The Study of "Fossil Brains": Tilly Edinger (1897–1967) and the Beginnings of Paleoneurology

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Paleoneurology, the study of the evolution of the brain, lies at the interface of neurology and paleontology. In its modern form, it was founded in Germany in the 1920s, the product of the unique educational background and inspiration of Ottilie ("Tilly") Edinger (1897–1967). Before Edinger's work, the history of the vertebrate brain was reconstructed almost exclusively by anatomists who compared the soft tissue brains of living fish, amphibians, reptiles, birds, and mammals. Structural variations among extant groups were documented and compared; their distribution was used to suggest the sequence of anatomical innovations in time. With strong preparation in both neurology and paleontology, Edinger was able to integrate comparative anatomy and the paleontologists' tool of stratigraphic sequence. More than anyone else, she introduced the concept of time to neurology, creating modern paleoneurology.

Here we relate the broad outlines of Tilly Edinger's life and describe how she changed the way that the evolutionary history of the vertebrate brain is reconstructed and understood. Her story is particularly compelling because she began much of her innovative work while she was enduring Nazi racial laws and terrors, completing it in exile after forced emigration from Germany.

Early biography and founding of paleoneurology

Tilly Edinger (Figure 1) was born in 1897 into an extended and well-to-do family that was part of the academic and cultural elite of Frankfurt am Main. Her father, Ludwig Edinger, was a pioneer comparative neurologist and the founder of Frankfurt's first neurological research institute (Kreft 1997). Before his early death in 1918, Edinger (Figure 1) provided his daughter with many contacts within the local and greater scientific community and with a role model for a life in science. She was educated first at home by private tutors, among them French and English governesses who instilled in her a lasting interest in foreign languages, and then at the Schiller-Schule, at that time the only secondary school for girls in Frankfurt.

Tilly Edinger's scientific interests led her to university studies in zoology and, later, in geology and paleontology. During preparation of her doctoral dissertation on the palate of the Mesozoic marine reptile *Nothosaurus*, Edinger encountered a skull with a natural brain cast. Such "fossil brains" are actually natural casts formed by sediments that filled the empty cranium of the animal after death and then became lithified. They can reflect the external features of brain anatomy in great detail. The description of the *Nothosaurus* specimen (Figure 2) was the subject of Edinger's first publication in 1921 (Edinger 1921). After attaining her degree, she worked as an unpaid volunteer at the Geological-Paleontological Institute of the University of Frankfurt (1921–1927) and later as the section head in vertebrate paleontology at the Senckenberg Museum (1927–1938).

Although she lacked close scientific mentors in Frankfurt, Edinger did have contacts with two eminent vertebrate paleontologists, Friedrich von Huene (1875–1969) in Tübingen and Louis Dollo (1857–1931) in Brussels. Dollo advised Edinger during her biannual three-day visits to Brussels and through letters, exchanged in both directions each week from

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the time of their first meeting in 1926 until Dollo suffered a stroke in 1929. Years later, Edinger wrote of the enduring debt that both she and the field of vertebrate paleontology owed Dollo: "We must admire Dollo as a revolutionary who led V[ertebrate] P[aleontology] in new directions.... Dollo was the first who urged that paleontology should be considered as a biological study, rather than associated with geology. It was Dollo who made the extinct vertebrates, so-to-say, re-enter life" (Edinger 1964, p. 42).

Edinger's curatorial work, meticulous descriptive papers, and numerous popular articles of the 1920s (see "Brief Biography") are far outweighed today by her self-assigned task, described in a letter to her father's famous student, Cornelius Ubbo Ariëns Kappers ("Uncle Kappers"), in the Netherlands: "You perhaps remember that in my first paper I described a fossil 'brain.' In the meantime, I have noticed that a large literature exists about such fossils, distributed widely in all the journals of the earth, and I have given myself the assignment not only to collect but also to rework this material into a book, 'Paleoneurology'" (undated letter in German from Edinger to Kappers, Netherlands Institute for Brain Research, Amsterdam).

Figure 1. Tilly Edinger (right) and her father, the pioneer comparative neurologist Ludwig Edinger (left). Tilly Edinger extended her father's insights on brain evolution by incorporation of the fossil record. She is shown with endocast and calipers at some time in the mid-1920s. Ludwig Edinger photo (probably taken in 1909), National Library of Medicine, Bethesda, MD; Tilly Edinger photo, Museum of Comparative Zoology, Harvard University, Cambridge, MA.

