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HISTORY OF NEUROSCIENCE

The gospel of the fossil brain: Tilly Edinger and the science of paleoneurology

Emily A. Buchholtz[1]* and Ernst-August Seyfarth[2]

[1]Department of Biological Sciences, Wellesley College, Wellesley, MA, USA; and [2]Zoologisches Institut, Biologie-Campus, J.W. Goethe-Universität, D-60054 Frankfurt am Main, Germany

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ABSTRACT: Tilly Edinger (1897–1967) was a vertebrate paleontologist interested in the evolution of the central nervous system. By combining methods and insights gained from comparative neuroanatomy and paleontology, she almost single-handedly founded modern paleoneurology in the 1920s while working at the Senckenberg Museum in Frankfurt am Main. Edinger's early research was mostly descriptive and conducted within the theoretical framework of brain evolution formulated by O. C. Marsh in the late 19th century. Nevertheless, she became immediately known in 1929 after publishing an extensive review on "fossil brains." Reconstructing evolutionary history from the fossil record instead of from the comparative analysis of living forms allowed her to identify the sequence of neural innovations within several mammalian lineages. Anti-Jewish terrorism forced Edinger to leave Nazi Germany in 1939. After finding refuge first in England, she continued her career at Harvard's Museum of Comparative Zoology. There she documented the occurrence of gross neural correlates of specialized behavior in several vertebrate lineages, and identified parallel evolution in mammalian sulcation patterns. Her insight that neural innovations need not be "correlated" with either non-neural innovations or with evolutionary "success" led her to reject Marsh's theory of progressive increase in brain size over time and other "anthropocentric" understandings of brain evolution. Edinger's research, her insistence on a stratigraphic and evolutionary framework for interpretation, and her massive compilations of paleoneurological literature established her as the leading definer, practitioner, and chronicler of her field. © 1999 Elsevier Science Inc.

KEY WORDS: Comparative neuroanatomy, Evolution, Female pioneers in neuroscience, History of neuroscience, Emigré scientist, Biography.

INTRODUCTION

Paleoneurology studies the brain and nervous system of fossil animals, in particular of fossil vertebrates. Its chief objective is to define trends in the evolutionary development of the various nervous systems. Initially, the study of "fossil brains" meant the mere collection and description of accidental finds of natural brain casts, that is, the fossilized sediments filling the endocrania (and spinal canals) of extinct animals. These can reflect characteristic features of external brain anatomy in great detail.

Modern paleoneurology was founded almost single-handedly by Ottilie ("Tilly") Edinger in Germany in the 1920s. She was one of the first to systematically investigate, compare, and summarize fossil brain data from the various collections in Europe and North America. She realized that insights into brain evolution could be extended considerably by focusing on animal groups whose lineages were already well-established from independent stratigraphic work, by taking artificial brain casts from existing museum specimens, and by utilizing established methods of comparative anatomy. Tilly Edinger's successful work in Germany came to an abrupt end in 1938 when she was expelled from her museum in Frankfurt am Main because she was of Jewish descent. She was forced to look for a position abroad and found refuge first in England and then at Harvard's Museum of Comparative Zoology in the United States.

We begin with a summary of Edinger's family background and her early training in Frankfurt. We then describe her initial career and work at the Frankfurt Senckenberg Museum, emphasizing the scientific themes that remained important to her throughout her life. Next, we give an account of the events that led to Edinger's forced emigration and exile. The final sections discuss her quick adjustment to life as an émigré (and later naturalized) scientist in the United States, her seminal contributions to the establishment of paleoneurology as a distinct field of inquiry, and her international recognition as spokeswoman for the entire discipline.

EARLY BIOGRAPHY

Tilly Edinger was the third and youngest child born (November 13, 1897) into a well-to-do Jewish family in Frankfurt am Main. Her father, Ludwig Edinger (1855–1918), was a physician and pioneer comparative neurologist; in 1914 he became the first Chair of Neurology in Germany, at the newly founded University of Frankfurt. Her mother, Anna Goldschmidt (1863–1929), was a

* Address for correspondence: Emily A. Buchholtz, Department of Biological Sciences, Wellesley College, 106 Central Street, Wellesley, MA 02481-8283, USA. Fax: (781) 283-3642; E-mail: ebuchholtz@wellesley.edu

leading social advocate and activist in Frankfurt [39,50]. Education in the Edinger family was first at home by governess (French, then English) and private tutor. At the age of 12 years, Tilly entered the only secondary school for girls in Frankfurt, the Schiller-Schule. Important to her later career were her familial introductions to various foreign languages, to travel, to some of the leading intellectuals of the day, and particularly the scientific example and interests of her prominent father.

Although not expected due to gender and wealth to hold a remunerated professional position, after graduation from secondary school Edinger was allowed to follow her own interests. These included science courses at the Universities of Heidelberg, Frankfurt, and Munich, and a doctoral degree (*magna cum laude*) in geology, zoology and psychology from Frankfurt University in 1921 (see her CV in Fig. 1). In a 1937 letter to her future mentor and colleague, the eminent Harvard paleontologist Alfred Sherwood Romer, she recalled what she described as "7 rather unhappy semesters studying zoology" after which she read Othenio Abel's *Grundzüge der Palaeobiologie der Wirbeltiere*—Principles of Vertebrate Paleobiology [1], and "a new life began, most happy ever since" [HARV]. Her research at Frankfurt was directed by Fritz Drevermann (1875–1932), a vertebrate paleontologist whose main energies went into his work as managing director of the Senckenberg Museum. She described the role that Drevermann played in her dissertation project on the Mesozoic marine reptile *Nothosaurus* in a 1939 letter to Romer: "Professor Drevermann gave me 4 papers on *Nothosaurus* on January 4th, 1920, suggesting that I should write my thesis on the *Nothosaurus* palate—his next step in the matter was to read my MS in his Easter holidays 1921 and to return it saying it was too long, and nothing else" [HARV].

Edinger's particular interest in paleoneurology began with this dissertation project, which included a study of the endocranial cast of *Nothosaurus*, later published separately [7]. The care she took in all her work is clear even in this first publication. For comparison and control, she used a prepared endocast of the brain cavity of a living reptile, the alligator; this also served to inform the range of inferences she could draw from the fossil specimen. The importance of her father's neuroanatomical work to her interests is also apparent. When C. U. Ariëns Kappers, the great Dutch neuroanatomist and former student of her father, commented on this first publication, she responded to him, "Isn't it wonderful, that although I am a paleontologist, I can still follow in Papa's path [trans]"? [NIBR]

EARLY CAREER IN FRANKFURT AM MAIN (1921–38)

