became the standard textbook of evolutionary morphology and was published in English in 1877. The work was, first and foremost, a compendium of descriptive comparative anatomy. Members of each major animal group were characterized as "lower" or "higher" in morphological complexity and differentiation. Gegenbaur wrote:

> The distribution of work amongst a number of different organs leads to the perfecting of the operations of such organs. Each organ is enabled to develop in a definite direction, with the particular function which is undertaken by it. The organism thus becomes more highly developed, as well as complicated. Division of labour leads to a perfecting of the whole organism. According as the division of labour involves only a few or many organs, a greater or less part of the organism is brought under its influence. (Gegenbaur, Bell, & Lankester, 1878, p. 14).

The differing development of brain regions, according to the demands that the animal's lifestyle placed on their function, was a concept of central importance to Edinger. Gegenbaur also speaks of a "vertebrate series" of ascending morphological complexity (Gegenbaur et al., 1878, p. 590), another idea that was of central importance to Edinger. Like Kielmeyer and some other pre-Darwinian morphologists, Gegenbaur supposed that embryonic development was the key to understanding evolutionary development, writing that "Ontogeny thus represents, to a certain degree, paleontological development, abbreviated and epitomized. The stages which are passed through by higher organisms in their ontogeny, correspond to stages which are maintained in others as the definitive organization" (Gegenbaur et al., 1878, p. 6).

Through his training of students, Gegenbaur founded a school of thought that dominated German morphology for the remainder of the century (Nyhart, 1995, 2003; Bowler, 1996; Gliboff, 2008). In 1872, when Ludwig Edinger began his studies of medicine at the University of Heidelberg, he studied for a year with Gegenbaur (Glees, 1952; Edinger, 2005, p. 50). Evolutionary morphology was considered a *wissenschaftliches* [pertaining to pure knowledge or basic research] field and was taught by medical faculties of the time (Nyhart, 1995). The results of such influence are evident in Edinger's work.

More than a decade prior to his encounter with Edinger, Gegenbaur was mentor to his most well-known student, Ernst Haeckel, who was considered the most vigorous exponent of Darwin's theory outside England in the nineteenth century (Nyhart, 1995, 2003; Bowler, 1996; Gliboff, 2008). Haeckel's *Generelle Morphologie der Organismen* [*General Morphology of Organisms*] published in 1866 and later works represented an attempt to meld Darwin's theory with the accomplishments of German morphology. Edinger read Haeckel's *Natürliche Schöpfungsgeschichte* [*Natural History of Creation*] (Edinger, 2005, p. 49), a widely read popular account of evolutionary theory published in 1868 (Haeckel, 1892; Richards, 2008), when he was a teenager. According to Kreft (2003), Edinger's interest in biology was sparked by Haeckel's writings.

Haeckel's account of evolution strongly emphasized progress as an increase in morphological complexity, and his works are full of references to "higher" and "lower" animals and developmental series of increasing morphological complexity (Haeckel, 1879, 1892). Haeckel advocated the theory that ontogeny repeats phylogeny as the "biogenetic fundamental law" and "one of the most important and irrefutable proofs of the [Darwinian] Theory of Descent" (Haeckel, 1892, p. 356). Regarding comparative anatomy, he wrote:

> The important parallelism of the paleontological and individual [embryonic] developmental series now directs our attention to a third developmental series, which stands in the closest relations to these two, and which likewise runs, on the whole, parallel to them. I mean the series of developmental forms which constitutes the object of investigation in *comparative anatomy*, and which I will briefly call the *systematic developmental series of species*. By this we understand the chain of different, but related and connected forms, which exist *side by side* at any one period of the earth's history; as for example, the present moment. While comparative anatomy compares the different forms of fully developed organisms with one another, it endeavours to discover the common prototypes which underlie, as it were, the manifold forms of kindred species, genera, classes, etc., and which are more or less concealed by their particular differentiation. It endeavours to make out the series of progressive steps which are indicated in the different degrees of perfection of the divergent branches of the tribe.. . . It shows us how far the succession of classes of vertebrate animals, from Fishes upward, through the Amphibia to the Mammals, and here again from the lower to the higher orders of Mammals, form a progressive series or ladder. (Haeckel, 1892, pp. 358–359; the work cited is the English translation of *Natürliche Schöpfungsgeschichte*, emphasis in original translation)

This idea of a progressive series or ladder, though clearly not a strictly linear one, takes center stage in Haeckel's discussion of brain evolution in his *Anthropogenie; oder Entwickelungsgeschichte des Menschen* [*The Evolution of Man*] (Haeckel, 1879). He writes that “Even among the higher Vertebrates themselves, numerous gradations occur in the structure of the brain. From Amphibians upward, the brain, and with it mental life, develops in two different directions, of which the one is carried out in Reptiles and Birds, the other in Mammals” (Haeckel, 1879, pp. 223–224). These ideas are central to Edinger’s approach to comparative neuroanatomy.

Controversy swirls about Haeckel and Gegenbaur. By the traditional account (Russell, 1916/1982; Gould, 1977; Bowler, 1983; Breidbach, 2002), they are said to have maintained the morphologists’ supposed commitment to transcendental idealism with minimal necessary modification to accord with Darwin. Evolution, like embryonic development, was supposed to represent deterministic progress up the scale of beings. As for pre-Darwinian morphologists, more recent historical research has prompted a revision of this view. Haeckel’s known philosophical commitments were wholly incompatible with transcendental idealism. He was an atheist and a proponent of monist pantheism, founding a society devoted to the promotion of this philosophy. He saw biological processes as the outgrowth of blind mechanistic physical laws (Bowler, 1996; Kleeberg, 2007; Gliboff, 2008; Richards, 2008). In his *Generelle Morphologie der Organismen* [*General Morphology of Organisms*] he wrote that “*We see in Darwin’s discovery of natural selection . . . the definitive death of all teleological and vitalistic interpretations of organisms*,” a clear rejection of the *Bildungstrieb* [the natural self-organizing force] of his pre-Darwinian predecessors (as cited in Gliboff, 2008, p. 173, emphasis in original). Although Haeckel accepted Lamarckian inheritance of acquired traits, he believed, as did Darwin, that neo-Lamarckian processes could function only in coordination with natural selection. He rejected Lamarck’s inner perfecting principle and the role of the will as contrary to a mechanistic account of living things. Progress was the result of unpredictable variation and natural selection, rather than of some teleological inner trend (Gliboff, 2008; Richards, 2008).

Haeckel sought to use paleontology, comparative morphology, and embryonic recapitulation to reconstruct Darwin’s divergently branching phylogenetic tree. Such a reconstruction involved a host of new and thorny questions. When are shared animal traits due to homology and indicative of a close genealogical relationship, and when are they due to parallel or convergent evolution of distantly related forms due to similar environmental demands? When can modern animals be taken as good representatives of ancestral forms? What is the relationship between an animal’s embryonic development and its phylogenetic history? What is the relationship between morphological complexity and genealogical history? Such questions concerning branching trees and their implications were at the core of evolutionary morphology (Bowler, 1996). Like Edinger’s modern critics, Dayrat charges that Haeckel’s method of tree reconstruction “was based on the acceptance of a revised *scala naturae* . . . Haeckel’s trees were branched only on the surface” (2003, p. 526) due to his preoccupation with scales of morphological complexity. It nonetheless remains the case that Haeckel’s trees, like Darwin’s, were divergently branched, and some of them were of strikingly modern appearance (see Figure 1).

Like their modern successors, Haeckel and his contemporaries were well aware of the problems posed by the project of reconstructing Darwin’s phylogenetic tree. In the theories of the evolutionary morphologists, hypothesized ancestors took the place of the hypothesized types of their forerunners. When possible, Haeckel sought living analogs of hypothesized ancestral forms. According to Bowler (1996, p. 60), he did this precisely because it gave them concrete form and thereby distanced him from the conceptions of the idealists. For such reasons, the search for “living fossils” was a common practice among evolutionary morphologists, but its problems were well appreciated. To argue that a given form is a living fossil, one must suppose that an ancestral form would survive unchanged,