This book, which Edinger would later title *Die fossilen Gehirne* (Fossil Brains) (Edinger 1929), formally defined a new field of inquiry. Gathering together references to the many endocranial casts that had been treated as isolated curiosities in earlier texts, Edinger organized them taxonomically and then summarized the inferences that could be drawn from them. Working almost entirely alone, she identified the broad outlines of a unique subdiscipline and for the first time raised many of the scientific questions that she would address for the rest of her career. Her book was widely praised and established Edinger's membership in the German and international paleontological communities. It also provided her with the reputation that would allow her, years later, to emigrate from Germany.

Science, Nazi threats, and forced emigration in the 1930s

Edinger's publications in the 1930s were natural outgrowths of approaches she identified in *Die fossilen Gehirne*. A major focus was the integration of geological and biological information. Particularly noteworthy is her recon- struction (Edinger 1933a) of the phylogenetic history of the brain within a single order of secondarily marine mammals, the Sirenia (seacows). Using both stratigraphy and comparative anatomy, she was able to identify the sequence of brain innovations in the order. Later in the decade (Edinger 1939) she predicted the extent and

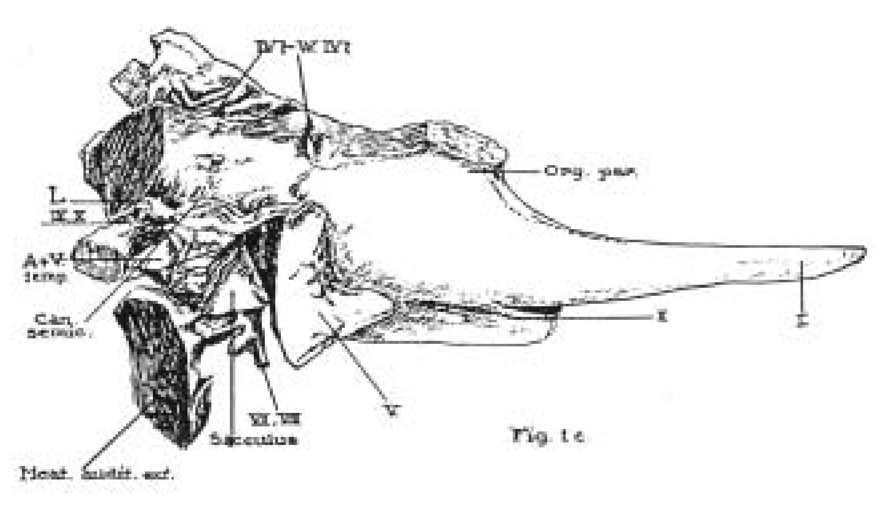

Figure 2. Right lateral view of the endocast of the extinct Mesozoic marine reptile Nothosaurus *that Edinger described in her first paper, published in the journal* Senckenbergiana *in 1921. Roman numerals indicate cranial nerve roots; Can. semic., semicircular canal; Meat. audit. ext., external auditory meatus; Org. par., parietal stalk. Edinger later (1975) reevaluated her identification of "IV? and WIV?" as nonneural structures, and of "VIII" as a branch of the facialis canal.*