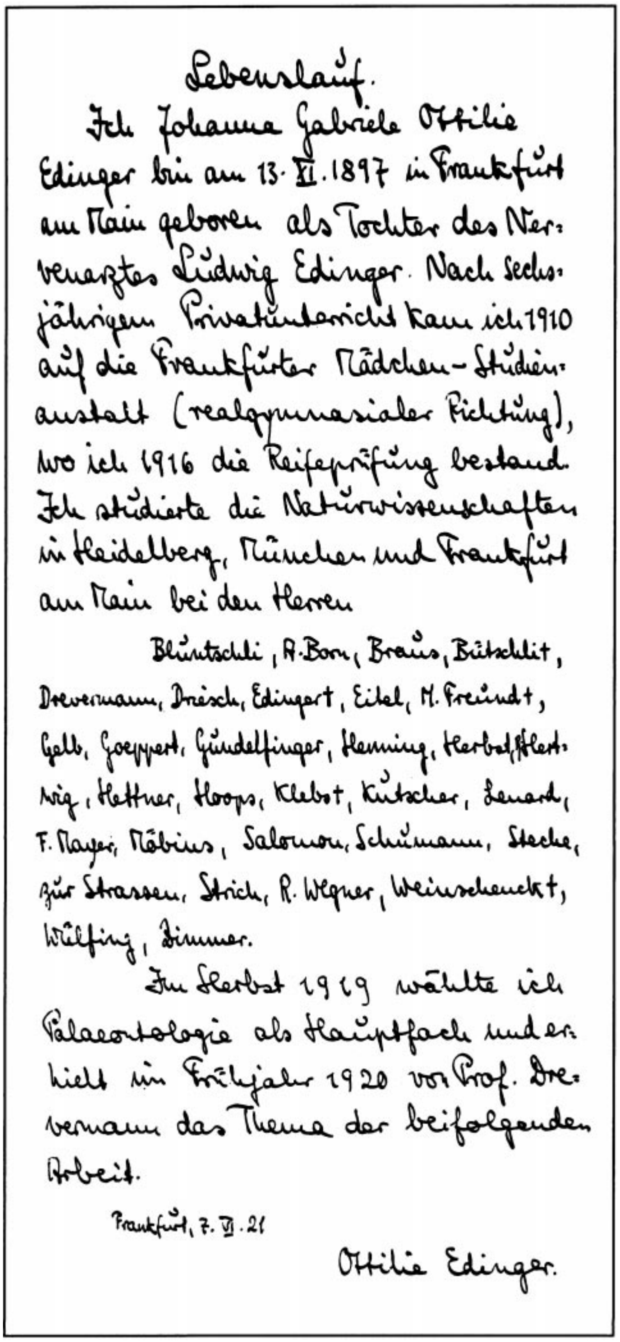
After her graduation from Frankfurt University in 1921, Edinger worked as an assistant in the Geological Institute of Frankfurt University and the Senckenberg Museum of Natural History. She was named Curator ("Sektionärin") of Fossil Vertebrates at the Senckenberg in 1927. Both positions were unpaid, but allowed her free rein to extend her paleontological education. She may have started with no particular career goal in mind (her mother apparently called vertebrate paleontology her "hobby"), but by the end of the decade she had established the field of paleoneurology and become its leading practitioner and chronicler.

With the exception of Drevermann, Edinger had no colleagues in vertebrate paleontology in Frankfurt. In the 1937 letter to A. S. Romer she described both the positive and negative aspects of this environment: "all fossil vertebrates [at the Senckenberg Museum] are entirely at my disposition . . . : nobody else is interested in them . . . On the other hand, this means that I am almost autodidact" [HARV]. She addressed this lack of colleagues by establishing long-distance professional and personal relationships with the leading European paleontologists of the day, most notably Schindewolf (Berlin), von Heune (Tübingen), and Dollo (Brussels). Summaries of her work at the museum for 1926–27 and 1927–28 [MCZH] indicate that much of her time was spent organizing the chaotic collections of fossil fish, amphibians, reptiles, and mammals in everything from cabinets to praline boxes, and exchanging casts of specimens with a wide variety of institutions. Among the new arrivals listed in the 1926–27 summary was "a collection of gypsum endocasts of endocrania of fossil mammals from the Yale Museum, New Haven, CT, USA [trans.]." These undoubtedly included copies of some of the specimens that Yale professor Othniel C. Marsh had described in the late 19th century in his early paleoneurological studies (see below). Edinger supplemented her curatorial work with occasional evening lectures on paleontology for coworkers (1927–28), with numerous published reviews of scientific papers and books (that would eventually number more than 1200!), and with radio programs on comparative anatomy and physiology for the public (1927–29). Further details of her curatorial work in Frankfurt are provided by Kohring [49].

First Evidence against Marsh's Rules

Almost all of Edinger's paleoneurological studies in the 1920s were descriptive; Fig. 1 shows her at work in a portrait taken in 1926. Notable among her early projects were descriptions of the endocranial casts of Mesozoic marine reptiles (*Placodus, Nothosaurus*) and of vertebrates specialized for flight (bats, pterosaurs, *Archaeopteryx*). In these early papers, she accepted the theoretical framework of brain evolution formulated by the 19th century American paleontologist O. C. Marsh (1831–99; Fig. 2, right). Marsh's interpretations of brain casts (see the example in Fig. 2, left) were summarized in a series of "laws" that predicted mammalian brain size and complexity on the basis of stratigraphic occurrence [51]. His statements that "all tertiary mammals had small brains" and that "there was a gradual increase in the size of the brain during this [Tertiary] period" were made without reference to the complicating factor of body size. Marsh also asserted that size increase "was confined mainly to the cerebral hemispheres, or higher, portion of the brain". Later he extended his observations taxonomically to include birds and reptiles, and predicted survival or extinction for taxa with larger or smaller than average brain size, respectively [53]. Therefore, his "laws" predicted not only how the brain changed during evolution, but also how the brain itself affected evolution. In her first paper Edinger [7] wrote that "according to Marsh's 'rules' *Nothosaurus* was predestined to extinction on the basis of its small brain size" [trans.]. Here she clearly accepted Marsh's argument that possession of a small brain was sufficient cause to explain the extinction of the genus. Only 5 years later, however, her description [9] of a small collection of tertiary bat brains led her to question Marsh's orderly scheme of progression in size and form: "In every case, these fossil bat brains already have the size and the form of recent ones" [trans]. As further discussed below, this was only the first of many expressions of Edinger's conflicts with Marsh's theoretical framework of brain evolution.

In addition to research papers, Edinger also wrote short and often light-hearted articles on a wide variety of topics, usually published in the Senckenberg house organ *Natur und Museum*. At Drevermann's request, she wrote a popular piece about the famous Solnhofen fossil *Archaeopteryx* [8]. This led to an inquiry about the natural endocranial cast of the British specimen, then a paleontological trip that included an extended visit in London in 1926, and finally a scientific article on the brain of



Lebenslauf.

Ich Johanna Gabriele Ottilie Edinger bin am 13. XI. 1897 in Frankfurt am Main geboren als Tochter des Nervenarztes Ludwig Edinger. Nach sechsjährigen Privatunterricht kam ich 1910 auf die Frankfurter Mädchen-Studienanstalt (realgymnasialer Richtung), wo ich 1916 die Reifeprüfung bestand. Ich studierte die Naturwissenschaften in Heidelberg, München und Frankfurt am Main bei den Herren

Bluntschli, A. Born, Braus, Bütschli†, Drevermann, Driesch, Edinger†, Eitel, M. Freund†, Gelb, Goeppert, Gundelfinger, Henning, Herbst, Hertwig, Hettner, Hoops, Klebs†, Kutscher, Lenard, F. Mayer, Möbius, Salomon, Schumann, Stecke, zur Strassen, Strich, R. Wegner, Weinschenck†, Wülfing, Zimmer.

Im Herbst 1919 wählte ich Palaeontologie als Hauptfach und erhielt im Frühjahr 1920 von Prof. Drevermann das Thema der beifolgenden Arbeit.

Frankfurt, 7. VI. 21

Ottilie Edinger.

FIG. 1. Tilly Edinger in Frankfurt in the 1920s. The portrait (right), taken in October 1926, shows her measuring an endocranial cast (photo reproduced with permission of Museum of Comparative Zoology, Harvard). She submitted the summary of her early life (left), in her own handwriting, together with her doctoral thesis in June 1921. In translation it reads: Curriculum Vitae. I, Johanna Gabriele Ottilie Edinger, was born in Frankfurt am Main on Nov. 13th, 1897, as a daughter of the neurologist Ludwig Edinger. After six years of private tutoring, I entered the Frankfurt secondary school for girls in 1910 ("Mädchen-Studienanstalt—realgymnasialer Richtung"), where I received my diploma in 1916. I studied natural sciences at Heidelberg, Munich and Frankfurt am Main under the following gentlemen: Bluntschli, A. Born, Braus, Bütschli +, Drevermann, Driesch, Edinger +, Eitel, M. Freund +, Gelb, Goeppert, Gundelfinger, Henning, Herbst, R. Hertwig, Hettner, Hoops, Klebst, Kutscher, Lenard, F. Mayer, Möbius, Salomon, Schumann, Stecke, zur Strassen, Strich, R. Wegner, Weinschenck +, Wulfing, Zimmer. In the fall of 1919, I chose paleontology as my main subject, and in the spring of 1920, Prof. Drevermann gave me the topic of the enclosed thesis.—Frankfurt, June 7, 21. Ottilie Edinger (courtesy of Universitätsarchiv, Frankfurt).

the London *Archaeopteryx* published in English [10]. She described the partially exposed endocast as "reptilian" in structure. Following more extensive preparation and study, the specimen is now typically regarded as intermediate in morphology and size between living reptiles and birds [5,44,45].

