

RESEARCH

Open Access



Flying turtles in the earliest trees of life: scientific transparency in the phylogenetic works of Ernst Haeckel

Ingmar Werneburg^{1,2*} and Uwe Hoßfeld³

Abstract

The evolutionary origin of turtles has long been debated, and recent studies continue to provide conflicting results. In some of the first trees of organisms ever drafted, Ernst Haeckel (1834–1919) placed turtles close to birds based on morphological arguments. He only later became convinced by novel embryological and paleontological discoveries that birds are rather placed within dinosaurs, far removed from turtles. We analyzed Haeckel's major publications on vertebrate phylogeny, with a focus on turtles and birds, and discuss his arguments for alternative interpretations of land vertebrate phylogeny. Haeckel carefully took the most recent developments in biology and paleontology into account to create his trees of life. While using his concept of the trifold parallelism between embryology, paleontology, and comparative anatomy, he understood his phylogenies as “fluent working hypotheses” with branches and taxon names floating, depending on available scientific evidence. Although Haeckel's trees resemble modern trees in many regards, he often pursued hypotheses not supported by recent data. We conclude that he committed those because of his strict attempts to order taxa by morphological homogeneity while not taking convergences into account.

Keywords Evolution, Birds, Morphology, Beaks, Paleontology, Turtles

Phylogenetic origin and the unique anatomy of turtles

The phylogenetic origin of turtles has been a topic of debate for over 150 years (Rieppel, 2008). Various extinct and extant taxa have been suggested as turtle ancestors or sistergroups, and turtles have been placed close to lepidosaurs (lizards + tuatara), archosaurs (crocodiles + birds), and even mammals, among extant groups.

This confusion arises from their highly derived anatomy, which is incomparable in many regards to that of other land vertebrates (Werneburg et al., 2024). Recent molecular studies consistently place turtles close to archosaurs (Field et al., 2014; Wang et al., 2013), forming the taxon Archelosauria (Fig. 1A).

The unique turtle shell (Figs. 1C, 2B) significantly restricts terrestrial locomotion. Additionally, internal organs such as the lungs and liver have been adapted to accommodate this “body plan” (Werneburg et al., 2024). In regard to their stiffened body, the Mesozoic Era's exclusively marine ‘sea dragons’ (Sauropterygia), for example, were also considered turtle relatives due to their robust bodies (Gregory, 1946), but their osteology differs in many details (Rieppel, 2004). Similar to marine reptiles, turtle limbs and necks are highly mobile and help to overcome the limitations of their body armor, making most turtles efficient underwater flyers (Krahl

Handling editor: Walter Joyce.

*Correspondence:

Ingmar Werneburg
ingmar.werneburg@senckenberg.de

¹ Senckenberg Center for Human Evolution and Palaeoenvironment
an der Universität Tübingen, Sigwartstraße 10, 72076 Tübingen, Germany

² Fachbereich Geowissenschaften, Universität Tübingen, Hölderlinstraße
12, 72074 Tübingen, Germany

³ Stoy'sches Haus/Institutsgebäude/Bienenhaus + AG Biologiedidaktik,
Am Steiger 3, 07743 Jena, Germany



© The Author(s) 2025. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

(See figure on next page.)

Fig. 1 A Time-scaled phylogenetic tree of modern amniotes (i.e., fully terrestrial land vertebrates) based on molecular data (timetree.org; access: 2024-08-28). Turtles (Testudines) and birds (Aves) are shown in red. Images adapted from Werneburg and Sánchez-Villagra (2009). **B** Reptile section of the phylogenetic “tree of man” from *Anthropogenie* (Haeckel, 1874) [here the version of the 3rd edition is reproduced, (Haeckel, 1877)], with the reptilian branch showing turtles (“Schildkröten”) as a sister group of birds [“Vögel (Aves)”] [Eidechsen = lizards; Schlangen = snakes; Crocodile = crocodiles]. **C** “Flying” and walking turtles with bird-like beaks in the upper part of plate 89 from Haeckel’s (1899) “Kunstformen der Natur”. The marine (“flying”) turtles include the Hawksbill sea turtle *Eretmochelys imbricata* (top left) and the leatherback *Dermochelys coriacea* (top right). Non-marine turtles: the anterior half of the Argentine snake-necked turtle *Hydromedusa tectifera* (bottom left), the mata-mata *Chelys fimbriatus*, and the head of the Aldabra giant tortoise *Aldabrachelys gigantea* (bottom right). **D** Mid-term embryos of a dog (Fig. C), human (Fig. D), a turtle [Fig. E, likely *Emys orbicularis*, (Rathke, 1848)], and a bird (Fig. F, chicken), published by Haeckel (1868). **E** The cleavage type (“Furchungstyp”) of animals is dependent on the egg type (“Eityp”), which is defined by the position of the fertilized egg cell (reddish circle) and the correlated amount and distribution of yolk cells (yellow circles). Conditions in E1: mammals, lancelet, many invertebrates; E2: amphibians, lungfish, lamprey; E3: reptiles, birds, monotremes, sharks, actinopterygian fishes; E4: insects, spiders, myriapods. This illustration shows a part of a wall chart of the zoological teaching collection of Tübingen university, Germany, and was drawn by the artist Heiner Bauschert (1928–1986); reproduced with permission. **F–G** Phylogenetic tree (“Pedigree”) of man (“Stammbaum des Menschen”) as a draft (**F**; made by Haeckel in 1863 at the earliest, see text) and in the published version (**G**) in the book *Anthropogenie* (Haeckel, 1874)