A Brief Biography of Tilly Edinger

1897	Born November 13 in Frankfurt am Main (Germany); third and youngest child of eminent neurologist Ludwig Edinger (1855–1918) and his wife Dora Goldschmidt (1863–1929)
1909–1916	Education at the Schiller-Schule, first secondary school for girls in Frankfurt
1916–1920	Studies at Universities of Heidelberg, Frankfurt, and Munich; first majors in zoology, later changes to geology/paleontology
Spring 1920	Formally begins work on doctoral dissertation “Über *Nothosaurus*” (About *Nothosaurus*) at the University of Frankfurt; her mentor is the paleontologist Fritz Drevermann (1875–1932)
July 1921	Oral examinations in geology, paleontology, psychology, and zoology; Dr. Phil. Nat.; parts of her doctoral thesis are published in the journal *Senckenbergiana*
1921–1927	Unpaid “Volontär-Assistentin” at Geologisch-Paläontologisches Institut and at Senckenberg Museum (located in same building) in Frankfurt; publishes variety of articles for general readership in *Natur und Museum*; writes numerous summaries, reviews, and translations for review journals (finally totaling more than 1,200)
1926	A major study trip to London, Paris, Brussels, and Amsterdam; establishes international scientific contacts
1927–1938	Sektionärin (unpaid curator) of fossil vertebrates at the Senckenberg Museum
1929	Publication of “Die fossilen Gehirne,” which outlines the methodology and questions of paleoneurology
1933–1938	Restrictive Nazi racial laws culminate in Kristallnacht on 9–10 November 1938; work in Germany is no longer possible
May 1939	Leaves Germany for temporary asylum in London with the help of the Notgemeinschaft (Emergency Association of German Scientists in Exile); supports herself as a translator of medical texts
1940	Arrives in New York aboard the SS Britannic on May 11; takes position as a research fellow at Harvard’s Museum of Comparative Zoology
December 1940	Present at the founding meeting of the Society of Vertebrate Paleontology
1943–1944	Guggenheim Fellowship awarded and renewed for a never-published study of tooth implantation in amphibians
1944–1945	Teaches comparative anatomy for three semesters at Wellesley College
1945	Becomes a naturalized citizen of the United States on 17 September; A. S. Romer and L. N. Jessner serve as her witnesses
1948	Publication of “Evolution of the Horse Brain,” which establishes the parallel and independent origin of many neural innovations in different mammalian lineages
1950	Honorary doctorate awarded by Wellesley College
mid-1950	First of several European trips to collect data for “Paleoneurology”
1957	Honorary doctorate awarded by the University of Giessen, Germany
1962	Elected vice-president of the Society of Vertebrate Paleontology; publication of “Bibliography of Fossil Vertebrates” (Romer et al. 1962)
1963	Elected president of the Society of Vertebrate Paleontology
1964	Honorary doctorate awarded by the University of Frankfurt am Main; formal retirement from the Museum of Comparative Zoology
May 1967	Hit by a truck as she walks to the Museum of Comparative Zoology; extensive head injuries result in death on 27 May
1975	Posthumous publication of “Paleoneurology 1804–1966,” an annotated bibliography of all works published in the field through 1966

timing of sirenian hind limb reduction on the basis of her interpretation of spinal cord anatomy. She also extended her reconstructions beyond the nervous system to the neuroendocrine organs, defining what she called “paleoendocrinology.” As outgrowths of the brain, both the parietal/ pineal complex and the hypophysis leave traces in the braincase, and Edinger (1933b, 1942) was able to make predictions about their phylogenetic history and the lifestyles of animals with particular expressions of these organs.

Beginning in early 1933, Edinger’s life and science in Nazi Germany were progressively complicated and restricted by the enactment of “racial laws” that had Jews as their primary targets. Initially her situation appeared tolerable because she was shielded to some extent by the protective actions of Senckenberg Museum Director Rudolf Richter (1881–1957) and by the voluntary nature of her work. On the night of 9–10 November 1938, however, Edinger’s German paleontological career ended abruptly. Later known as “Kristallnacht” (Night of the Broken Glass) the date marks the first large-scale pogrom organized by the Nazis all over Germany; nearly 100 Jews were killed and thousands were imprisoned. By 11 November Edinger was no longer permitted to enter the Senckenberg Museum or any other public building. Shortly thereafter, the contents of her office arrived at her home without comment, and the university library ordered her to return all books she had taken out for her work.

By mid-1938, the worsening political climate had already prompted Edinger to take a few preliminary steps toward emigration, a solution she was very reluctant to consider. Her first contact was her childhood classmate Lucie Jessner (1896–1979), a psychiatrist who had immigrated first to Switzerland in 1933 and then to the United States in early 1938 (see portrait in Figure 3). Working as a resident psychiatrist at McLean Hospital outside Boston, Jessner contacted the eminent Harvard paleontologist Alfred S. Romer (1884–1973), writing: “My friend—Dr. Tilly Edinger, paleontologist in Frankfurt am Main, Germany—wants me to ask you about different matters, very important for her. She believes you might know her name by several of her papers and you might be friendly enough to give me the opportunity to speak with you” (letter dated 28 June 1938, Harvard University Archives, Cambridge, MA).

Romer not only spoke with Jessner but also corresponded with Alice Hamilton, an industrial chemist recently retired from Harvard University. Hamilton had been a student of Ludwig Edinger in her youth and had maintained a friendship with the family ever since. Prompted by his knowledge of Tilly Edinger’s scientific reputation and these contacts, Romer set in motion a series of requests for an (unpaid) position for her at Harvard’s Museum of Comparative Zoology. Although he had never met her, he also signed a personal affidavit—required before a visa could be issued—that guaranteed financial support should it become necessary. These actions are in keeping with his reputation, still honored by former colleagues today, as a man of high intelligence, good spirits, and great heart (Figure 3).