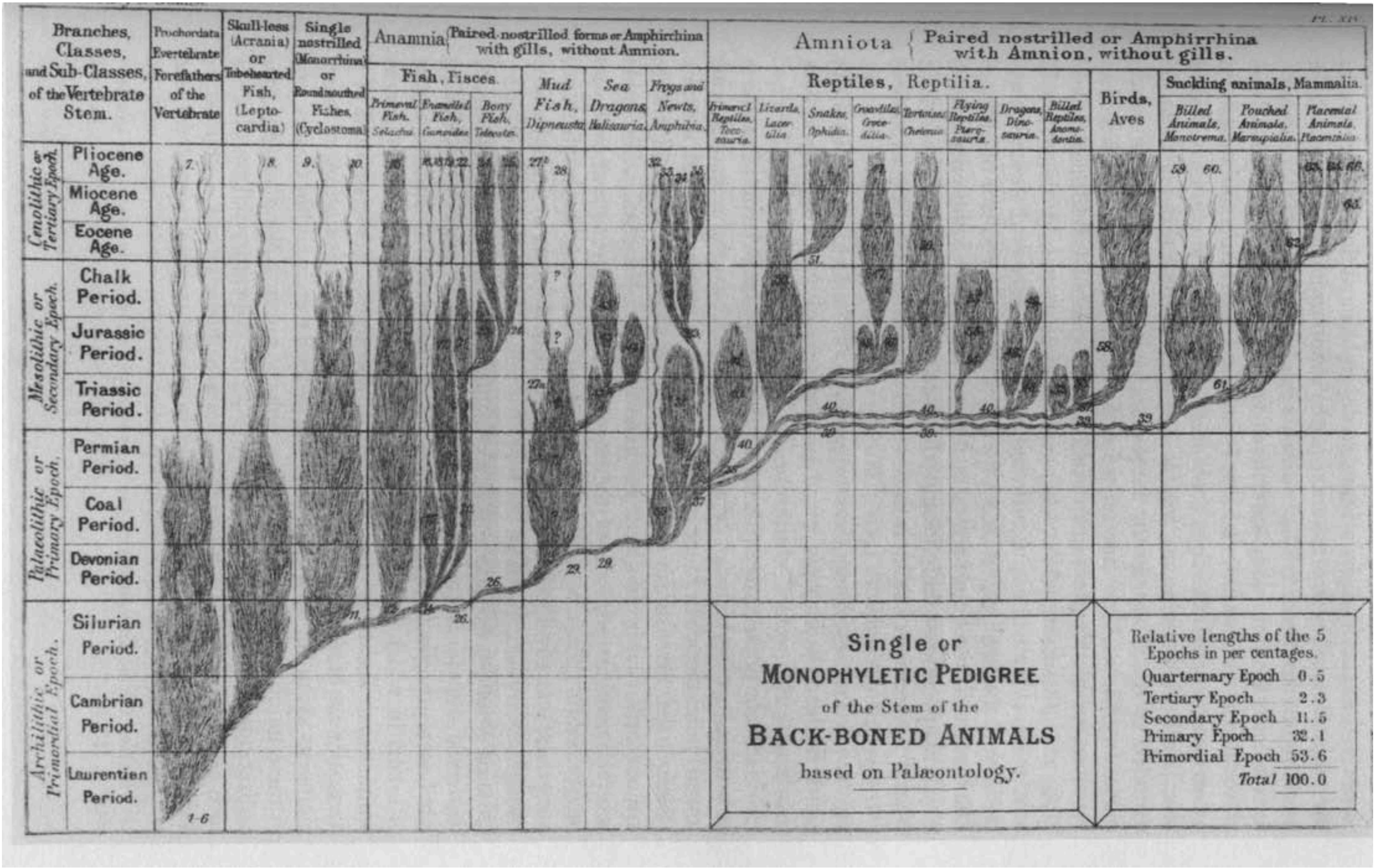

Figure 1. Ernst Haeckel's "Monophyletic pedigree of back-boned animals" from his *Natürliche Schöpfungsgeschichte* [*Natural History of Creation*] (1883) II, Plate XIV, illustrates how phylogenetic relationships were conceived of in Edinger's times. Despite Haeckel's interest in scales of morphological complexity, the diagram depicts a divergently branching genealogy of basically modern appearance. In Haeckel's terminology an "anatomical series" is the series of forms coexisting at one time in Earth's history, corresponding to any horizontal band of the diagram.

while its descendants radiated into more specialized forms. One must also cope with the possibility that some simple forms, rather than having retained the simplicity of an ancestral form, might have evolved from more complex forms by the degenerative loss of traits. To give one example, the lancet *Amphioxus*, a chordate lacking a backbone, was specifically identified by Haeckel and others as a living fossil of the vertebrate common ancestor. Contemporary critics charged that *Amphioxus* had instead become simplified due to its burrowing lifestyle (Bowler, 1996).

Such debates made Edinger's contemporaries well aware of the complexity of the relationship between morphological complexity and genealogical ancestry. American ichthyologist Theodore Gill (1837–1914) expressed his frustration over the wide disagreement about which fishes were the "highest." Few doubted that the teleosts, or bony fishes, were the most specialized and thus highly developed forms. Yet, the line that led to land tetrapods—"higher" vertebrates—appears to have come from a group that stood "lower" among the fishes, the lungfish. Writing in 1872, he complained that "Perhaps there have been no words in science that have been more productive of mischief and more retarding the progress of biological taxonomy than those words, pregnant with confusion, HIGH and LOW, and it were to be wished that they might be erased from scientific terminology" (as cited in Bowler, 1996, p. 207, emphasis original).

In the early-twentieth century, morphology, a highly productive and successful field for much of the nineteenth century, began to decline in popularity in relation to a new set of problems and approaches presented by experimental biology. Evolutionary morphology was mired in controversy about such matters as the status of "living fossils" and many other things. Its major problems had generated multiple inconsistent hypotheses, without the methods or the evidence needed to decide among them (Nyhart, 1995; Bowler, 1996). Interest in this set of problems revived in the latter half of the twentieth century with the new methods of cladistic analysis and evolutionary developmental biology being brought to bear. It was the use of these new methods by comparative neurobiologists that brought them into conflict with the interpretations of Edinger.

Neuroanatomy

The first comparative studies of animal brains were made in the seventeenth century. In the early-nineteenth century many monographs were published on the gross morphology of the brains of nonmammals (Edinger, 1899a, p. 11). Although invented in the early-seventeenth century, microscopes were of limited value in the investigation of living things prior to the nineteenth century because of their poor optical quality. In that century, better glasses and lenses were invented, and German physicist Ernst Abbe (1840–1905) worked to develop a better understanding of the optical theory of the microscope. Germany led in the field of microscopy, with high-quality instruments manufactured by Carl Zeiss (Coleman, 1977). By the latter half of the nineteenth century, improvements in microscopy and tissue preparation had made it possible to study the internal microanatomy of brains (Shepherd, 1991; Northcutt, 2001; Hakosalo, 2006; Edinger, 1899a, p. 4). Ludwig Edinger's first encounter with microscopy came at the age of 14, when he was given a small microscope as a gift. This gift is said to have played a role in his selection of medicine as a career (Glees, 1952; Kreft, 1997, 2003).

German anatomist Benedikt Stilling (1810–1879) introduced serial sectioning into neuroanatomy in 1842, in which the brain is hardened by chemical fixatives, carefully sliced into uniform thin sections by a new device called a microtome and placed on slides for microscope viewing (Hakosalo, 2006). Anatomists garnered an understanding of the three dimensional microstructure of the brain by sequentially observing such slides. A variety of selective stains were developed to visualize brain structures (Edinger, 1899a, p. 5; Shepherd, 1991; Northcutt, 2001). From 1874–1877, while studying at the University of Strasbourg with Adolf Kussmaul, Edinger worked on the anatomy of the spinal cord, learning the new techniques of serial sectioning and histological fixation and staining. At the time, these novel techniques afforded substantial technical challenges (Glees, 1952; Stahnisch, 2008). Edinger's knowledge of them made it possible for him to undertake his comparative studies of vertebrate brains.

A conceptual framework for interpreting observations made using the new methods soon emerged. Early in the nineteenth century, two German microscopists, Matthias Jacob Schleiden (1804–1881) and Theodor Schwann (1810–1882) formulated the cell theory, maintaining that living cells were the microscopic building blocks of all organisms (Coleman, 1977). The cell theory proved difficult to apply to the nervous system with its thicket of fine processes and nerve fibers. Some contended that the nervous system uniquely consisted of an interconnected reticulum (Shepherd, 1991). By the end of the century, however, the "neuron doctrine" of Spanish neuroanatomist Santiago Ramón y Cajal (1852–1934) had triumphed. Ludwig Edinger's thesis advisor, eminent anatomist Wilhelm von Waldeyer (1836–1921), played a central role in the formulation and acceptance of this doctrine. The doctrine maintained that nerve cells or neurons were distinct units conforming to the Schleiden-Schwann theory (Edinger, 1899a, 1911; Shepherd, 1991).

Neurons came to be seen as the structural and functional units of the nervous system, with their cell bodies clustered into nuclei or layered cortices and their axonal processes forming pathways of connection. The elucidation of these structures and their connections became the fundamental task of neuroanatomy (Shepherd, 1991). The task these ideas set for Edinger's comparative neuroanatomy was to determine how such microscopic structures and connections vary across those animals possessing nervous systems (Edinger, 1899a, 1911).

Edinger's Scientific Career

Ludwig Edinger was born into a prosperous Jewish family in Worms am Rhein, Germany, in 1855. His father owned a clothing manufacturing company, and his mother was the daughter of a prominent doctor. In 1872, at the age of 17, he began his studies at the University of Heidelberg with Carl Gegenbaur, with whom he eagerly studied zoology and comparative anatomy (Glees, 1952; Edinger, 2005, p. 50). From 1874–1877, he studied at the University of Strasbourg, including three years of work as a resident with Adolf Kussmaul, who was known primarily as a medical clinician (Matteson & Kluge, 2003). There he gained his first research experience and his knowledge of the new neuroanatomical techniques of microscopy, serial sectioning, and staining (Glees, 1952; Stahnisch, 2008).

Edinger's MD thesis, completed at Strasburg Municipal Hospital under the supervision of Wilhelm von Waldeyer, was titled *Über die Schleimhaut des Fischdarmes, Nebst Bemerkungen Zur Phylogenese Der Drüsen Des Darmrohres* [*On The Histology Of The Mucosa of Fish and Some Remarks on the Phylogenesis of the Glands of the Small Intestine*] (Edinger, 1877; Stahnisch, 2008). The topic indicates his interest in nonmammals and evolutionary morphology. With Waldeyer, Edinger continued to study the works of Gegenbaur and Haeckel, including Haeckel's *Generelle Morphologie der Organismen* [*General Morphology of Organisms*] (Edinger, 2005, p. 62). Waldeyer's own interest in comparative neuroanatomy is evident in his later activities. After he became director of the *Anatomisches Institut der Universität Berlin* [Anatomical Institute of the University of

Berlin] in 1883, such work became his prime focus. He studied the brains and crania of various primate species and human races (Shepherd, 1991).

Edinger earned his habilitation[2] in 1881 and spent time as a researcher in London, Berlin, and Leipzig. In Leipzig, Edinger met Carl Weigert, who had developed a new stain that selectively stained the bundles of axons that constitute nerve fibers, making it possible to trace the courses of such bundles in microscope slides. Weigert was to become a close collaborator, and his stain proved of central importance to Edinger's neuroanatomical work (Glees, 1952; Kreft, 1997; Stahnisch, 2008).