In the 1920s Edinger worked concurrently on a major bibliog-

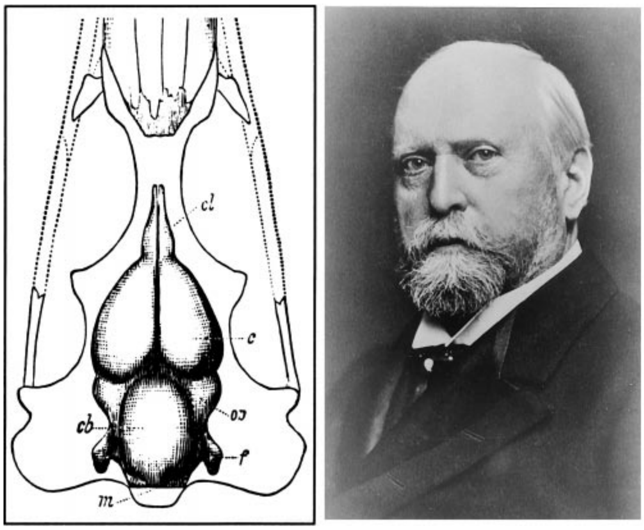


FIG. 2. Othniel C. Marsh (1831–99, right), Professor at Yale College (later Yale University), and author of a series of "laws" concerning brain evolution (courtesy of the Peabody Museum of Natural History, Yale University). Edinger challenged both the imaginative reconstructions of some of his endocasts, such as that of the toothed bird *Hesperornis regalis*, (left, reproduced with permission from [52], but with truncation of anterior skull) and also their interpretation. Her restudy of the skull fragments supported avian, instead of reptilian, similarities for the brains. ol, olfactory lobes; c, cerebral hemispheres; op, optic lobes; cb, cerebellum; f, flocculi; m, medulla.

raphy and summary of the field of paleoneurology ("meine große Gehirnarbeit"—my great brain treatise), published in 1929 as *Die fossilen Gehirne* [11], and dedicated to the memory of her father, who had described the comparative brain anatomy of living vertebrates. The 250-page review, which she much later called "a rather childish compilation" [29], nevertheless laid out not only the history, but also the contemporary state of knowledge and the outstanding questions of the field that would prove to be her life's work. Its phylogenetic section is a point-for-point examination, and in some cases refutation, of Marsh's "general law of brain growth." *Die fossilen Gehirne* received positive reviews from paleontologists across Europe. Later, when she was forced to leave Nazi Germany, this work would serve as the major scientific support for her wartime immigration to the United States.

Paleoneurology versus Comparative Brain Anatomy

Two lines of paleoneurological inquiry that became major themes of Edinger's work in later decades have origin in the early 1930s. The first was the description of endocasts of multiple members of a single taxon from different geological horizons. In contrast to the simple catalog of differences allowed by comparative study of only modern brains, this method allowed Edinger to reconstruct the sequential order of neural innovations in the history of a group. She later contrasted the two methods as "paleoneurology versus comparative brain anatomy." The first taxonomic group given such treatment was the mammalian order Sirenia; equids and camelids were similarly analyzed after her emigration. After a short article on Steller's seacow [12], Edinger wrote a thorough description of the known endocasts and a summary of brain evolution within the Sirenia (Fig. 3). She established that reduction of the olfactory brain was already present in the middle Eocene *Eotherium and Protosiren*, and was postdated by kyphotic bending

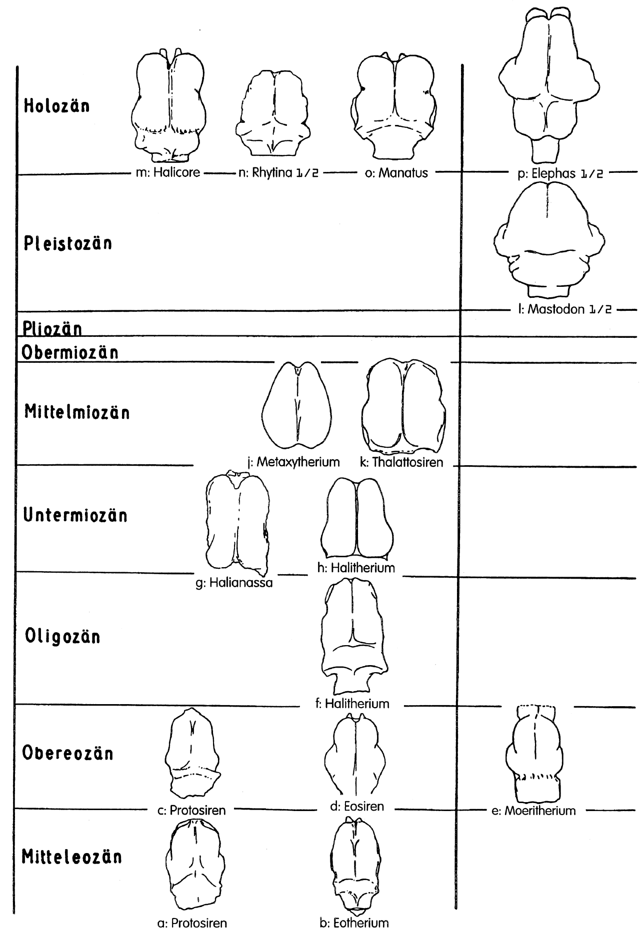


FIG. 3. Stratigraphic distribution of sirenian endocasts (dorsal views) as noted by Edinger in 1933. Edinger noted the retention of many aspects of sirenian brain structure throughout the history of the order, as well as the relative decrease in brain:skull proportions over time. This was Edinger's first example of interpretation of cerebral innovations in a vertical (paleoneurological) versus a horizontal (comparative anatomical) framework. Reproduced with permission from [13, Fig. 11], but with enlarged lettering of taxon names.

of the brain stem, first seen in the Miocene *Halianassa* [13]. Contrary to the most direct reading of Marsh's predictions, the cranium of recent sirenian taxa (as opposed to extinct groups) actually comprised a smaller, rather than a larger, part of the entire skull, and the distinctive features of sirenian gross brain structure were already established in early members of the order. A final short sirenian paper described changes in the postcranial central nervous system of sirenians inferred from neural canal anatomy. She correlated the reduction in the size of the spinal cord's lumbosacral enlargement with progressive reduction of the posterior extremities [16].

A second major theme was paleoendocrinology, a field that Edinger "named" in a brief article summarizing previous references to endocrine function in fossil vertebrates [14]. A second article [15] catalogued the taxonomic occurrence of patent parietal foramina in living mammals. Later, while in London during her first emigration year, Edinger worked on a survey of relative pituitary body size in living and fossil vertebrates, an extension of a discussion initiated by Nopcsa [54,55]. Published in 1942 [20], her work cited recent experimental work on rats, dogs, and chickens, and pathological data on humans of extreme body size to support her hypothesis that an increase in body size, both within and between species, is accompanied by an increase in the size of the anterior lobe of the pituitary gland relative to the brain as a whole, and a resulting relative increase in the secretion of growth hormone. She documented this trend among small and large representatives of reptiles, birds, and mammals, concentrating particularly on giantism in dinosaurs. A proposal to predict relative size of the parietal eye (parapineal organ) in extinct taxa by comparison of the relative sizes of parietal foramen and foramen magnum was published in 1955 [25]. It suggested a much larger relative size and role for the parietal eye in extinct marine reptiles and therapsids than in living reptiles. Finally, she described the structure and location of variously asymmetrical and partially divided foramina in the skull roofs of Devonian and Carboniferous placoderm, dipnoan, and paleoniscid fish [27]. The paired foramina, she argued, corroborated the "bilateral theory" of comparative zoologists that the pineal and parapineal organs were historically a bilateral pair, and that the midline location of the pineal organ is therefore secondary—a notion that is also valid today.

FIG. 4. Tilly Edinger (left), in a photo she sent to A. S. Romer in 1938 shortly before her emigration from Nazi Germany (courtesy of Harvard University Archives). Alice Hamilton (right) in 1935, who intervened on Edinger's behalf (courtesy of The Schlesinger Library, Radcliffe College).