Figure 3. The four scientists whose combined intervention enabled Edinger to emigrate from Germany. Top left, the retired Harvard chemist and Edinger family friend Alice Hamilton, who petitioned Harvard for a position for Edinger and (with A. S. Romer) signed an affidavit that allowed temporary residence in England (photo from the National Library of Medicine). Top right, Edinger’s childhood classmate, the psychiatrist Lucie Ney Jessner, who first approached A. S. Romer on Edinger’s behalf (photo from the National Library of Medicine). Lower left, the pathologist Philipp Schwartz, founder of the Notgemeinschaft, whose offer of temporary translation work allowed Edinger to seek refuge in London while awaiting her American visa (photo from the National Library of Medicine). Lower right, Alfred Sherwood Romer, paleontologist at Harvard’s Museum of Comparative Zoology and Edinger’s cherished mentor throughout her American career, in June 1952 (photo courtesy of Robert Romer); Romer’s offer of a position at Harvard and a financial guarantee were critical to the issuance of Edinger’s visa, which allowed her emigration from Germany.

With the positive response from Romer, Edinger applied for an American visa at the American Consulate in Stuttgart on 1 August 1938, receiving a visa quota number that would allow entry into the United States in two years at the earliest. Fully aware that such a wait could be potentially life-threatening, she attempted unsuccessfully to be classified as a "nonquota" immigrant. She was forced to look for another, short-term solution.

By December 1938 such a solution had been arranged, again with the aid of the scientific community (Figure 3). Philipp Schwartz (1894–1977), a former pathology professor at the University of Frankfurt, had immigrated to Switzerland in the spring of 1933. There he had established the Notgemeinschaft Deutscher Wissenschaftler im Ausland (Emergency Association of German Scientists in Exile), a society dedicated to helping scientific refugees from Nazi Germany. Among the scientists aided were many, including Schwartz himself and Tilly Edinger's brother-in-law Werner Lipschitz, who took positions at the newly organized University of Istanbul. From Turkey, Schwartz offered Edinger the opportunity to earn a small stipend (£15 per month) translating German medical articles into English, if a place of temporary asylum could be found. In London, the Society for Protection of Science and Learning was helpful in resolving bureaucratic hurdles and in securing a place of refuge, ultimately provided by the British Museum of Natural History, where Edinger could carry out this translation work.

Waiting for details of this solution to be finalized, Edinger wrote to Rudolf Richter to thank him for his supportive testimonial. She shared her conviction that "One way (England) or the other (United States), fossil vertebrates will save me" (letter in German dated 18 December 1938, Archives: Senckenbergische Naturforschende Gesellschaft, Frankfurt am Main, Germany). As it happened, both England and the United States were critical to her successful emigration. Edinger left Germany for London in May 1939, with 10 marks in her pocket. She worked at the British Museum of Natural History for the next year, alternately translating texts for Dr. Schwartz and working on her own paleoneurological projects. Despite being in drastically reduced financial circumstances and having travel restrictions due to her classification as an "enemy alien," Edinger described her life in London as considerably freer than in Germany: "It sounds funny, to one who was 'at home' not allowed to enter even an open museum, or a cinema, or a café, to apply the word 'restrictions' anywhere in the beautifully free life I am leading here" (letter dated 27 October 1939 to A. S. Romer, Harvard University Archives, Cambridge, MA). A year after her arrival, her visa number was unexpectedly called, and she sailed to the United States in May 1940 to begin her new life.

A new career in the United States: Edinger pursues four main areas of inquiry

Edinger found the United States in general, and the Museum of Comparative Zoology in particular, a comfortable match for her informal personality. She was almost immediately incorporated into the academic and social atmosphere that then existed at Harvard's Museum of Comparative Zoology (Figure 4). Her arrival in Cambridge was also conveniently timed to allow her to attend the founding meeting of the Society of Vertebrate Paleontology in December 1940, at which she was the only female present. Her colleagues became, to a large degree, her extended family. Looking back during a personal interview in 1962, Edinger recalled sitting around a table with eminent paleontological colleagues and suddenly realizing that she called them all by their first names, something that would not have happened in Germany (Radio Bremen 1962). It reminded her of Edinger family get-togethers in Frankfurt.