At this point in his career, Edinger faced discrimination because he was a Jew and was unable to obtain university posts or a professorship. On the advice of Jewish colleagues, he became a practicing physician (Glees, 1952; Stahnisch, 2008). In 1883, he settled in Frankfurt am Main, just 30 miles from his childhood home in Worms, to establish his practice. Frankfurt was very liberal, and Jews had benefited from this tolerant culture. Although there was no university, the Senckenberg Institute provided research facilities and meeting space for local medical and scientific societies. Edinger was eventually given a room at the institute, but, at first, he had to set up a lab in his bedroom. His studies there concerned the development of the nervous system in human embryos, using material sent by a gynecologist in Giessen. Edinger later wrote that it was easier to trace the course of nerve tracts in the brains of embryos than in adults (Edinger, 1899a). He worked during the day at his clinical practice and in the evenings at his neuroanatomy. The publications that resulted from this work garnered the attention of the noted anatomist Theodor Meynert, who journeyed from Vienna to Frankfurt to see his anatomical preparations first hand (Glees, 1952; Kreft, 1997).

In 1883, the Medical Society of Frankfurt asked Edinger to give a series of lectures on the brain for a medical audience. These were held for several years and were a great success. He published them as *Zehn Vorlesungen über den Bau der nervösen Centralorgane: für Ärzte und Studierende* [*Ten Lectures on the Structure of the Central Nervous System: for Medical Doctors and Students*]. The book first appeared in 1885 and was followed by eight editions until 1911. It was translated into every modern language and garnered Edinger an international reputation (Herrick, 1908; Glees, 1952; Stahnisch, 2008). Also in 1885, Carl Weigert, his academic career destroyed by anti-Semitic discrimination, joined Edinger at Frankfurt as a pathologist and neuropathologist. The two shared laboratory space at the Senckenberg Institute for the next 17 years. They were successful teachers and attracted students to the institute from across the entire continent. Edinger was the first to make extensive use of the Weigert stain for examination both of the human brain and of the brains of nonmammalian vertebrates (Glees, 1952; Kreft, 1997).

From 1890 onward, a continuous stream of publications in comparative neuroanatomy issued from the work of Edinger and his pupils. The fifth edition of Edinger's neuroanatomy text, published in German in 1896, was expanded to include 150 pages of systematic comparative neuroanatomy of nonmammalian vertebrates and a greatly expanded treatment of the brains of nonhuman mammals. He billed the volume as the first attempt at a comparative microanatomy of the vertebrate nervous system and retitled it *Verlesungen über den Bau der Nervösen Zentralorgane des Menschen und der Thiere* [*Lectures on the Anatomy of the Central Nervous System of Man and of Animals*]. It was republished in English translation in 1899 as *The Anatomy of the Central Nervous System in Man and of Vertebrates in General* (Edinger, 1899a; Hall, 1899). The seventh edition was expanded to two volumes,

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[2] Habilitation is the highest academic qualification in European academia, requiring work of greater quantity and quality than a PhD.

the first (*Band I, Das Zentralnervensystem der Menschen und der Säugetiere-* [*Volume I, The Central Nervous System of Man and Mammals*]) published in German in 1904 (Edinger, 1904), and the second (*Band II, Vergleichende Anatomie des Gehirns-* [*Volume II, Comparative Anatomy of the Brain*]) in 1908 (Edinger, 1908b). The first volume focused on the needs of medical students and practitioners, and the second expanded his treatment of comparative neuroanatomy and brain function (Herrick, 1908).

Between 1888 and 1903 Edinger also published a five-volume series; *Untersuchungen über die vergleichende Anatomie des Gehirns* [*Investigations of the Comparative Anatomy of the Brain*]. Topics dealt with include the forebrain in fish, amphibia, and reptiles, the diencephalon in cartilaginous fishes, amphibians, and reptiles, and, in collaboration with Adolf Wallenberg (1862–1949), the forebrain in birds (Reviewer, 1893; Edinger, 1899b; Edinger, Wallenburg, & Holmes, 1903). A 1908 English language review, revealed a growing interest in the relationship of the brain to behavior, including his own observations in comparative psychology (Edinger, 1908a).

Edinger obtained his own laboratory space in 1902, and in 1907, at the age of 52, his laboratory comprised the entire second floor of the newly built Dr. Senckenberg Pathology Institute. In 1914, this institute was incorporated into the new University of Frankfurt and Edinger was made a full professor of Neurology. Unfortunately, 1914 also marked the onset of World War I, which caused a major reduction in funding for the new university. In 1918, Edinger died of a coronary thrombosis at the age of 63 (Glees, 1952; Kreft, 1997, 2003).

Edinger's student and collaborator, Dutch neuroanatomist Cornelius Ubbo Ariëns Kappers (1877–1946) carried on his work and himself became an important figure in comparative neurobiology (Meerloo, 1946; Glees, 1952; Northcutt, 2001; Butler & Hodos, 2005). His daughter, Tilly Edinger (1897–1967), also became an important scientist in her own right, founding the field of paleoneurology, the study of fossil braincases (Buchholtz & Seyfarth, 2001; Northcutt, 2001; Kreft, 2003). Inspired by her father, who died when she was 21, Tilly studied zoology, geology, and paleontology and became fascinated by fossil braincases. In 1929, she published *Die fossilen Gehirne* [*Fossil Brains*], thereby establishing this new field. Fleeing Germany for the United States with the rise of the Nazis, she continued her career at the Harvard Museum of Comparative Zoology (Buchholtz & Seyfarth, 2001).

Other important European contributors to early comparative neuroanatomy in the 20 years bracketing the turn of the twentieth century included Sir Grafton Elliot Smith (1871–1937) in England and Nils Holmgren (1877–1954) in Sweden. Several Americans also made noted contributions during this period, including G. Carl Huber (1865–1934), Elizabeth C. Crosby (1888–1983), J. B. Johnston (1868–1939), C. Judson Herrick (1868–1960), James Papez (1883–1958), and Olaf Larsell (1886–1964) (Northcutt, 2001). In 1936, Cornelius Ubbo Ariëns Kappers, G. Carl Huber, and Elizabeth C. Crosby jointly authored a three-volume compendium of comparative neuroanatomy (Ariëns Kappers, Huber, & Crosby, 1936; Northcutt, 2001). This compendium summarized the accomplishments of the early period and extended Edinger's theories of brain evolution. The field was then inactive until well after the Second World War (Northcutt, 2001).

Edinger's Comparative Neuroanatomy

Overview

I will here focus on the fifth edition of Edinger's neuroanatomical text, which is available in English (Edinger, 1899a), as well as his seventh and eighth editions (Edinger, 1908b, 1911),[3] which are available only in German, and a 1908 English-language synopsis (Edinger, 1908a). The fifth edition consists of three sections concerning general features of the microanatomy of the vertebrate brain, comparative vertebrate neuroanatomy, and mammalian and human neuroanatomy, respectively. In the seventh edition, the second comparative section is expanded to fill an entire 334-page volume of its own. The comparative work described was largely the product of Edinger's own laboratory (Herrick, 1908) and included 283 hand-drawn figures.

The opening chapter for both editions deals with the history and techniques of neuroanatomy and summarizes past studies of neuroanatomy in nonmammals. But while Edinger attempts to situate his work within the broader context of other workers in neuroanatomy, he makes no comparable attempt to situate his work within the context of evolutionary morphology. The works of Stilling, von Gerlach, Golgi, Ramón y Cajal, and many others are explained; those of Darwin, Bronn, Haeckel, and Gegenbaur pass unmentioned.[4]

A contemporary reviewer of Edinger's seventh edition, American zoologist and comparative neuroanatomist C. Judson Herrick writes, "Comparative neurology has been and is extremely difficult because of the fragmentary nature of the mass of intricate detail and the lack of co-ordinating principles" (1908, pp. 283–284). Much of Edinger's comparative volume does indeed consist of descriptive anatomical detail. However, he also employs a clear evaluative framework and, by his seventh edition and later writings (Edinger, 1908a), draws theoretical conclusions about both brain function and evolution.

Edinger's Evaluative Framework: The Vertebrate Series

In the introduction to his fifth edition, the first to feature comparative material, Edinger explains his motivation for studying nonmammals:

> The central nervous system has formerly been studied mostly by physicians. To them, naturally, the first task was to gain a better understanding of the human brain, only the mammalian brain being brought in for comparison. . . . By comparing animals low down in the vertebrate series, the attempt is here made to determine where particular structures appear, how they vary, and what functions they perform at different stages of their [evolutionary] development. It has also been attempted to determine what belongs to each part of the nervous system as essential and fundamental. . . . There must be a number of anatomical mechanisms which are alike present in all vertebrates: those which make possible the simplest expression of the activity of the central nervous system. It is only necessary to find that animal, or that stage of development of any animal,

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[3] The seventh edition appears to have been the last complete, two-volume edition. The first volume of an eighth edition was published in 1911. I can find no trace of a second volume. Its publication was perhaps precluded by the outbreak of World War I in 1914 and Edinger's death in 1918. All references to the text of the first volume are to the 1911 eighth edition, and all references to the text of the second volume are to the 1908 seventh edition.

[4] While their work is not discussed, in Edinger's (1908b) *Vorlesungen über den Bau der nervösen Zentralorgane des Menschen und der Tiere-Zweiter Band Vergleichende Anatomie des Gehirns, Vol. 2*, Karl Gegenbaur's *Vergleichende Anatomie der Wirbeltiere, mit Berücksichtigung der Wirbellosen* [*Comparative Anatomy of the Vertebrates, with Consideration of the Invertebrates*], (1898) and H. G. Bronn's *Klassen und Ordnungen des Tierreichs* [*Classes and Orders of the Animal Kingdom*], Vol. 6 (1907) are cited.

> in which this or that mechanism appears in so simple a form that it may be completely understood. (Edinger, 1899a, pp. v–vi)

By his own admission, Edinger's quest for simplicity amongst the lower vertebrates did not meet with success. His prior expectations for success may have been due to the explanatory framework that permeates his work—the vertebrate series. Denounced by his successors, it was also recognized as problematic by Edinger himself.