FORCED EMIGRATION AND EXILE

During the 1930s, Edinger's personal and scientific life was progressively constrained by the anti-Jewish decrees and finally the terror initiated by the Nazi regime. The influence of the new rules on Edinger's professional life was slower than on many other persons of Jewish descent because the Senckenberg was a private institution, and her position there was unsalaried. Nevertheless, in 1937 she heard from the Munich vertebrate paleontologist Ferdinand Broili (1974–46) that she could no longer serve as a reviewer for the journal *Neues Jahrbuch für Mineralogie, Geologie, und Paläontologie*, and in 1938 a similar, albeit regretful, notice came from Otto Schindewolf (1896–1971) in Berlin concerning the *Zentralblatt and Fortschritte*. Rudolf Richter (1881–1957), the invertebrate paleontologist who had succeeded Drevermann at the Senckenberg in 1932 was, she wrote in the 1937 letter to Romer, "fighting like a hero to keep me in the house: it is me who brought order to the collection and goes on determining, labeling, etc., since taking my degree in 1921" [HARV].

With characteristic humor, Edinger compared her retention at the museum to "ein Ammonit im Holozän"—an ammonite in the Holocene [SNG]. She was literally among the very last scientists of Jewish ancestry to retain a work situation in prewar Germany. Although urged by friends and by her sister Dora's example to leave the country, she nevertheless chose to stay, as did their brother, Friedrich, who later (1942) became a victim of the Holocaust [Edinger letter (April 5, 1951) to R. M. Yerkes; LBI]. Alice Hamilton (1869–1970), then a recently retired Harvard University faculty member, a former student of Ludwig Edinger, and a family friend for many years, reported a September 1938 dinner conversation in which Tilly Edinger stated, "So long as they leave me alone I will stay. After all, Frankfurt is my home, my mother's family has been here since 1560, I was born in this house. And I promise you they will never get me into a concentration camp. I always carry with me a fatal dose of veronal" [41].

Nevertheless, Edinger must have considered plans for leaving, because in July 1937 she allowed Lucie Jessner (1896–1979), a schoolgirl friend who was then working as a psychologist at McLean Hospital in Boston, to make first inquiries of A. S. Romer about possibilities for study, employment, or research at Harvard. Romer responded positively, but deferred active intervention until Edinger indicated that her departure from Germany would actually be necessary. She subsequently (August 1938) applied to the American consulate for entry into the United States, and was issued quota number 13,814, expected to be reached sometime in the summer of 1940. Among the letters sent to the State Department in her support was one from George Gaylord Simpson (December 31, 1938) that included this testimonial: "She is a research scientist of the first rank and is favorably known as such all over the world. She is everywhere recognized as the leading specialist on the study of the brain and nervous system of extinct animals and on the evolution of the gross structure of the brain. She is so preeminent in this field that she may really be said to have created a new branch of science, that of paleo-neurology, a study of outstanding value and importance" [WELL].

"The Fossil Vertebrates Will Save Me"

Despite Edinger's reluctance to leave, the organized Nazi terrorism of "Kristallnacht" (November 9–10, 1938) forced her hand. Forbidden to enter the Senckenberg, and virtually restricted to her flat, she decided to leave as soon as possible. A flurry of letters in late 1938 from Alice Hamilton (portrait: Fig. 4, right) to A. S. Romer urged him to press for an immediate Harvard appointment for Edinger, hoping to bypass the lengthy quota list and fearing "that our only hope lies in such action" [HARV]. A temporary solution was provided by the Society for the Preservation of Science and Learning (SPSL) in London, which secured a visa on the recommendation of (among others) the renowned British paleoichthyologist D. M. S. Watson (1886–1973), contingent on a financial guarantee and a pledge to leave England for a position in the United States by the summer of 1940. Although tight, the financial resources were provided by a combination of extended family members living in London and the offer of a part-time job translating medical texts from German to English for the émigré pathologist Philipp Schwartz (1894–1977), previously at the University of Frankfurt and then a professor of pathology at the University of Istanbul. Alice Hamilton and Alfred Romer filed affidavits for the guarantee of her welcome into the United States. As part of her application to the SPSL, Edinger gathered testimonials from scientific colleagues (Fischer-Wasels, Broili, and Richter). They indicate the high esteem in which she was held by the European paleontological community in 1938, and justify her belief stated in a letter to Richter that, one way or another, "werden mich also die fossilen Wirbeltiere retten"—the fossil vertebrates will save me [SNG]. Forfeiting most of her family's wealth, she left Germany for London in May 1939, carrying only hand luggage.

Temporary Refuge in London

Edinger spent the year from May 1939–May 1940 in London. Her time there was somewhat dampened by a government restriction on travel, her fear (not realized) that she might be incarcerated as an "enemy alien," and temporary closure of the British Museum of Natural History due to the war. Although much of her time was committed to her translating job, Edinger still did research in her "spare" time. Three paleoneurological papers, on Chinese ovibovines [17], on the pituitary body in giant vertebrates [20], and on the endocranial anatomy of æpyornithids published with the Swedish paleontologist Carl Wiman [64], were partially or completely produced during her year in London. The languages in which they were written (English and French) and their places of publication (Sweden, United States, and France) demonstrate how definitively her professional, as well as her personal, life was changing.

Anxious to speed her emigration, Edinger attempted to qualify as a "nonquota" immigrant to the United States, typically reserved for individuals who had held teaching appointments in "institutions of learning." Despite attempts to describe her work experience in ways that would meet this standard, and the appeals of both Romer and Hamilton, Edinger was not granted nonquota status. Lack of the support she requested from Rudolf Richter in this process was a source of pain, and appears to have soured their future relationship. Nevertheless, her number on the quota list was called earlier than she had anticipated, in early 1940, and after a dangerous Atlantic crossing on the *Britannic*, she arrived in New York on May 11, 1940.

A NEW INTELLECTUAL ENVIRONMENT AND CAREER AT THE MCZ

Almost immediately after her arrival, Edinger was given the title Research Associate in Paleontology by Harvard University. She found a tiny apartment within several hundred yards of the Museum of Comparative Zoology (MCZ), and began her new life as a salaried paleontologist. Among her assigned jobs at Harvard was assistance with the massive *Bibliography of Fossil Vertebrates exclusive of North America* [62], on which she worked with Romer, Nelda Wright, and Richard von Frank for nearly 20 years, and for which her painstaking attention to detail and facility with European languages were tremendous assets. She supplemented the meager stipend the MCZ was able to give her with sporadic translation work and by teaching comparative vertebrate anatomy for three semesters at Wellesley College just outside Boston (1943–45). In addition, she abstracted German language articles for the Geological Society of America, and received temporary aid from the Emergency Committee in Aid of Displaced Foreign Scholars (1940–43), and from a Guggenheim award (1943, renewed 1944) for a (never published) study of tooth replacement.

Edinger found the atmosphere at Harvard much more lighthearted and congenial than at the Senckenberg, with "Gelachter, Gesinge und Gepfeife"—cheerful laughter, singing and whistling in the prep room [SNG], and the powerful impact of A. S. Romer's good spirits and kindness, which even now decades after his death are remembered with great fondness by his colleagues. She also participated somewhat marginally in paleontological field work, attending occasional field conferences, and prospecting in the Permian fossil beds of Archer County, Texas in the summer of 1951 with Romer's field crew (Fig. 5).

Moreover, Edinger had entered an academic environment with a different understanding of the mechanism of evolution from that

FIG. 5. In the summer of 1951, Edinger (far right) joined (from the left) Stanley Olsen (Romer's preparator and later professor at the University of Arizona), A. S. Romer, and Nelda Wright (Romer's research assistant) for field work in Archer County, Texas (photograph courtesy of Donald Baird).

common in her homeland. Although the fact of evolution was accepted early in Germany, the microevolutionary role of natural selection described by Darwin was not seen as sufficient to explain the macroevolutionary trends visible in the fossil record. Instead, macroevolution was held to have its own internal "driving forces" (variously named by different workers, including notably Edinger's colleague and friend Otto Schindewolf) that could result in the saltational origin of new taxa from old, and an inertia that could lead to hypertrophied, nonadaptive organs and extinction. Paleontology, recognized as a subdivision of geology in German institutions, often operated outside an overt theoretical framework. In the United States, Edinger was surrounded by vertebrate paleontologists with zoological training, and was in an intellectual atmosphere dominated by Ernst Mayr and George Gaylord Simpson, and by the gradual and adaptationist ideas of the Evolutionary Synthesis—as described, for instance, by Reif [59,60] and Gould [40]. Influences of this atmosphere on Edinger's later work can be seen in her emphasis on the relationship between brain anatomy and behavior, and by her reluctance to accept either the inevitability of progressive increase in brain size or biological "success" as its predestined result.