Figure 4. Tilly Edinger and colleagues at the Museum of Comparative Zoology, 1955. Sitting left to right: Tilly Edinger, Harry B. Whittington, Ruth Norton, Alfred S. Romer, Nelda Wright, and Richard van Frank. Standing left to right: Arnold D. Lewis, Ernest E. Williams, Bryan Patterson, Stanley J. Olsen, and Donald Baird. Photo courtesy of David Roberts.

In Romer's words, Edinger's work at the Museum of Comparative Zoology was "ad majorem musei gloriam" (for the greater glory of the museum), but she earned her living during the early Harvard years by continuing to translate papers for Philipp Schwartz, by abstracting for the Geological Society of America, and by teaching laboratory sections of comparative anatomy at Wellesley College. She was also a key contributor (with Romer, Nelda Wright, and

Richard van Frank) to the museum's major project, the assembly of a bibliography of fossil vertebrates (exclusive of North America), finally published in 1962 (Romer et al. 1962). Here her proficiency in several languages and her attention to detail were major advantages. The outside work diminished over the years as her research was funded by internal grants at Harvard, by the Guggenheim Foundation, and by the American Association of University Women. She was then able to concentrate more fully on paleoneurology. Her research contributions may be grouped into four main areas of inquiry (see also Buchholtz and Seyfarth 1999).

To what extent do endocasts reflect the actual anatomy of ancient brains? Edinger devoted the first two chapters of her 1929 treatise to a discussion of the nature of "fossil brains" and to the relationships between the brain, the braincase of the skull in which it was originally housed, and the endocast that was later made by infilling this braincase. Natural endocasts existed as a "miscellany of unpublished specimens in various museums" (Edinger 1975), but had never been systematically documented. Further, they were not the only source of paleoneurological information. The brains of extinct animals could also be reconstructed from natural or artificial (prepared) endocasts, from serial sections of skulls, or from photographs of the inside of the cranium. In each case, however, a distinction must be made between the brain itself and the size and shape of the cavity that supported the brain in life. In addition to neural tissues, the braincase houses support (meningeal) and vascular tissues and may be incompletely ossified, with the result that the endocast is inevitably larger than the corresponding brain. Such mismatches are particularly marked in fishes, amphibians, and reptiles, but are much less dramatic in birds and mammals, in which the brain is closely appressed against the braincase's interior surface. Instead of concluding that the shape of the braincase was of no reliable use in reconstructing that of the brain, Edinger documented the brain/braincase relationship in different vertebrate classes. This approach began with her very first publication in 1921 concerning the endocranial cast of the Mesozoic marine reptile *Nothosaurus*, in which she used a modern *Alligator* brain and its relationship to its braincase as a model for her interpretation. A more extensive example is provided by her paper on amphibian paleoneurology with A. S. Romer (Romer and Edinger 1942), in which a series of brain/endocast comparisons in modern amphibians allowed them to correlate variations in endocasts with systematic and functional differences (Figure 5). "Study of recent amphibians therefore encourages us to proceed with greater confidence to the interpretation of the endocasts of extinct forms," they concluded.

Is comparative anatomy adequate to answer questions of brain evolution? Working with the methods of comparative neurology, Ludwig Edinger (1885) had identified the existence of both ancient (palaeëncephalon) and modern (neëncephalon) areas of the vertebrate brain. His daughter extended his work by adding the time component offered by stratigraphic occurrence. She reasoned that the ancestral anatomical form is not present in any living vertebrate, so that determination of the sequence of innovations requires fossils. Additionally, neontological comparisons could not identify possible independent origins of the same trait in two different groups. Having predicted that a series of horse endocasts could be assembled from the rich equid record in the United States, Edinger was challenged to do so almost immediately after her arrival in 1940 by the paleontologist George Gaylord Simpson. She found the endocasts more difficult to collect than she had assumed they would be, but spent most of the following decade writing her major monograph on the evolution of the equid brain (Edinger 1948). Her analysis strongly suggested that both brain enlargement and superficially similar patterns of cortical sulcation (surficial folds and grooves) had arisen independently in different orders of mammals (Figure 6). Additionally, she documented that the origins of neural and osteological innovations in horses were