In the major works of Edinger considered (Edinger, 1899a, 1911), classes of animals were ranked along a sequence varyingly referred to as the "vertebrate series," "animal series," or "taxonomic series" on which they were designated "lower" or "higher" (i.e., from lowest to highest, invertebrates, fishes, amphibians, reptiles, birds and mammals, humans). The rank of a vertebrate class in the series is taken to be derived from more general considerations outside the scope of Edinger's neuroanatomy. Edinger's series of coexistent modern species corresponds to the "systematic developmental series of species" in Haeckel's *Natürliche Schöpfungsgeschichte* as discussed above. Edinger seeks to interpret differences in brains across modern vertebrate classes in relation to the series, generally as additions or differentiations over evolutionary time. Here are a few illustrative examples:

> From the reptiles upward through the vertebrate series, one recognizes that, besides the two nuclei mentioned, new ones arise which, among the fish and amphibians, are present in only rudimentary form. (Edinger, 1899a, p. 92)
>
> From birds upward in the vertebrate series there is formed a tract from the cerebral cortex to the optic center. (Edinger, 1899a, p. 136)
>
> Though these nuclei exist in the lower vertebrates, it is only in the highest of the series that the cerebral tracts are added. (Edinger, 1899a, p. 136)
>
> Thus in the vertebrate series there is added to the lower olfactory mechanism a higher one, which gradually increases in extent. (Edinger, 1899a, p. 152)

As discussed above, ranking organisms as "high" or "low" based on morphological complexity was an accepted, though controversial, practice among evolutionary morphologists contemporary with Edinger. The concept of the vertebrate series appears in the works of both Gegenbaur and Haeckel (Gegenbaur, Bell, & Lankester, 1878; Haeckel, 1879, 1892; Bowler, 1996) and was in widespread use in the scholarly literature of the period. Of 10,350 English language scholarly papers published between the years 1860 and 1919 as indexed on Google Scholar and containing the word "vertebrate" in their title or abstract, 386 or 3.7% use the phrase "vertebrate series." Use of the phrase subsequently declines in frequency, reaching 0.05% for the 20-year period between 1980 and 1999. Examination of a sampling of older papers indicates that other authors use it in much the same way as does Edinger, ranking vertebrate classes as "higher" or "lower" along the series. Edinger nowhere feels the need to justify his use of the series (and he sometimes criticizes it harshly) indicating, along with the literature survey, the wide acceptance of the framework. Edinger's contemporary reviewer, C. J. Herrick (1908), writes of the vertebrate series in a matter-of-fact way and even questions some of Edinger's claims to departure from its expectations.

We have already seen that any necessary connection between the linear scales sometimes invoked by German morphologists and the transcendentalist metaphysics of the *scala naturae* has been challenged (Rehbock, 1990; Nyhart, 1995; Bowler, 1996; Gliboff, 2008). Specifically, the influential Ernst Haeckel espoused a contingent, Darwinian view of evolution that was wholly inconsistent with such metaphysics (Gliboff, 2008; Richards, 2008).

The basis in Darwinian genealogy for the vertebrate series is actually straightforward. Fishes are the oldest vertebrate class, and land-dwelling vertebrates must have been derived from a piscine ancestor of some sort. Nor does anyone doubt that the first land-dwelling vertebrates would have exhibited the defining characteristics of the class amphibia. Given an aquatic starting point, reptiles, animals capable of reproducing on land, must, on Darwin's theory, have been derived from animals lacking this ability. The only available such class of vertebrates—for a theory that posits that change can happen only in small increments—are the amphibians. Thomas Huxley once argued that mammals evolved independently of reptiles from an amphibian ancestor (Bowler, 1996). By the time of Edinger's works, however, fossil evidence had convinced most morphologists that the mammals had evolved from a reptilian ancestor (Bowler, 1996). Therefore, any modern mammal must have had a reptilian, amphibian, and piscine ancestor. Seen simply as such a temporal sequence for the major classes, then the vertebrate series appears unproblematic for Darwinians. From Darwin on, it was clear to evolutionary morphologists that birds evolved independently from a different reptilian stock than did mammals (Bowler, 1996). Edinger made reference to this divergence (Edinger, 1908b, p. 277) and, thus, could not have seen vertebrate brain evolution as strictly linear.

The use of "higher" and "lower" implies more than a temporal sequence; it also implies a scale of ascending morphological complexity among modern vertebrates. The Darwinian rationale for such a scale was recounted by the American writer and science popularizer Charles Morris (1881).[5] Animals may survive, he supposed, by adaptation to a few simple conditions or to many and complex conditions. Fishes, now as in the primordial past, were said to be constrained by the properties of water to do the former. The limited supply of oxygen limits their vital activity. Their sensory acuity is supposedly limited because light comes to them dimmed, sound dulled, and taste and smell blunted by water. Buoyancy renders rapid motion easy, and with no places of ambush, predator-prey relations are unchallenging. Thus, modern fishes supposedly retained their primordial morphological simplicity.

Land dwelling is said to impose greater demands on locomotion, blood pumping, and a host of other functions, providing greater pressures and opportunities for the evolution of morphological complexity. Therefore, successively more land-adapted vertebrate classes are successively more morphologically complex and, given the fixed demands of their environment, retained this ascending scale of complexity to the present.

As for Darwin, morphological complexity involves internal specialization and division of labor. The mammalian form is said to be exposed to the widest range of opportunities and perils and to have, therefore, achieved the greatest morphological complexity. Upright stance frees the forelimbs and hindlimbs for different specializations, and man's upright stance is therefore an advance over the quadrupeds. Man is said to have sensory acuity "in advance of all other animals" (Morris, 1881, p. 795).[6]

For a sequence among modern vertebrate classes to retain information about the evolutionary history of their bodies as a whole or of some particular set of traits, it must be the case that at least some members of each vertebrate class retain the traits in question from their primeval ancestors. On the Darwinian account, evolutionary change or stasis is not a

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[5] Morris is unmistakably a Darwinian. He begins his paper with an explanation of Darwin's mechanism of natural selection but makes no mention of neo-Lamarckian or orthogenetic alternatives.

[6] This claim is, of course, woefully at odds with modern understanding. A wide variety of animal species are now known to have sensory abilities excelling those of humans in a wide variety of ways. Many animals can detect features of their environment (ultraviolet light, polarized light, ultrasound, electrical fields, etc.) to which humans are completely insensitive.

matter of some internal or necessary trend; it is rather a contingent consequence of environmental demands or lack thereof. Darwin argued that simple creatures persist in the world beside complex ones precisely because selective pressures prompting increases in morphological complexity do not always exist (Ruse, 1996). Perspectives such as that of Morris (1881) would have rendered it plausible to suppose that some environments inhabited by entire vertebrate classes, such as aquatic environments, would be devoid of pressures for evolutionary change. For a Darwinian, the question of whether or not the vertebrate series preserves a record of sequential historical increase in morphological complexity is thus one that can only be answered empirically. This is precisely the question to which Edinger's carefully collected comparative data provided an answer for the brain. His answer was, in many instances, negative.

Edinger's Findings and Theories

Edinger's search for simplicity in the brains of the lower vertebrates was not successful. He lamented:

> Simple and clear as are the outer features of the lower vertebrate brain, the inner structure is nevertheless, hardly less complicated, especially in those regions posterior to the Thalamecephalon [diencephalon], than in the mammals themselves . . . they are not altogether simple and clear even in so low a form as the larva of the cyclostomii [the jawless fishes that evolutionary morphologists viewed as the lowest vertebrates]. (Edinger, 1899a, p. 12)

The comparative sections of Edinger's fifth (Edinger, 1899a) and seventh editions (Edinger, 1908b) are organized according to major brain divisions progressing rostrally along the axis of the vertebrate central nervous system (CNS). He accordingly begins with the spinal cord. Edinger reports that *amphioxus*—the chordate that Haeckel had identified as a possible surviving common ancestor of the vertebrates—"practically possesses only a spinal cord" with only barely discernable brain structures (Edinger, 1899a, p. 48). More generally, he reports that spinal cords of lower vertebrates are disproportionately large, with fish having small brains and relatively enormous cords. "This striking relation," he writes, "may be followed even to the mammals. The brain of the horse or ox is much smaller than that of man, but their spinal cord is more than twice as thick as the human cord" (Edinger, 1899a, p. 74). Alongside such putative progressive trends, however, he noted extensive variability from species to species, without regard for rank along the vertebrate series. Of spinal commissures, he writes that "they are very unequally developed in different animals, even in animals of related species" (Edinger, 1899a, p. 66).

Rostral to the spinal cord is the medulla oblongata, a major brain region containing sensory and motor nuclei associated with the cranial nerves. Here Edinger found unexpected complexity in the lower vertebrates. In ray-finned fishes, "the nerve nuclei of the medulla have such a development and such complicated relations that the same structures in reptiles, birds, and mammals seem, in comparison, small and simple" (Edinger, 1899a, p. 84). The enormous development of the terminal nucleus of the vagus in goldfish led Edinger to describe it as a "veritable tumor" (Edinger, 1899a, pp. 85–86) (see Figure 2). By contrast, the same structure was relatively obscure in some other fishes, as well as in birds and mammals.

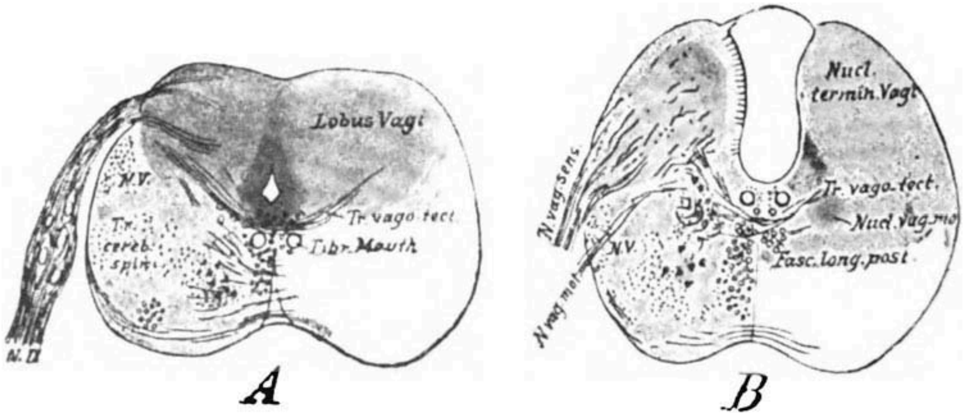

Figure 2. Edinger's drawing of transverse sections through the medulla oblongata of a goldfish at (A) a more posterior and (B) a more anterior level, from Edinger (1899a), Figure 45, p. 86. The vagal lobe (Lobus Vagi) and the terminal nucleus of the vagus (Nucl. termin. Vagi) are prominent. Edinger noted that structures associated with the vagus nerve were highly developed in the goldfish, a "lower" vertebrate, though not in some other fish such as the sturgeon, or in "higher" vertebrates such as birds and mammals, an indication that the complexity of such structures is determined by the demands of the lifestyle of a species rather than by its position along the vertebrate series.