Edinger's publication record after her emigration reflects her dramatic changes in institutional affiliation, working language, available specimens, and publication vehicles. Her first American article described the neurocranium of an MCZ specimen of the pterosaur *Pterodactylus elegans*, and was published in the flagship scientific journal of Yale University, the *American Journal of Science* in 1941 [18]. The following year, she published her pituitary body study in the *Quarterly Review of Biology* [20] and coauthored a paper with A. S. Romer on the endocranial casts of his taxonomic specialty, fossil amphibia [61]. These publications also reflect Edinger's postemigration pattern of producing a relatively small number of long articles that not only described gross anatomy, but also attempted to relate anatomical features, when possible, to both behavior and phylogeny.

ESTABLISHING A PALEONEUROLOGY IN HER OWN TERMS

Evolution of the Horse Brain

Edinger's major project during most of her first decade in the United States was the description and analysis of equid brain

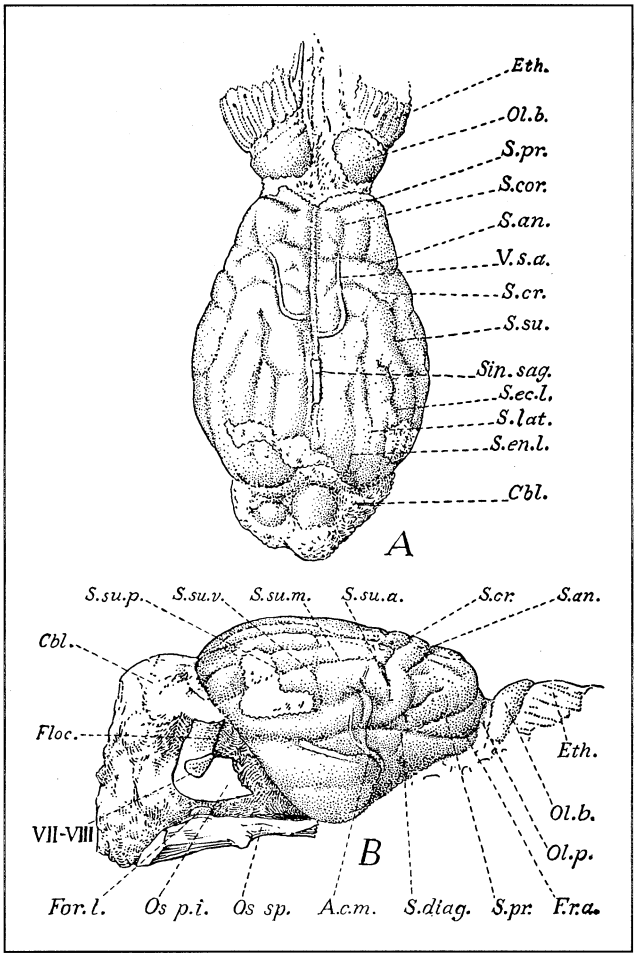


FIG. 6. Endocranial cast of a three-toed horse, *Mesohippus* (YPM-PU 12304) from the Oligocene of South Dakota, reproduced with permission from [22] (A) Dorsal; (B) lateral view from the right. In numerous series of such "fossil brains," Edinger determined features such as the relative size of the olfactory bulbs (Ol.b.), the complexity of the cerebellum (Cbl.), the pattern of sulci (s.), and the position of the rhinal fissure (F.r.a.), which marks the border between "paleocortex" and "neocortex." She found that *Mesohippus* had the sulcal pattern of modern horses, and—in contrast to the brains of earlier equids—a more ventral position of the rhinal fissure indicating a marked expansion of the dorsal "neocortex."

evolution. First proposed as a challenge to American paleontologists by Edinger in her 1929 review, this project was thrown back into her lap by George Gaylord Simpson "the moment we met" [22]. Her first abstract of work in progress appeared in 1941 [19], and her correspondence during the 1940s contains repeated references to the difficulties of obtaining suitable specimens and of reserving time for this project while earning her living.

Edinger meticulously described the gross anatomy of natural and artificial endocasts taken from Lower Eocene to modern equids (see the example in Fig. 6), placing them in geologic and phylogenetic context based on Stirton's *Phylogeny of North American Equidae* [63]. Using brains of extant mammals as a basis, she carefully documented variations in form, relative size of brain areas, and sulcal patterns of each endocast, noting individual variation when multiple specimens were available and comparing occurrence of neuroanatomical changes to those of teeth, skull, and the postcranial skeleton. Edinger's innovations lay in her exhaustive treatment of the known endocranial record of a single mammalian family, and her insistence on the use of fossil specimens, instead of the "horizontal" comparison of living specimens, to determine the pattern of change in brain evolution. Her observations on equids were the basis for conclusions concerning the history of sulcation and about the relationship between changes in the brain and those in other body systems. They also presented an opportunity to reexamine both the relationship between body size and brain size and the relative merits of "paleoneurology" and "comparative anatomy."

The earliest specimen she analyzed, then identified as the Eocene horse "Eohippus" [=*Hyracotherium*], was "in a primitive stage of mammalian brain evolution" and displayed minimal sulcation. However, a modern fissuration pattern existed in the upper Miocene *Merychippus*. As an important result, she concluded that the similarities of sulcation pattern between living horses and other modern mammals must have arisen separately and in parallel in different orders. The later recognition by Radinsky [58] that misidentification of this specimen had led her to underestimate the degree of sulcation in the early equid cerebrum slightly modifies her conclusion, but does not detract from its general relevance.

Edinger also noted the apparent independence of skeletal and brain changes, the first statement of her principle of "noncorrelation." As an example, she documented that expansion of the equid neocortex occurred in the Eocene, while increase in body size occurred later, in the Oligocene. In her own later assessment of this project [31], she wrote: "the absolute increase and elaboration of the cerebrum in the Equidae was not at all times closely correlated with progress in body size, limb or tooth structure in the manner that the so-called 'scale' of extant mammals would suggest if regarded as representing steps in evolution; but the fact that enlargement was greater in the cerebrum and its neocortex, i.e. in the neëncephalon than in the palaeëncephalon, and greater also in the neocerebellum than in the palaeocerebellum, brilliantly justifies these distinctions which my father derived from comparing brains of lower and higher extant animals."

Although she carefully documented the size of each endocast, Edinger did not attempt a quantitative analysis of relative brain size over time, largely because of her stated reluctance to predict brain:endocranial volume relations, the lack of postcranial material for most of the individuals she studied, and the unknowable range of individual variation within her fossil species. In agreement with many previous workers, however, she noted that "when body size increases in evolution, the brain to body ratio decreases." Many small, early mammals had greater brain to body volume ratios than did larger, more recent species. However, her further conclusion that "the history of the Equidae may be regarded as a final refutation of the idea that a high ratio of brain volume to body volume is a sign of a high evolutionary level" did not take into account the fact that the brain to body relationship is not linear; this would become a source of future frustration and contention (see below).

Finally, the equid monograph gave Edinger the opportunity to contrast histories reconstructed from comparative analysis of living species and from sequences of fossil species. She noted a series of "trends and conditions" that could be observed in equid fossils, but could not be found by a comparative study of extant brains. Among these were the independence of degree of sulcation and increase in body size, the relative timing of expansion in median and lateral lobes of the cerebellum, and the surprisingly constant size of the olfactory lobes during periods of neocortical expansion. Edinger's language, especially her use of terms such as "progressive," "lower," and "higher" in reference to individual animals and lineages, appears outdated today. Nevertheless, its reference was to documented changes within the geological record of Equidae, instead of to a comparison of living mammals (often primates), from which history was then inferred. The importance of the monograph was recognized from the moment of its publication. G. G. Simpson, writing later to support her nomination for an honorary doctorate at Wellesley College, noted that it marked "a new era in the significance and broad value of paleoneurology and of paleontology in general" [WELL].