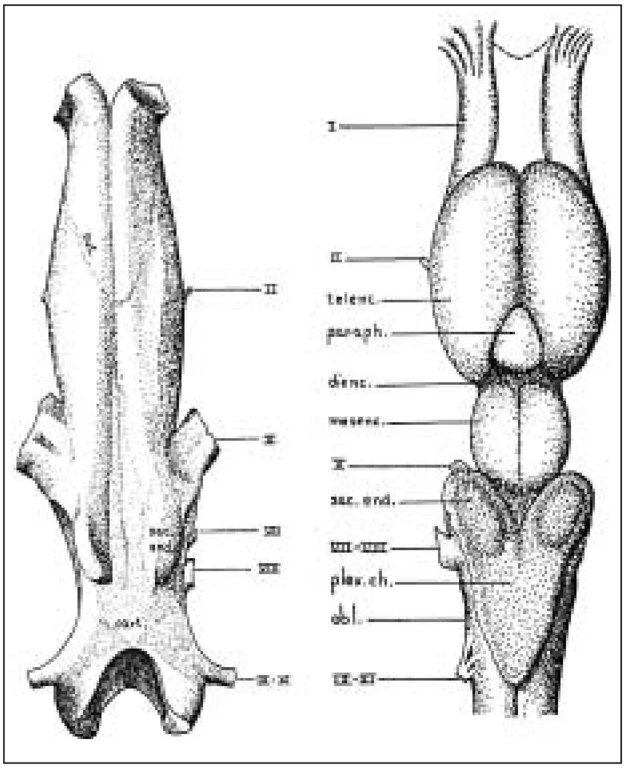

Figure 5. Endocranial cast (left) and brain of the living hellbender* Cryptobranchus alleganiensis *used by Romer and Edinger (1942) to document the relationship between the endocranial cast and the soft tissue brain in a living amphibian. Roman numerals indicate cranial nerve roots; paraph., parapophysis; sac. end., endolymphatic sacs; plex. ch., choroid plexus. Note that the major brain regions (telenc., telencephalon; dienc, diencephalon; mesenc., mesencephalon; obl., medulla oblongata) visible on the brain are only poorly differentiated on the endocast.

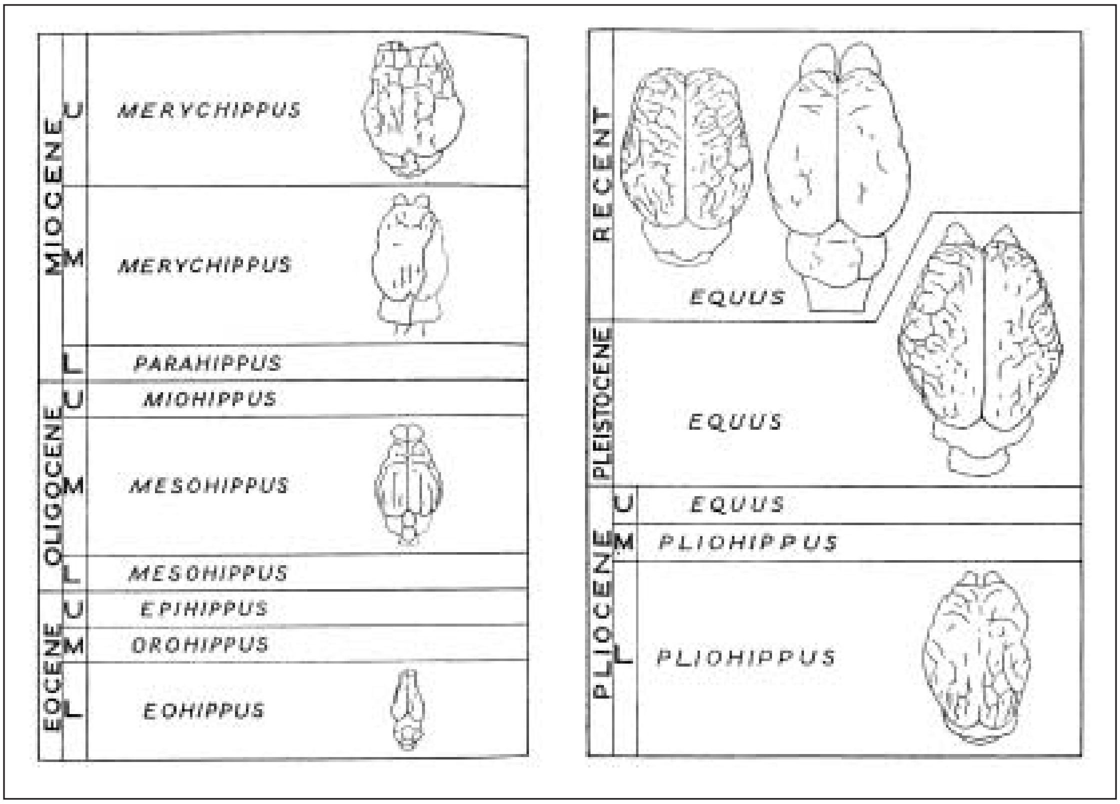

Figure 6. Edinger's series of horse brains, showing differences in size and external anatomy as well as order of stratigraphic occurrence, from Edinger's classic monograph, "Evolution of the Horse Brain" (1948). Vertical labels identify geologic epochs of the Cenozoic and their subdivisions (L, lower; M, middle; U, upper); horizontal labels identify equid genera found in those rock units.