Regarding other medullar nuclei, he writes:

> In many teleost fishes the sensory portion of the nucleus of the facial nerve, the very same that in humans . . . stands as a minor remnant, is an enormous nucleus to which taste receptors on the outer skin of the head project. In the octaval nuclei, which in mammals only the auditory nerve and the vestibular nerve supply, there is in all aquatic animals also a massive nucleus to which fibers of the head and lateral line project, this is the sense organ for the reception of the magnitude of pressure of moving water. (Edinger, 1908b, p. vii, translation mine)

Contrary to the views reflected by Morris (1881), some sensory systems were highly developed in fishes that were less developed or wholly absent in land vertebrates.

The cerebellum is located at the rostral end of the medulla oblongata on its dorsal surface. Of this structure, Edinger wrote: "no other part of the brain—the cerebrum probably excepted—manifests so many variations in its degree of development as does the cerebellum. The cerebellum is not more highly developed in the higher animals than in the lower.. . . [O]n the other hand, we meet, even between closely related animals, very striking differences" (Edinger, 1899a, p. 101) (see Figure 3). Edinger attributes this variation to differing locomotor requirements, noting that:

> In most amphibians there is only a minimal lamina in the position where the cerebellum is found. In the birds and again in the best swimmers [among teleost and elasmobranch fishes], such as shark and salmon, it is so enormous, that in this giant organ one can no longer recognize the thin lamina from which it originated and is in many cases present. . . . Not only does the flounder, which seldom swims, exhibit a very small cerebellum, among the turtles the

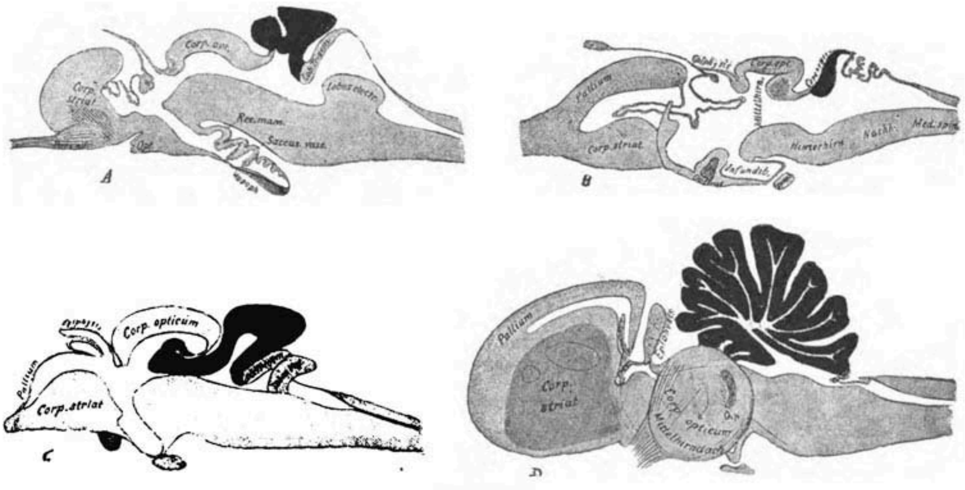

Figure 3. Edinger's drawings of midsaggital sections through the brains of four vertebrates, (A) a ray, (B) an amphibian, (C) a trout embryo, and (D) a bird, Edinger (1908b), Figure 94, p. 126. The cerebellum, shown in black, varies greatly in size and complexity from species to species. Other structures indicated include the corpus striatum (Corp. striat.) in the floor of the forebrain, and the pallium, its roof, as well as the optic tectum (corp. opt.).

> land dwelling often have only half as large a cerebellum as the swimming species. One observes the same with land dwelling lizards and giant dinosaurs that swam. (Edinger, 1908b, p. viii, translation mine)

Far from being undemanding, swimming had imposed its own peculiar demands on aquatic vertebrates.

The midbrain is located rostral to the medulla along the axis of the brain. Edinger draws similar conclusions regarding it. The midbrain and its connections are highly developed in "lower" vertebrates (see Figure 4) , and its structure is:

> . . . as far as is known, in all animals the same, except that those portions of the fibers which pass downward from the roof of the organ . . . are much more highly developed in fishes and birds than in mammals. In the latter therefore, there has taken place a relative retrogressive development. . . . So the midbrain offers again a good example of the fact that in the animal series (Taxonomic Series) no one segment of the brain undergoes a step-by-step progressive development which is even approximately parallel to the rank of the animal as determined by its general structure. (Edinger, 1899a, p. 124)

As Herrick (1908) notes, nearly half the pages of Edinger (1908b) are devoted to the "rhombencephalon [hindbrain—medulla oblongata and cerebellum] and its peripheral connections" (p. 275). More than two thirds of the book is devoted to structures other than the forebrain. In the introduction to the seventh edition, Edinger states his conclusions regarding these structures quite clearly and forcefully:

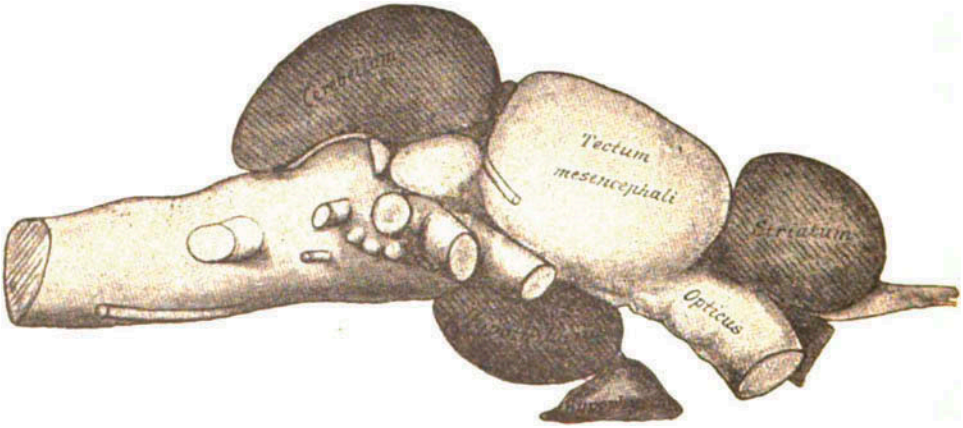

Figure 4. Edinger's drawing of a lateral view of the brain of a cod (*Gadus aeglefinis*), from Edinger (1899a), Figure 63, p. 112. The highly developed midbrain is indicated by the huge optic tectum (labeled Tectum mesencephali). The cerebellum, a hindbrain structure, is also prominent. The forebrain is labeled striatum, a forebrain floor structure, reflecting Edinger's belief that teleost fish lacked a forebrain roof.

> [W]hen we consider these brain components, we find that adaptations to particular living conditions have made them even more complicated and excellent, in certain respects, than the corresponding parts in mammals. In this respect the concept of higher and lower standing brains must be greatly qualified or curtailed (*durchaus eingeschränkt*). (Edinger, 1908a, p. v, translation mine)

Edinger elaborates later in the text:

> The study of the nuclei of the medulla oblongata is again very instructive for the view that I have earlier expressed, namely that it is not consistently the case that there are brains higher or lower in development in the animal series. Only individual brain components are sometimes here, sometimes there more developed, and this development depends in no way on the placement of an animal in the phylogenetic series, but rather entirely on the demands this or that adaptation has imposed on its bodily characteristics. (Edinger, 1908a, p. 80, translation mine)

Edinger is here describing a phenomenon known to modern evolutionary biologists as mosaic evolution (Mayr, 2001; Butler & Hodos, 2005). Traits are acted upon independently by natural selection, becoming more elaborate, retaining their simplicity, or becoming simpler based on such disparate pressures. While any particular trait of an animal may be described as primitive (if retained unchanged from an ancestral form) or derived (if altered from that state), animals cannot, as a whole, be so described. For brainstem structures, Edinger understood its implications just as well as do his modern critics—the vertebrate series, as a rank ordering of modern vertebrates, does not retain a record of the evolutionary history of vertebrate brainstems:

> It is not possible to retrace the genealogical history of the structure of the brain upward, nor to infer the phylogenesis of the brain from its structure. Where, in one animal, there is only undeveloped tissue, in all of its nearest relatives one

> finds a well-developed brain part. Due to the fact, of which many examples will be shown in what follows, that the development of the central nervous system in all its parts depends only on the requirements imposed by lifestyle. (Edinger, 1908a, p. v, translation mine)

Edinger (1908a, 1908b) divides the vertebrate brain into two parts (see Figure 5). He calls the first part the *palæëncephalon*. It includes all of the brainstem structures already discussed along with the structures in the floor and at the rostral end of the forebrain: the basal ganglia and the olfactory lobes. Edinger wrote:

> The palæëncephalon appears, with all its characteristic subdivisions, from cyclostomes to man. No part is ever entirely absent; its type remains unchanged whether we have before us the brain of a shark or the brain of an elephant. It is the oldest portion of the entire central nervous system, and many animals possess nothing but it. (Edinger, 1908a, p. 438)

It is the palæëncephalon whose component parts become independently adapted to the life circumstances of each modern vertebrate species and for which the basic premise of the vertebrate series—a progressive increase in morphological complexity—must therefore be rejected.