Many years later Edinger noted [35] that her equid monograph served as "jet propulsion for paleoneurology. Jet is a wrong word insofar as the influence went in many directions." Almost single-handedly, she had established the field of paleoneurology, and had become not only its dominant practitioner but also its chronicler. She wrote articles and delivered oral reports at professional meetings concerning "the state of paleoneurology."

Spreading the Gospel of the Fossil Brain

In 1948, the Society of Vertebrate Paleontology voted unanimously "that Tilly shall be forced to rewrite, in the English language, her *Die fossilen Gehirne* of 1929." The reworking of her 1929 book required travel to almost every major museum with paleoneurological material in the United States and abroad, a daunting physical and financial drain for Edinger, who suffered from a series of physical ailments (of which the most limiting was progressive deafness) and had almost no cash reserves. She received travel funding from the American Association of University Women, from the Milton Fund of Harvard University, and from the Penrose Fund of the American Philosophical Society. Her trips took her all the way across the United States to major museums of natural history, and back to Europe in 1950 and 1955, where she reestablished personal and scientific relationships with many of her prewar colleagues. Her Harvard colleague, mammalogist Bryan Patterson, referred to this intense activity as "spreading the gospel of the fossil brain" [32]. With the help of several coworkers, she was engaged with this "maximum opus" throughout the rest of her life.

After Edinger's death, Bryan Patterson wrote [37] that Edinger's increasing deafness progressively cut her off from much of the give and take that is central to the exchange of scientific ideas. For example, during the later years of her career, functional mapping of the mammalian cortical surface was an emerging field that could have been correlated with the sulcation patterns revealed on endocasts. Unlike younger paleoneurologists, in particular Leonard Radinsky [57], Edinger restricted her interpretations to relative sizes of brain regions, without exploiting this new information source. Edinger's isolation was at least in part self-chosen, as she is remembered by many for leaving her hearing aid off, and switching it on only to facilitate conversation. Nevertheless, her disability and the solitary habits typical of concentrated museum work did not keep her from extensive personal interaction, as documented by voluminous preserved personal and scientific correspondences, and by the fond memories of many former colleagues.

In addition to the work on her paleoneurological summary and on the Romer bibliography, Edinger continued to publish shorter research papers of her own. She continued her prewar interest in the parietal foramen [25], and published the work on pineal organs previously discussed [27]. She also published primarily descriptive papers on nonneurological features of the skull, notably the frontal sinuses [23] and the foramen ovale (with D. B. Kitts) [38]. Edinger also extended the range of possible paleoneurological insights to behavior. For example, a 1955 paper correlated the relative hypertrophy and diminution of the acoustic and olfactory brain regions in Cetacea with an increasing dependence on hearing and loss of olfaction in the order over time [26]. Her most cherished example demonstrating that "fossil brains reflect specialized behavior" was a Paleocene endocast with enlarged and dorsally exposed acoustic colliculi found by Princeton paleontologist Glenn Jepson, and referred to in a voluminous correspondence between them as the "Tillybat" (Fig. 7). They carried on an animated multiyear argument debating whether the specimen was a microchiropteran bat whose large colliculi indicated acoustic navigation (Edinger) or a miacid carnivore (Jepson, and many others). Bryan Patterson, called in to mediate, found that the braincase possessed a greater resemblance to that of a miacid than to that of a bat, but that this resemblance "bars the problematical specimen from the Chiroptera is by no means certain" [GAPU]. Resolution sufficient for publication was never reached, and today the specimen (in the Princeton collection of the Yale Peabody Museum) is still classified as a miacid. Edinger further used the presence of an exposed tectum in both the Paleocene specimen and in some living bats as an argument against the necessity of "progression" in brain anatomy over time.

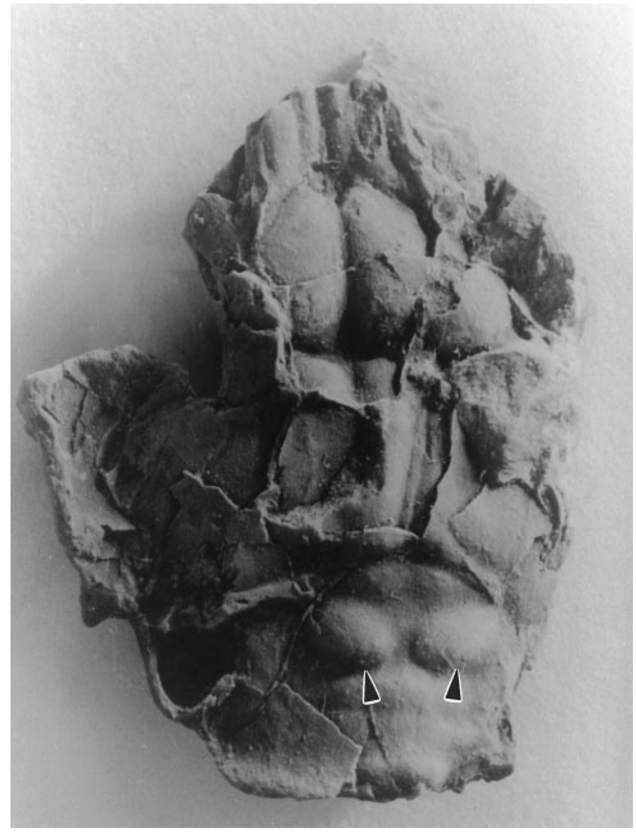


FIG. 7. The "Tillybat" specimen (YPM-PU 16494). Edinger described the specimen [30], from anterior to posterior, as showing "large olfactory bulbs behind a proximal fragment of the nasal cavity; the anterior tips *in situ* of the wing-shaped cerebral hemispheres, the midline then displaced to the right (and much of the right hemisphere lost) but median again posteriorly; small optic colliculi, and acoustic colliculi conspicuous by size and height; and a broad cerebellum with large floccular lobes." The dorsally exposed and relatively large posterior colliculi (*arrowheads*) were used by Edinger to support her argument that the specimen was a microchiropteran bat capable of auditory navigation (photo permission of Yale Peabody Museum).

Edinger was increasingly willing to attack the work of previous paleoneurologists, most often Marsh, in print. In "The brains of the

Odontognathae" [24] she challenged not only Marsh's interpretation of the braincasts of the toothed birds *Hesperornis and Ichthyornis* as "reptilian" instead of "avian," but also his scientific honesty. The skull figured in his Odontornithes monograph [52] and partially reproduced here in Fig. 2 was, she asserted, reconstructed from "a number of fragments scattered over a slab" the braincast represented "Marsh's idea of a *Hesperornis* brain." What sparse evidence of brain anatomy Edinger was able to document from a restudy of the skull fragments suggested a broader cerebrum and smaller olfactory lobes than diagrammed by Marsh, both indicative of avian, instead of reptilian, neuroanatomy. Many years later in a 1966 letter to the renowned Berkeley paleobiologist E. C. Olsen, she referred to Marsh as "the man who fooled all the people all the time (really! and still does)". Despite her justified criticisms, Edinger's statement that "the differences of the bird brain from the reptilian are, of course, connected with the higher evolutionary level which the avian organism has achieved" [24], still has a decidedly *Scala Natura* ring to it today.

In an oral presentation to the American Society of Zoologists in 1958 Edinger not only reattacked Marsh, but also formulated her own theory of "noncorrelation," stated as an amendment to Cuvier's theory of correlation. By this she meant that there are often different selective pressures on different parts of the body during evolution, and that changes in, for instance, the postcranial skeleton need not be accompanied by parallel changes in brain size. She also challenged "the ancient, enduring concept of progressive brain evolution as an important factor in success, as shown by survival." She used the long survival of both seacows and bats as examples of lineages in which there had been little change in brain anatomy, without extinction, since the Paleocene or Eocene [28].