"mosaic"—the changes in gross neural patterns had not necessarily occurred at the same time or at the same rate as those in other body systems.

Can the lifestyle of extinct animals be predicted from brain casts? Early descriptions of endocasts were restricted almost entirely to reports of size and sometimes to the extent of cerebral convolutions. The function of the brain, however, is based on the huge number of its neurons and their complex cellular interactions, none of which is preserved in endocasts. Edinger's familiarity with neuroanatomy allowed her to extend the range of information recoverable from endocasts. Neural input from different sense organs is initially processed in different areas of the brain; hence, variable development of these processing areas allows evaluation of the relative importance of smell, sight, and hearing in the life of the animal. This correspondence is particularly easy to infer in those vertebrates whose processing areas are exposed on the surface of the brain.

Edinger used this approach to predict the sensory dominance of sight and the possession of flight capabilities in reptilian pterosaurs (Edinger 1941) on the basis of the enlarged optic lobes and cerebellum of *Rhamphorhynchus* specimens. Similarly, she traced the reduction of the sense of smell over the course of whale evolution by the relative reduction of olfactory lobes in their endocasts (Edinger 1955). Perhaps most notably, she carried on a protracted dispute with her Princeton colleague Glenn "Jep" Jepsen over the identification of a Paleocene fossil braincase and endocast. Although many aspects of the braincase suggested it belonged to an early (miacid) family of carnivores, Edinger insisted instead that it was an early bat based on the enlargement of the acoustic colliculi, a site of auditory processing in the midbrain that is enlarged in living bats. The dispute was never resolved, despite the intervention of the paleomammalogist Brian "Pat" Patterson at Harvard, but its good-natured tone is indicated by Jepsen's composition of this poem (letter dated 11 June 1957 from Jepsen to Edinger, Special Collections, Museum of Comparative Zoology, Harvard University, Cambridge, MA):

The Tilly-bat

A curious beast is the Tillybat
It surely seems odd and quite silly that
With a brain shape so batty,
We'd find glenoids so catty!
You see why we call it a dilly, Pat?

"The midbrain is hilly, —
and further", says Tilly,

"Look here *quick* and see
Those coll*ic*uli!
It had to squeak, not mew, —
it never walked, it flew!
Jep, don't be so placid,
It's not a miacid!"

Has brain size increased over geologic time? In the late 19th century, the American paleontologist Othniel Charles Marsh (1831–1899) described a variety of reptilian and mammalian endocasts from the Mesozoic and Cenozoic Eras. Marsh summarized his observations as the "General Laws of Brain Growth." Most memorable were his assertions that "all Tertiary [early Cenozoic] mammals had small brains" and that "there was a gradual increase in the size of the brain during this period" (Marsh 1885). Early in her career Edinger supported Marsh's interpretations, but she later became one of his most strident critics (e.g., Edinger 1962). She argued that brain size in two animals of different lineage or body size should not be compared; she complained further that very few fossil endocasts were associated with skeletons complete enough to allow estimates of body size. Using her horse sequence as an example, Edinger noted that as equid body size increased over the Tertiary Period, brain size actually decreased in proportion to body size. Similarly, she rejected any constant trend toward an increase in brain size by noting the almost modern anatomy and size of very early bat brains (Edinger 1926), but the retention of very primitive anatomy in modern sirenians (Edinger 1933a). Edinger's discomfort with logarithms restricted her ability to analyze brain size and body size allometrically. A series of workers, notably including Harry Jerison in his classic *Evolution of the Brain and Intelligence* (Jerison 1973), have recognized that although brain size increases with body size, it does not increase as fast as body size. As a result, large animals have relatively smaller brains than do small animals. Because Marsh had not explicitly taken body size into account, and because Edinger had not taken allometric scaling into account, neither was able to make a definitive statement about brain size over time.