The roof and sides of the forebrain comprise the pallium. In mammals, a component of the pallium elaborates to become the cerebral cortex. Edinger (1908a, 1908b) coins the term neëncephalon to refer to the pallial mantle of the forebrain. In the same paragraph where Edinger rejects the general possibility of reconstructing the genealogical history of the brain using the neuroanatomy of modern forms, he adds a major caveat: “A true ascending line without relapse can only be established for the forebrain, and here it can indeed be shown that this brain part is only a primordium in the lowest vertebrates, and becomes ever more complicated and larger in the higher classes” (Edinger, 1908b, p. vi, translation mine). Later, he asserts that “Now that we know something of the quantitative development of the neëncephalon, we can indeed speak of higher and lower standing brains” (Edinger, 1908b, p. ix, translation mine).

Edinger regarded the forebrains of teleost fishes to consist entirely of the striatum and olfactory area (Edinger, 1899a, 1908a, 1908b) (see especially Edinger 1899a, Fig. 36, p. 76 and Fig. 86, p. 138). The “mantle” consisted only of a “simple epithelial plate” with no neural tissue (Edinger, 1899a, p. 146) (see Figure 6). The teleost thus represents the primitive vertebrate neural condition; its brain consisting exclusively of palæëncephalon. In rays and sharks, Edinger writes that “the mantle is developed; indeed the most anterior portion is so enormously thickened and the lateral portions project so far inward that in a greater part of the forebrain of selachians [rays and sharks] the ventricle is obliterated . . . in this way the brain of the selachian diverges much in form from the brains of other vertebrates” (Edinger, 1899a, p. 159). Edinger notes that “larger and smaller portions—according to species” (Edinger, 1899a, p. 159) of the epithelial mantle become neural tissue among selachians.

Above the fishes in the vertebrate series, “nearly the complete mantle may be transformed to brain-substance, only the most posterior part retaining its epithelial character and persisting as the Tela choroidea” [a membranous structure that secretes cerebrospinal

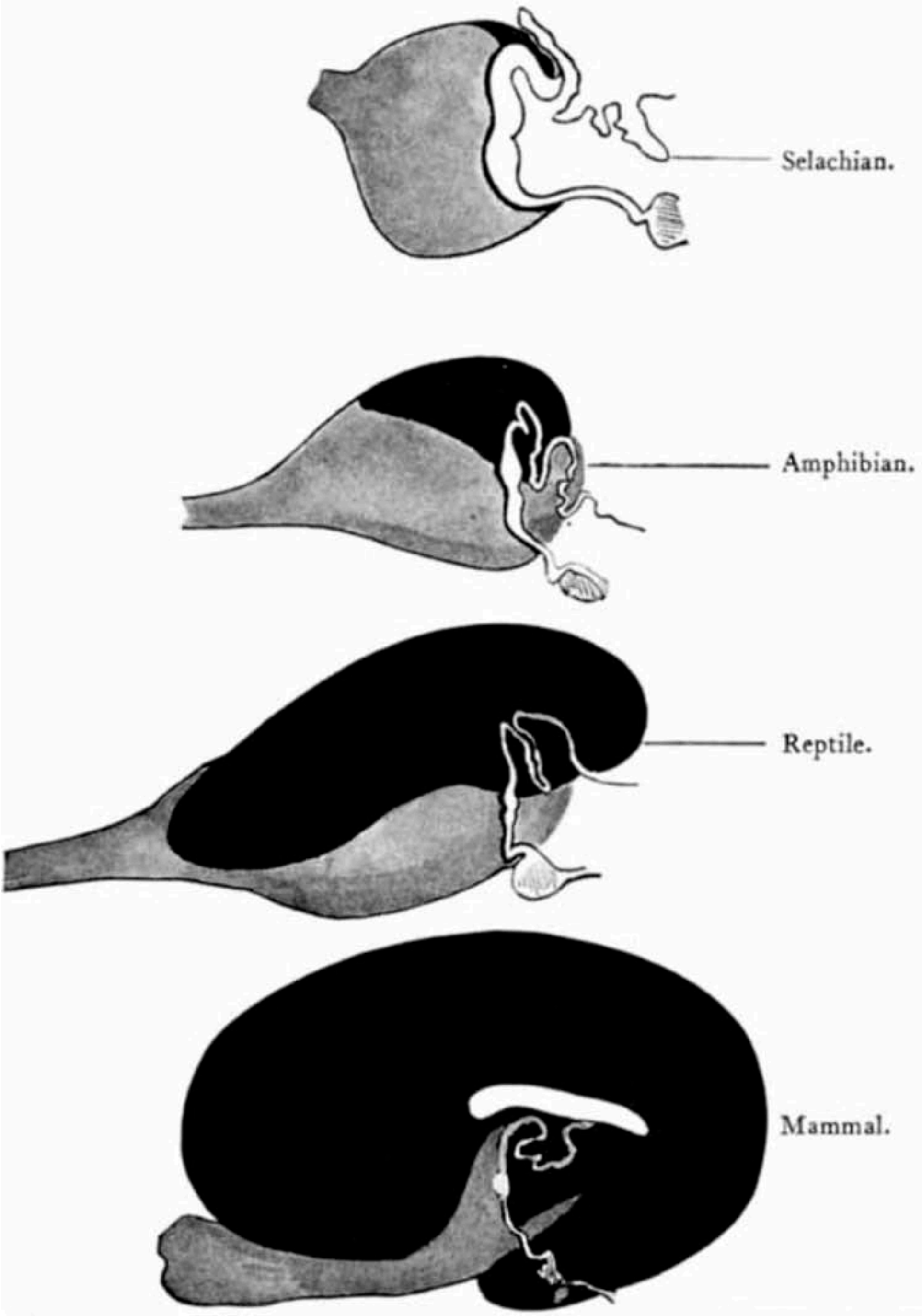

Figure 5. Edinger's drawing of the brains of a series of vertebrates showing the expansion of the neëncephalon (black) and the regression of the palæëncephalon (grey) with progression along the vertebrate series, from Edinger (1908a), Figure 3, p. 447. The brain of a selachian (a group of elasmobranch fishes that includes sharks and dogfishes), amphibian, reptile, and mammal are shown.

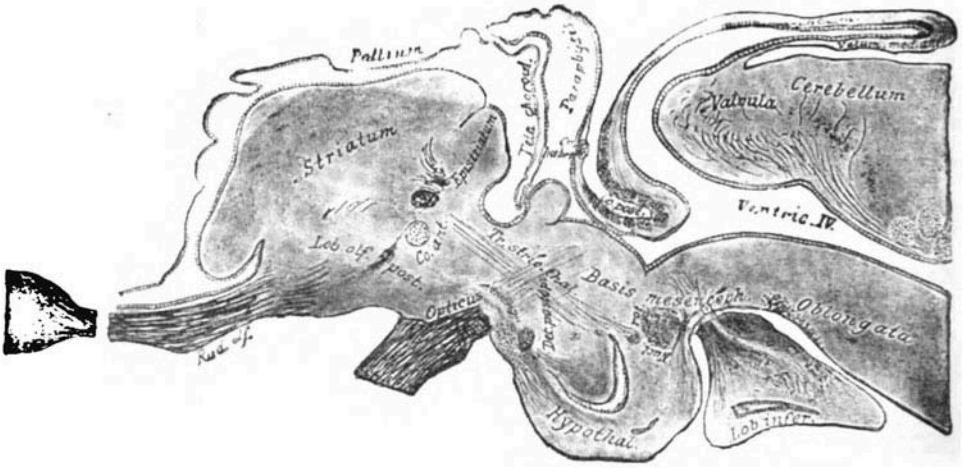

Figure 6. Edinger's drawing of a midsaggital section through the brain of a barbel—a small carp-like fish (*Barbus fluviatus*), from Edinger (1899a), Figure 95, p. 148. Note that the entire forebrain lobe of the fish is labeled "Striatum," reflecting Edinger's belief that the entire forebrain lobe of teleost fish consisted of forebrain floor derived structures. A purely membranous covering over the forebrain, the tela chorioidea, is labeled "pallium" reflecting Edinger's belief that the forebrain roof in teleosts is non-neural. From our modern perspective, Edinger appears to have been confused by some unusual features of the structure and development of teleost forebrains. During embryonic development, all vertebrate brains begin as a hollow tube. A fold occurs along its dorsal surface. In most vertebrates, the developing forebrain folds inward, producing paired pallial lobes, with the tela chorioidea tucked between. In teleost fishes, the tube instead splays outward, resulting in an unusual placement of the pallium, and the coverage of the forebrain by the membranous tela choriodea. Edinger's collaborator Cornelius Ubbo Ariëns Kappers (Ariëns Kappers, 1929, p. 110) correctly described this process in his later work.

fluid] (Edinger, 1899a, p. 146). In amphibians, "the mantle has become a nervous mechanism. This mechanism, which is not much developed in amphibians, reaches, in reptiles, the condition of a well-marked brain-cortex" (Edinger, 1899a, p. 160). In amphibians and reptiles, he regards the cortex to be devoted largely to olfaction (Edinger, 1899a, p. 174).