In 1960 Edinger presented a lecture entitled "Anthropocentric misconceptions in paleoneurology" to the Rudolf Virchow Society in New York, and later published an enlarged version of the speech [31]. Here she vigorously attacked assumptions shared by both the general public and by the paleontological community about the pattern of changes in the brain during vertebrate evolution. Among her topics were claims that the extinction of individual fossil taxa could be ascribed to their "absurdly small" brains (often compared in size and shape to fruit or vegetables!), and, again, the contention by Marsh that mammalian brain evolution is characterized by progressive increase in brain size throughout time. Edinger wrote [31] that "the obligation to demonstrate that he in fact did not show [that there had been a gradual increase in (brain) size with the passage of geologic time] devolves upon me because I have had the privilege to see what may well be a thousand fossil brains." Chief among her many complaints against Marsh were his failure to evaluate brain size relative to body size, his insistence that all mammals followed similar trajectories of increasing brain size over time, and the assumption that evolution of all body systems was somehow "synchronized" and progressive, rather than mosaic in showing both the retention of conservative traits as well as origin of derived ones. She ascribed one source of Marsh's misunderstandings to his training in "earth sciences," and contrasted it to the background in comparative anatomy of Marsh's competitors, Joseph Leidy and Edward Drinker Cope.

Despite her energetic attacks, the quantitative work of some of Edinger's contemporaries revealed that although formulated without control for body size, Marsh's generalization of an increase in brain size over time in mammals could be defended as a general trend with isolated exceptions. As long ago as 1897, E. Dubois [6] had developed an exponential equation that described the relationship of brain size to body size. Von Bonin [2], Count [4], and later Jerison [42,43] calculated the exponent to be approximately 0.67. Jerison [43] further documented that a "family" of lines of the same slope, but of different y (= brain size) intercepts, could describe brain-to-body relationships of mammals of different geological periods. This y intercept (identified as k in Jerison's papers) did, in fact, increase over time, documenting a general trend of increasing brain size over time for mammals *of a given body weight*.

From 1958 until 1964, Edinger carried on a lively and even fond correspondence with Jerison, much of it dedicated to a discussion of the brain-to-body size relationship. Jerison urged Edinger to consider the mathematical relationships he had documented, but she repeatedly resisted, as in a 1958 letter to Jerison: "As I never can understand formulas and logarithmic graphs, I do not understand yours" [Harry J. Jerison, pers. papers]. In a 1962 letter to Julian Huxley [l.c.] she further insisted that such quantitative work should not be applied to paleoneurology, which of necessity used specimens from isolated and possibly nonrepresentative individuals, usually without enough postcranial material to reliably predict body size. She concluded, "Briefly, paleontologists, including myself, keep out!" This she largely did for the rest of her career, leaving quantitative methods to her younger colleagues, notably Jerison [45–48] and Radinsky [56]. Despite differences in approach and background, the respect and affection that Jerison and Edinger had for each other is clear from their letters. Jerison later dedicated his groundbreaking treatise, *Evolution of the Brain and Intelligence* [45] to Edinger.

SERVING THE SCIENTIFIC COMMUNITY AND FINAL YEARS

Very soon after her arrival in the United States, Edinger was present at the Cambridge, Massachusetts organizational meeting of the Society of Vertebrate Paleontology (December 1940), which grew out of the Vertebrate Paleontology Section of the Paleontological Society. For many years she was an active contributor at annual meetings and a frequent contributor to the society's news bulletin. Many of her contributions were travelogues of her visits to foreign museums for access to specimens, and short biographies of European paleontologists unfamiliar to her American colleagues.

During and immediately after the war she also served on the society's committee on foreign membership, evaluating the applications of non-American scientists for membership. In this role, and as a recent émigré, she was often questioned about the propriety of providing testimonials for German paleontologists who had joined the Nazi party, and were subject to "denazification" trials. While acknowledging the difficulty of advising in particular cases, she noted [21] that "those colleagues over there who have a clean sheet politically do not ask because they have no need for American statements." Evidence of her ambivalence and discomfort in supplying such testimonials is also provided by the very short and crisply worded example she wrote for her former colleague at the Senckenberg, Rudolf Richter, in May of 1947. The "denazification" of Richter occurred the month before her letter. He was reinstated as Professor of Geology and Paleontology at the University of Frankfurt in November of 1947, but not as Director of the Senckenberg Museum.

In the fall of 1963, Edinger was elected president of the Society of Vertebrate Paleontology, the first woman to serve in this role. In a humorous mode, she wrote, "this most beloved of scientific societies has also now chosen for president a woman who to me seems unfit for that post" [33]. Neither the administrative job for the Society nor her formal retirement in 1964 kept Edinger from her research. In 1966, reporting to the Society of Vertebrate Paleontology [35], she described a diverse list of projects that she either hoped "to forget," "to finish myself," or to find collaborators for. Among the projects she finished was a phylogenetic treatment of a third group of mammals, the camelids [34,36], which paralleled her works on Sirenia and Equidae. She also coauthored a description of the brain of the modern emu [3], which initiated a discussion of "what primitive means."

These new studies contributed to a body of work that was now recognized not only by the paleontological community, but also by the broader scientific establishment. Edinger repeatedly served as a foreign ambassador for the Society, and as an observer and historian of the field of paleontology as a whole. Her unique role in the establishment of paleoneurology earned her honorary degrees from Wellesley College (1950), from the University of Giessen (1957), and from the University of Frankfurt am Main (1964), the last a particularly welcome tribute after her painful departure from that city in 1939.

Most of Edinger's time in her last decade, however, was dedicated to the "comprehensive summary of paleoneurology." Over the years its content had changed from a textual summary to an annotated bibliography, but it was still massive in size and rich in detail. When Edinger died at the age of 69 years on May 27, 1967 as the result of a traffic accident, it was still unfinished. Colleagues completed the remaining work, and it was published posthumously in 1975 with a foreword by Bryan Patterson [37]. It still serves as the essential reference for all who follow her path in the study of "fossil brains."

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SOURCES CITED

GAPU Department of Geosciences Archives, Princeton University, Princeton, NJ
HARV Harvard University Archives, Pusey Library, Cambridge, MA
LBI Leo Baeck Institute, New York, NY
MCZH Museum of Comparative Zoology, Harvard University, Special Collections, Cambridge, MA
NIBR Netherlands Institute for Brain Research, C. U. Ariëns Kappers Archive, The Netherlands
SNG Senckenbergische Naturforschende Gesellschaft, Archiv, Frankfurt am Main
WELL Wellesley College Archives, Wellesley, MA