Career culmination

By the early 1950s, Tilly Edinger had become not only the major contributor to the field of paleoneurology but also chronicler, promoter, and finally mentor to a younger generation that was following in her footsteps. These roles were only minimally affected by her familial progressive deafness, which was by then quite acute. She wrote a series of articles detailing the "present state of paleoneurology" and sent letters, reprints, and advice to an amazingly large number of correspondents. Many of these letters survive, documenting not only her work but also her cheerful, generous, and vibrant personality. During these years Edinger's unique contributions to paleontology and dominant role in paleoneurology were recognized by the award of honorary degrees from Wellesley College (1950), the University of Giessen (1957), and the University of Frankfurt am Main (1964). In 1962 and in 1963, she was elected and served first as vice-president and then as president of the Society of Vertebrate Paleontology. Perhaps the largest time commitment of her later years was to the production of an annotated bibliography of all known literature references to fossil endocasts (Edinger 1975), initially

Paleoneurology Today

Early in her career, Edinger complained that "the neurology corner of the paleontology field is not plowed as much as it deserves." But by the 1960s she reported (1961) that paleoneurology was "swamped with so much fertilizer from so many sorts of brilliant minds." The insights of Edinger's nearly 50-year-long career were the major impetus to this upsurge in activity both during and after her lifetime. Many of her original questions still remain on the modern research agenda, although the range of techniques available to today's workers has expanded dramatically. Digital imaging of skulls (Figure 7) now permits the reconstruction and measurement of endocranial space without sectioning or casting the skull, potentially allowing many more endocasts to be studied (Brochu 2000). Such casts may be compared with the soft-tissue brains of living taxa using extensive banks of images on the Internet.

Electrophysiological mapping studies (Welker and Campos 1963) permit much finer localization of functionally distinct cortical areas in living animals, expanding the range of behavioral inferences to be drawn from fossil specimens (especially mammals) that show surface sulcation (e.g., Radinsky 1968). Perhaps most significantly, body- and brain-size relationships have been more quantitatively addressed. Recent statistical analyses (Barton and Harvey 2000, de Winter and Oxnard 2001) demonstrate that the relative sizes of functionally linked brain structures evolved in concert within an individual mammalian order, but did so independent of brain structures serving other functions. Moreover, functionally integrated neural structures varied independently between different mammalian orders. These results directly support Edinger's more qualitative observation of the same phenomenon in fossil taxa.

The encephalization quotient devised and extensively developed by Jerison (1973) allows the comparison of brain size in animals of different body size. Its applications include the examination of trends in encephalization and intelligence within a single lineage (e.g., hominid ancestors of humans) and the changing distribution of brain sizes in entire faunas that existed at different geologic times. It has also been the basis of predictions of behavioral patterns (Hopson 1979) and metabolic regimes in various dinosaur subgroups.

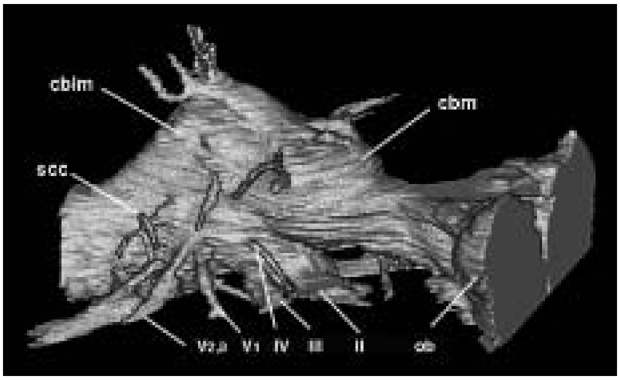

Figure 7. Digital endocast of the braincase of the saurischian dinosaur* Tyrannosaurus rex *generated by computed tomographic analysis without damage to the skull. Anterior is to the right, and the view is right anterolateral; the olfactory bulbs are truncated anteriorly. Roman numerals indicate cranial nerve roots; cblm, cerebellar region; cbm, cerebrum; ob, olfactory bulb; scc, semicircular canal. Many of the extensions of the endocast probably represent canals that housed vascular structures. Identifications taken from Brochu (2000); image courtesy of C. A. Brochu, Field Museum of Natural History, Chicago.

undertaken as an update of *Die fossilen Gehirne.* To assemble data for it, she traveled extensively to the major museums of Europe, reestablishing close ties with many of her prewar friends and colleagues. After she died in 1967 as the result of a traffic accident, her nearly finished "magnum opus" was completed by several of her colleagues. Even today, this dense and comprehensive volume is the necessary starting point for any project in paleoneurology.

Acknowledgments

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