Edinger wrote that "The mantle in birds is, so far as we now know, not much more extended than that of reptiles" (Edinger, 1899a, p. 177). In his view, the corpus striatum, the forebrain component of the palaëncephalon, dominates the brains of reptiles and birds. He writes that "in birds, where the corpus striatum reaches remarkable size, it makes the major part of the forebrain, notwithstanding the presence of a fairly developed mantle" (Edinger, 1899a, p. 156). Among reptiles, the corpus striatum exhibits a particular size and prominence in turtles. As noted earlier, evolutionary morphologists of Edinger's time, like modern evolutionary biologists, regarded birds and mammals to have evolved independently from different groups of reptiles (Bowler, 1996). Edinger wrote that birds had followed:

> . . . a very different path of brain evolution than that which travels from the amphibians, through the reptiles, and on to the mammals. Apparently two different brain types have been derived from the reptile; the mammalian, and the bird type." (Edinger, 1908b, p. 277, translation mine; see Figure 7)

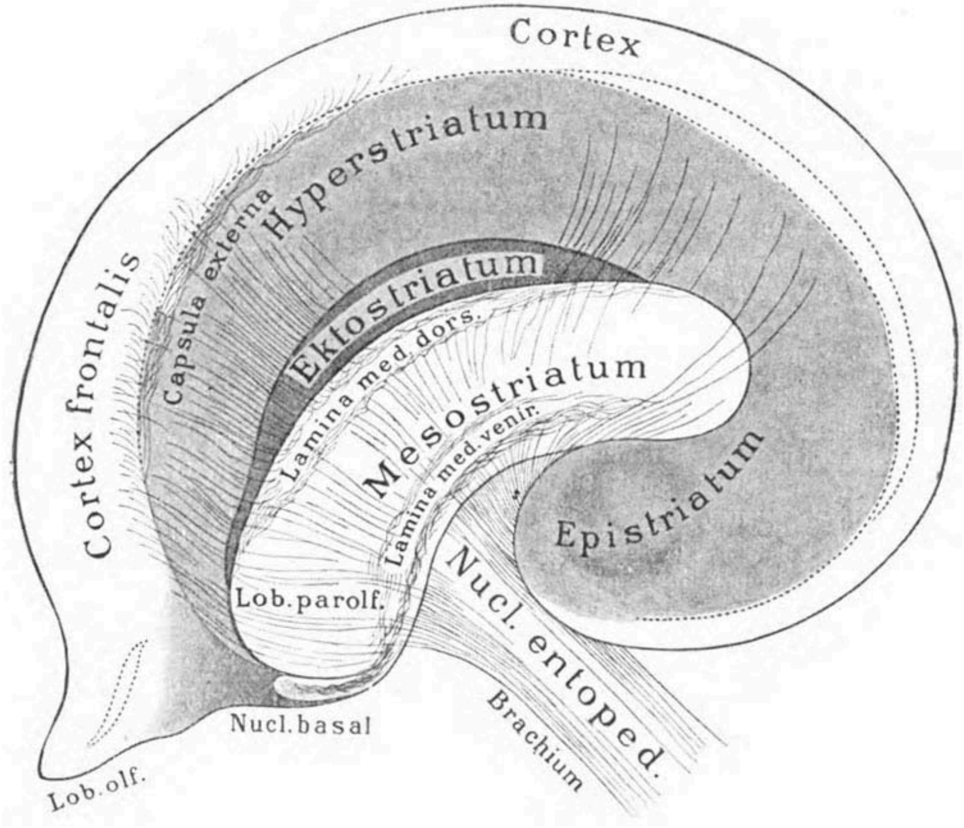

Fig. 251.

Figure 7. Edinger's drawing of a sagittal section through the forebrain of a bird from Edinger (1908b), Figure 251, p. 281. The terminology reflects Edinger's belief that the bird forebrain is dominated by a hypertrophied basal ganglia, of which the striatum is a part. In 2002, the avian brain nomenclature forum changed the terminology used for the avian forebrain to reflect the modern recognition that many of the structures that Edinger took to be part of a hypertrophied basal ganglia are, in fact, part of the forebrain roof or pallium. Hyperstriatum was changed to hyperpallium, mesostriatum to mesopallium, neostriatum to nidopallium, and Archistriatum to arcopallium.

In birds, the basal ganglia had hypertrophied, in mammals, the mantle or neëncephalon.

Edinger acknowledged a good deal of within-group variability among the forebrains of birds and mammals. His Figure 249 illustrates variation in the external morphology of the forebrains of birds (see Figure 8). He commented that "the bird families exhibit as great a range of differences in their brains as do the mammalian families, and the brain of a goose is no more similar to that of a pigeon than that of a hedgehog is to a human" (Edinger, 1908b, p. 279, translation mine). Although he cast his theories in the language of the vertebrate series, Edinger was aware of both divergent branching and within-group variability of forebrains within vertebrate lineages.

Citing the work of Australian-British anatomist, Sir Grafton Elliot Smith, Edinger (1908b) divides the neëncephalon into the archipallium, which consists of the olfactory and parolfactory cortex and the hippocampus, and the neopallium, consisting of the remaining pallial structures. The archipallium is seen as the older structure, existing alone, perhaps,

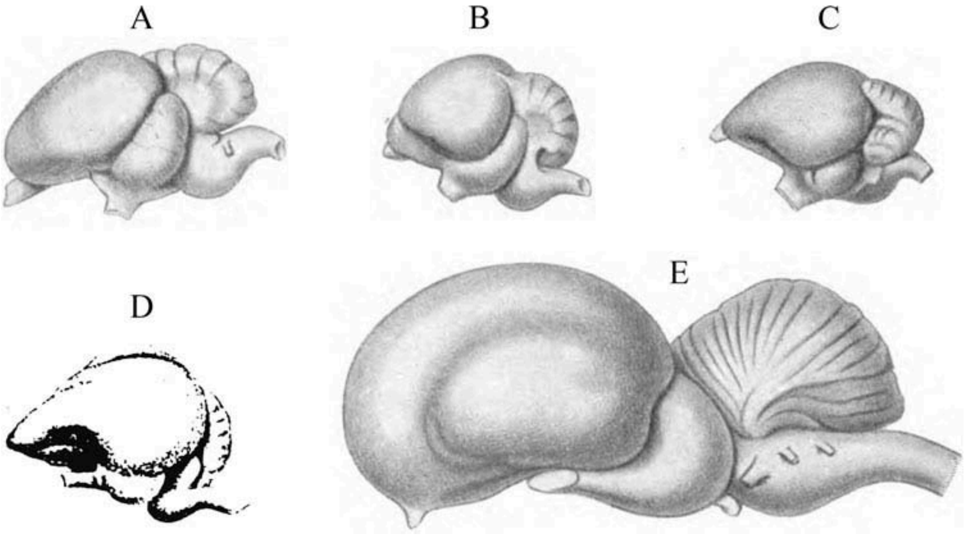

Figure 8. Edinger's drawing of a lateral view of the brains of five species of bird in their correct relative sizes from Edinger (1908b), Figure 249, p. 279: (A) Grey-necked wood rail (*Aramides cayennensis*), (B) Noddy Tern (*Sterna stolida*), (C) Ruff (*Machaetes pugnax*), (D) Parakeet (*Sittace*), (E) Ostrich (*Struthio*). Note the extensive variation of size of forebrain.

in amphibians. The neopallium is the newer structure, making its first appearance in reptiles and increasing in relative size along the vertebrate series, becoming the enormous cortical lobes of mammals. He illustrated these presumptive evolutionary relationships using a sequence of modern species in Edinger (1908b, Fig. 5) (see Figure 9). Edinger wrote:

> Very gradually then, the mantle increases in extent ascending in the vertebrate series. In the apes, belonging to the class of primates, it has attained an expansion which borders closely on the relations found in man. The frontal lobe, still very small in the lower apes, attains a large size in the higher apes, but always remains very much inferior to that of man. (Edinger, 1899a, p. 210)

In his 1908 paper, Edinger reaches beyond comparative neuroanatomy into comparative psychology, presenting views of the behavioral roles of the palaëncephalon and neëncephalon. Of the palaëncephalon he writes:

> *All sense impressions and movement combinations belong to the palaëncephalon. It is able to establish simple new relations between the two . . . It is the bearer of all reflexes and instincts.* (Edinger, 1908a, p. 444, emphasis in original).
>
> *With the appearance of the neëncephalon, the behavior of the animal becomes completely changed*. (Edinger, 1908a, p. 446, emphasis in original)

He holds that the neëncephalon is "a mechanism which by means of numberless connections within itself provides the possibility for association" (Edinger, 1908a, p. 446) and makes possible flexible learned behavior at the level of reptiles and higher along the vertebrate series:

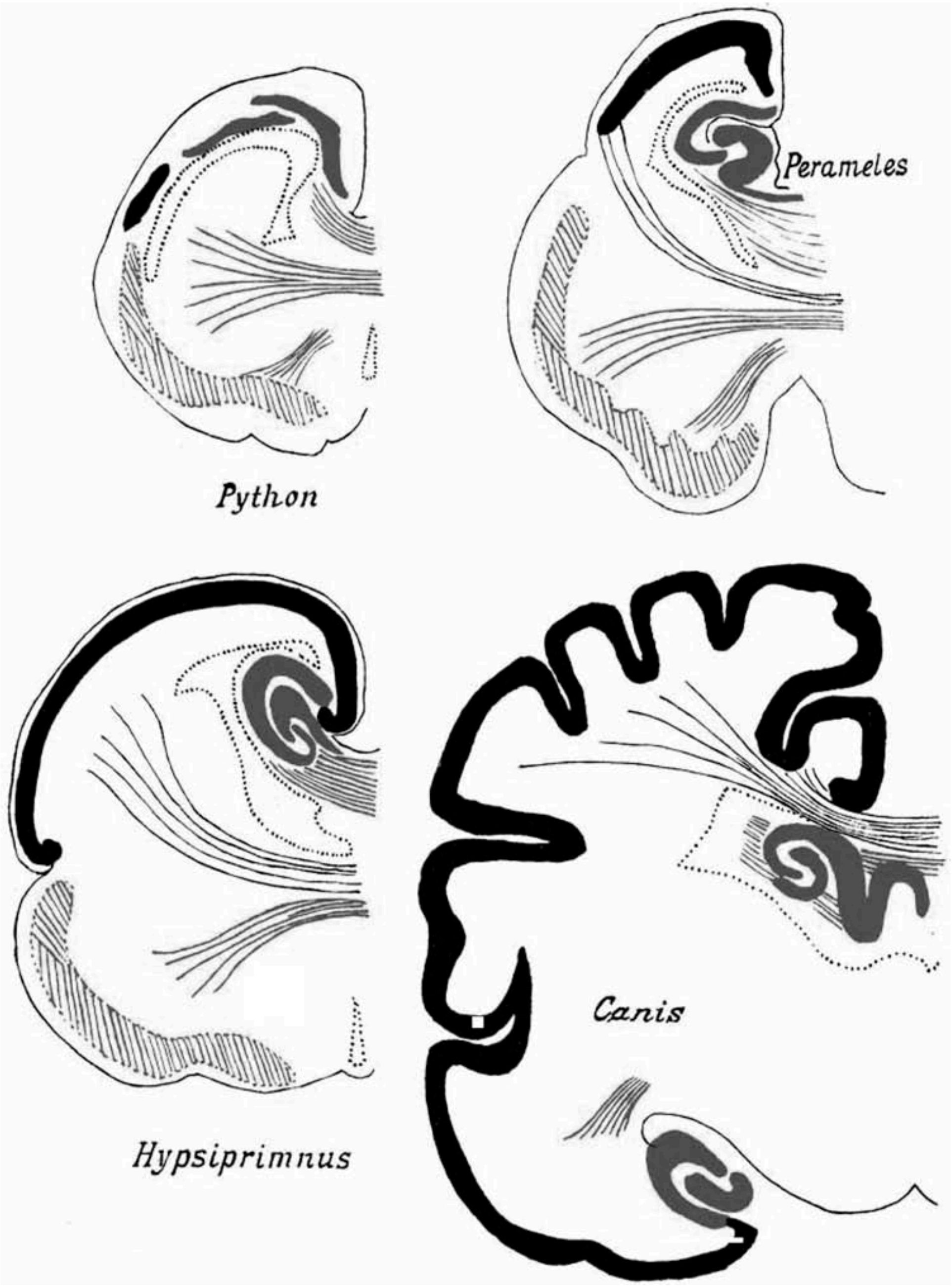

Figure 9. Edinger's drawing of the evolution of the archipallium (grey solid and cross-hatched) and the neopallium (black) from the reptilian type, from Edinger (1908a), Figure 5, p. 455. Both structures are constituent parts of the neëncephalon. Transverse sections through the forebrains of the constricting snake python (*Python*), the long-nosed bandicott (*Peremeles*), a marsupial mammal, the kangaroo rat (*Hypsiprimnus*), and a dog (*Canis*).

> We have come to know fishes as strictly palaëncephalic animals. In reptiles and birds a small neëncephalon cooperates. Finally, in mammals we meet a brain which has so large a neëncephalon that we may expect a subordination of reflexes and instincts to associative and intelligent actions. (Edinger, 1908a, p. 454)

Edinger proposes that the behavior of fishes be carefully compared with that of higher animals, in order to elucidate the role of the palaëncephalon and neëncephalon in behavior, and presents his own preliminary observations.

Though possessing vastly greater neuroanatomical sophistication, Edinger's assignment of behavioral roles to the palaëncephalon and neëncephalon is strongly reminiscent of Jean-Baptiste Lamarck's distinction between the brain proper and its "accessory organ" the "hypoencephalon" a century earlier (Lamarck, 1809/1963). Lamarck's hypoencephalon "is the special organ in which ideas and all acts of intelligence are carried out" (Lamarck, 1809/1963, p. 309). As with Edinger's neëncephalon, Lamarck's hypoencephalon consists of the "two wrinkled hemispheres" in mammals but makes its first appearance "in the most imperfect of these [vertebrate] animals (viz. the fishes)" (Lamarck, 1809/1963, p. 309). As with Edinger's palaëncephalon, the brain proper is "that part of the main medullary mass which contains the centre of communication of the nerves, and where the nerves of the special senses meet" (Lamarck, 1809/1963, p. 309).

Edinger in Modern Perspective

Modern commentators (Northcutt, 2001; Butler & Hodos, 2005; Jarvis et al., 2005; Reiner, 2005, 2009; Striedter, 2005) have at least partially erred in their assessment of Edinger. First, under the influence of older historiographic perspectives (Russell, 1916/1982; Gasman, 1971; Gould, 1977; Bowler, 1983) and a modern debate about the use phylogenetic scales in comparative psychology and neurobiology (Hodos & Campbell, 1969; Campbell & Hodos, 1991), they have misunderstood his scientific context. Nineteenth-century morphologists did not typically espouse the transcendental metaphysics of the *scala naturae* or hold a linear, non-Darwinian view of evolution. They instead were largely united in their acceptance of Darwin's theory of common descent with its divergently branching genealogies (Bowler, 1996). Some of the principle players, such as Ernst Haeckel, vigorously rejected the metaphysics of the *scala naturae* and a role for inner perfecting principles in evolution (Gliboff, 2008; Richards, 2008). Their use of linear scales was grounded in a struggle to understand the relationship between morphological complexity and Darwinian genealogy and the relationship between modern forms and ancestral forms (Bowler, 1996). While neuroscientist commentators may be correct, in a general sense, in perceiving some relationship between the *scala naturae* and the vertebrate series, the relationship is a distant and indirect one.

Influenced, in part, by the older historiographic views of German evolutionary morphology (Nyhart, 1995; Gliboff, 2008; Richards, 2008), modern commentators suppose that Edinger's perspective was anti-Darwinian. While Edinger never expressed support for a particular mechanism of evolutionary change, the vertebrate series is not inconsistent with Darwinism as it was understood at the time. If evolutionary change is historically contingent, as it is under Darwinism, then it is possible in principle that some or all of the modern members of historically older vertebrate classes might have remained morphologically simpler than the members of more recently emerged classes. Such a hypothesis can only be evaluated empirically, and this is precisely what Edinger did for the case of the vertebrate brain.

Modern commentators have erred in supposing Edinger consistently accepted a linear progressive view of brain evolution. In fact, he vigorously rejected such a view for all brain structures except the pallium. He did assess all of his results in relation to the vertebrate series, a progressively ascending scale of morphological complexity that seemed to have been established on grounds of general vertebrate morphology by others. But, he found that brain structures typically varied in ways that did not fit its expectations. Edinger reported that individual brainstem structures varied in morphological complexity from species to species independently of one another and without regard to the animal's position in the series. He believed that this species-to-species variation was due to the differing demands of different animal lifestyles and environments. This is quite similar to the modern concept of mosaic evolution. Based on these findings of species-to-species variability, Edinger rejected the notion that it was possible to use modern brains as "living fossil" stand-ins for ancestral brains in a reconstruction of evolutionary history.

The principle object of interest for modern critics of Edinger is the forebrain roof, or pallium, which was the one structure for which Edinger did accept progressionism. This progressionism led him, late in his career, to advocate a progressionist comparative psychology. Even for the forebrain roof though, it would be somewhat misleading to characterize his views as linear, since he was well aware of the importance of Darwinian branching in the case of birds and acknowledged within-group variability in forebrain size for a number of vertebrate classes.

The first major anatomical finding to call Edinger's views regarding the forebrain roof into question was made by Karten (1969). He showed that a surprisingly limited portion of the structure that Edinger had identified as the striatum in reptiles and birds stained positive for the enzyme acetylcholinesterase. In mammals, acetylcholinesterase is abundant in the striatum but absent in the pallium. Subsequent investigations, based on multiple lines of evidence, indicated that a sizable portion of what Edinger considered the striatum in reptiles and birds is, in fact, a pallial structure now referred to as the dorsal ventricular ridge (DVR; Ulinski, 1983; Butler & Hodos, 2005; Striedter, 2005). As discussed above, Edinger, and Haeckel before him, had long ago concluded that forebrain evolution followed a "different path" in birds than in mammals. This finding indicates that the different path involved development of a distinctive pallial component rather than hypertrophy of the striatum. More crucially, it demonstrated that both modern reptiles and modern birds, with their distinctive DVR, were the end product of a different path of forebrain roof evolution than that followed by mammals. The forebrains of modern reptiles thus could not, as Edinger supposed, preserve an earlier step in the mammalian path. A central claim of Edinger's progressionist theory of the evolution of the neëncephalon had been struck down. Other findings showed that olfactory input did not, as Edinger claimed, dominate the forebrain roof in "lower" vertebrates, and that all such forebrains receive nonolfactory sensory input (Northcutt, 2001).

In the early-twentieth century, taxonomists developed a new method of reconstructing phylogenetic trees known as cladistic analysis (Striedter, 1998; Bowler, 2003). Grounded in the concept of mosaic evolution, this formalized and logically rigorous method was said to resolve many of the seemingly intractable conundrums that had plagued evolutionary morphology. Rather than comparing modern vertebrate classes and grades of organization in hopes that they preserved a sequential record of vertebrate evolution, the new methods used patterns of similar and dissimilar traits across groups of modern species to infer evolutionary branch points based on an assumption of parsimony. That is, the method assumed that the smallest number of independent evolutionary changes had occurred. The new method could be applied to similarities and dissimilarities of all sorts, including genetic ones to reconstruct increasingly robust phylogenetic trees. In the early 1980s, Northcutt and his collaborators (Northcutt, 1981, 1984, 1995) undertook a comprehensive analysis of the evolution of the forebrain using the new techniques of cladistic analysis. These techniques indicated that the size and complexity of the forebrain roof has undergone numerous independent expansions across modern vertebrates, including expansions among the teleosts, sharks, birds, cetaceans, and primates. They concluded that forebrain expansion is the result of local trends within particular vertebrate groups rather than of any global trend across the vertebrates.

Edinger's contributions to modern comparative neuroanatomy extend far beyond a compendium of comparative anatomical facts and a failed progressionist theory of forebrain evolution. More than two thirds of Edinger's final comparative volume dealt with structures other than the forebrain roof. Perhaps his most important contribution was his demonstration that, for these structures, a progressionist view of brain evolution must be rejected. Despite the sophistication of modern cladistic analysis, the reasoning that Edinger used to dismiss progressionism for the brainstem was not different in kind from the reasoning his modern successors used to dismiss it for the forebrain. Modern investigators should properly view Edinger as their forerunner in rejecting a linear view of brain evolution. This study highlights the need for a more balanced and sympathetic understanding of the history of nineteenth-century German biology.

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