REFERENCES

1. Abel, O. Grundzüge der Palaeobiologie der Wirbeltiere. Stuttgart: Schweizerbart; 1912.
2. Bonin, G. v. Brain weight and body weight in mammals. J. Gen. Psychol. 16:379–389; 1937.
3. Cobb, S.; Edinger, T. The brain of the emu (*Dromaeus novaehollandiae* Lath.). I. Gross anatomy of the brain and pineal body. Mus. Comp. Zool. Breviora 170:1–18; 1962.
4. Count, E. W. Brain and body weight in man: Their antecedents in growth and evolution. Ann. N. Y. Acad. Sci. 46:993–1122; 1947.
5. de Beer, G. Archaeopteryx lithographica. London: British Museum; 1954.
6. Dubois, E. Sur le rapport du poids de l'encéphale avec la grandeur du corps chez mammiferes. Bull. Soc. Anthrop. Paris [Ser. 4] 8:337–376; 1897.
7. Edinger, T. Über *Nothosaurus*. I. Ein Steinkern der Schädelhöhle. Senckenbergiana 3:121–129; 1921.
8. Edinger, T. Die *Archaeopteryx*. Natur und Museum 55:491–496; 1925.
9. Edinger, T. Fossile Fledermausgehirne. Senckenbergiana 8:1–6; 1926.
10. Edinger, T. The brain of *Archaeopteryx*. Ann. Mag. Nat. Hist. 18:511–156; 1926.
11. Edinger, T. Die fossilen Gehirne. Ergeb. Anat. EntwGesch. 28:1–249; 1929.
12. Edinger, T. Von der Stellerschen Seekuh. Natur und Museum 60:221–225; 1930.
13. Edinger, T. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. V. Tertiäre Wirbeltiere. 5. Über Gehirne tertiärer Sirenia Ägyptens und Mitteleuropas sowie der rezenten Seekühe. Abh. Bayer. Akad. Wiss., Mathem.-naturwiss. Abt., N.F. 20:5–36; 1933.
14. Edinger, T. Paläo-Endokrinologie. Naturwissenschaften 21:486–487; 1933.
15. Edinger T. Die Foramina parietalia der Säugetiere. Z. Anat. EntwGesch. 102:265–289; 1933.
16. Edinger, T. Two notes on the central nervous system of fossil Sirenia. Bull. Fac. Sci. Fouad I Univ. (Cairo) 19:43–57; 1939.
17. Edinger, T. The brains of three Pontian ovibovinae from China. Bull. Geol Inst. Uppsala 28:133–140; 1940.
18. Edinger, T. The brain *of Pterodactylus*. Am. J. Sci. 239:665–682; 1941.
19. Edinger, T. Phylogeny of the equid brain [Abstract]. Bull. Geol. Soc. Am. 52:1966; 1941.
20. Edinger, T. The pituitary body in giant animals fossil and living: a survey and a suggestion. Q. Rev. Biol. 17:31–45; 1942.
21. Edinger, T. News from abroad. News Bull. Soc. Vert. Paleontol. 21:24–28; 1947.
22. Edinger, T. Evolution of the horse brain. Mem. Geol. Soc. Am. 25:1–177; 1948.
23. Edinger, T. Frontal sinus evolution (particularly in the Equidae). Bull. Mus. Comp. Zool. 103:411–496; 1950.
24. Edinger, T. The brains of the Odontognathae. Evolution 5:6–24; 1951.
25. Edinger, T. The size of parietal foramen and organ in reptiles. A rectification. Bull. Mus. Comp. Zool. 114:1–34; 1955.
26. Edinger, T. Hearing and smell in cetacean history. Monatsschr. Psychiatrie Neurologie [Festschrift E. Grunthal] 129:37–58; 1955.
27. Edinger, T. Paired pineal organs. In: Ariëns Kappers, J., ed. Progress in neurobiology [Proceedings of the First International Meeting of Neurobiologists, Groningen]. Amsterdam: Elsevier; 1956:121–129.
28. Edinger, T. Noncorrelation. Typescript of paper presented to the Symposium on Vertebrate Zoology of the American Society of Zoologists and AAAS. 1–5; 1958.
29. Edinger, T. The present state of paleoneurology. Typescript of remarks to the Society of Vertebrate Paleontology. 1–3; 1961.
30. Edinger, T. Fossil brains reflect specialized behavior. World Neurology 2:934–941; 1961.
31. Edinger, T. Anthropocentric misconceptions in paleoneurology. Proc. Rudolf Virchow Med. Soc. 19:55–107; 1962.
32. Edinger, T. Tübingen meeting of the Palaontologische Gesellschaft. News Bull. Soc. Vert. Paleontol. 67:8–13; 1963.
33. Edinger, T. Partial report on 1963 work. Typescript of paper presented at the Annual Meeting of the Society of Vertebrate Paleontology, Nov. 20, 1963. 1–9; 1963.
34. Edinger, T. Brains from 40 million years of camelid history [Abstract]. International Symposium on Phylogenesis and Ontogenesis of the Forebrain. Frankfurt-Sprendlingen Aug. 15–19 1965:12; 1965.
35. Edinger, T. A report on unfinished work. Typescript of paper presented at the Annual Meeting of the Society of Vertebrate Paleontology, Nov. 16, 1966. 1–16; 1966.
36. Edinger, T. Brains from 40 million years of camelid history. In: Hassler, R.; Stephan, H., eds. Evolution of the forebrain. Stuttgart: Georg Thieme; 1966:153–161.
37. Edinger, T. Paleoneurology 1804–1966. An annotated bibliography (with a foreword by Bryan Patterson). Adv. Anat. Embryol. Cell Biol. 49:1–258; 1975.

38. Edinger, T.; Kitts, D. B. The foramen ovale. Evolution 8:389–404; 1954.
39. Emisch, H. Ludwig Edinger—Hirnanatomie und Psychologie. Stuttgart: Gustav Fischer; 1991.
40. Gould, S. J. Foreword. In: Schindewolf, O.H. Basic questions in paleontology. Chicago: University of Chicago Press; 1993: ix–xiv.
41. Hamilton, A. Exploring the dangerous trades. Boston: Little, Brown; 1943.
42. Jerison, H. J. Brain to body ratios and the evolution of intelligence. Science 121:447–449; 1955.
43. Jerison, H. J. Quantitative analysis of evolution of the brain in mammals. Science 133:1012–1014; 1961.
44. Jerison, H. J. Brain evolution and *Archaeopteryx*. Nature 219:1381–1382; 1968.
45. Jerison, H. J. Evolution of the brain and intelligence. New York: Academic Press; 1973.
46. Jerison, H. J. Paleoneurology and the evolution of mind. Sci. Am. 234:90–101; 1976.
47. Jerison, H. J. Animal intelligence as encephalization. Phil. Trans. Roy. Soc. Lond. B. Biol. Sci. 308:21–35; 1985.
48. Jerison, H. J. Fossil evidence on the evolution of the neocortex. In: Jones, E. G.; Peters, A., eds. Cerebral cortex, vol. 7. New York: Plenum Press; 1990:285–309.
49. Kohnng, R. Senckenbergische Forscher: Tilly Edinger (1897–1967). Natur und Museum 127:39–410; 1997.
50. Kreft, G. The work of Ludwig Edinger and his neurology institute. In: Korf, H.-W.; Usadel, K.-H., eds. Neuroendocrinology—retrospect and perspectives. Berlin: Springer-Verlag; 1997: 407–423.
51. Marsh, O. C. Small size of the brain in Tertiary mammals. Am. J. Sci. 8:66–67; 1874.
52. Marsh, O. C. Odontornithes: A monograph on the extinct toothed birds of North America. U. S. Geol. Exploration 40th Parallel, volume 7; 1880.
53. Marsh, O. C. Dinocerata. Monogr. U. S. Geol. Surv. 10:1–243; 1886.
54. Nopcsa, F. v. Über Dinosaurier. 2. Die Riesenformen unter den Dinosauriern. Cbl. Min. Geol. Palaeontol. 1917:332–351; 1917.
55. Nopcsa, F. v. Heredity and evolution. Proc. Zool. Soc. Lond. 1926: 633–665; 1926.
56. Radinsky, L. Relative brain size: a new measure. Science 155:836–837; 1967.
57. Radinsky, L. Evolution of somatic sensory specialization in otter brains. J. Comp. Neurol. 134:495–505; 1968.
58. Radinsky, L. Oldest horse brains: more advanced than previously recognized. Science 194:626–627; 1976.
59. Reif, W.-E. Evolutionary theory in German paleontology. In: Grene, M, ed. Dimensions of Darwinism. Cambridge: Cambridge University Press; 1983 173–203.
60. Reif, W.-E. Afterword. In: Schindewolf, O. H. Basic questions in paleontology. Chicago: University of Chicago Press; 1993:435–453.
61. Romer, A. S.; Edinger, T. Endocranial casts and brains of living and fossil Amphibia. J. Comp. Neurol. 77:355–389; 1942.
62. Romer, A. S.; Wright, N. E.; Edinger, T; Frank, R. v. Bibliography of fossil vertebrates exclusive of North America 1509–1927. Mem. Geol. Sci. Am. 87:1–1544; 1962.
63. Stirton, R. A. Phylogeny of North American Equidae. Bull. Univ. Calif. Dept. Geol. Sci. 25:165–198; 1940.
64. Wiman, C.; Edinger, T. Sur les cranes et les encephales d'*Æpyornis* et de *Mullerornis*. Bull. L'Acad. Malgache 24:1–10; 1942.

NOTE: A FULL BIBLIOGRAPHY OF TILLY EDINGER'S SCIENTIFIC PUBLICATIONS IS AVAILABLE FROM THE AUTHORS.