& Werneburg, 2023; Werneburg et al., 2024; Werneburg et al., 2015b).

Turtle skulls are significantly different from those of other land vertebrates because they lack temporal fenestrae (Abel & Werneburg, 2021). This feature was considered reminiscent of archaic, so-called anapsid reptiles, for more than 100 years. However, details in bone architecture differ (Müller, 2003; Schoch & Sues, 2015), and it has been demonstrated that the well-known neck retraction behavior has led, by tensional stresses, to the formation of a compact skull, making it difficult to make an unequivocal association with other vertebrate skulls (Werneburg & Preuschoft, 2024; Werneburg et al., 2015b, 2024; Werneburg, 2024a, 2024b).

Haeckel kept turtles at a distance

Ernst Haeckel (1834–1919) produced the first phylogenetic tree of vertebrates in his book *Generelle Morphologie* (Haeckel, 1866; Hoßfeld & Levit, 2016), which was based on comprehensive morphological insights. Given the unique anatomy of turtles, it is surprising that Haeckel, except for his famous drawing in his book *Kunstformen der Natur* (Haeckel, 1899) (Fig. 1C),¹ only rarely mentioned turtles in his publications. In his letters (Bach, 2024), however, he emphasizes the importance of turtle specimens for the scientific collection of the Phyletische Museum in Jena, Germany (Fischer et al., 2008; Knorre, 1983; Uschmann, 1959a).² Indeed, Haeckel recognized the general importance of turtles for zoology, as becomes obvious in a letter to the ruler of Sachsen-Weimar-Eisenach (including Jena city), the Grand Duke

Carl Alexander, dated July 19th, 1874, which lists turtle shells as particularly valuable objects that he received for the Phyletische Museum from the colonies of the Dutch East Indies (Bach, 2024).

Also, for education, turtles served a special role at Jena University. In a letter dated October 19th, 1873 (Bach, 2024), with some kind of humor, Haeckel mentioned to an animal trader that turtles were ‘sacrificed’ for dissection courses: “Your chamaeleons are still alive and cause the Jena people great amusement. I have also fed them with earthworm cutlets. / Some of the Smyrna tortoises [likely: *Testudo graeca ibera* sensu (Türkozan et al., 2023)] have already been processed by the students as victims of science in the summer. This fate awaits the other part of them in the coming winter.”³

In Jena, Haeckel and his colleague Carl Gegenbaur (1826–1903) divided their field of study into invertebrate and vertebrate morphology, respectively (Hoßfeld & Olsson, 2003; Maier, 1994). As such, by this agreement (Uschmann, 1959b), Haeckel did not come to develop a great interest in turtles. Gegenbaur, in contrast, used turtles in many of his studies (Wagner, 1997), such as in his original textbooks on vertebrate morphology (Gegenbaur, 1859, 1878, 1898) and monographic treatments, such as on the shoulder girdle of vertebrates – in which turtles played a particular role (Gegenbaur, 1865). On March 16th, 1861 (Bach, 2024), shortly after both Haeckel and Gegenbaur came to Jena as professors of zoology, Gegenbaur wrote: “Dear Häckel [sic]! You will receive the turtle with the request that you kindly take care of it. The

¹ Note that the marine turtles are shown above the more terrestrial ones, suggesting them as “flying”. See also text below: Haeckel considered leatherback-turtles as most ancestral within turtles.

² See for example letters to Haeckel from Johannes Schild, March 20th, 1901, and from Wilhelm Foerster (1856–1908) (zoology preparator in Tübingen), October 29th, 1902 – as well as a letter from Haeckel dated June 29th, 1861, regarding the Berlin collection.

³ Our translation from: „Ihre Chamaeleons leben noch und verursachen den Jenensern großes Ergötzen. Ich habe sie auch mit Regenwurm-Coteletten gefüttert. / Die Schildkröten von Smyrna sind zum Theil bereits als Opfer der Wissenschaft im Sommer von den Studenten verarbeitet worden. Zum andern Theil steht ihnen dieses Schicksal im kommenden Winter bevor.“ Letter to the archaeologist, ingenieur, and architect Carl Humann (1839–1896), who lived in Smyrna (today Izmir) and has apparently sent living animals to Jena.

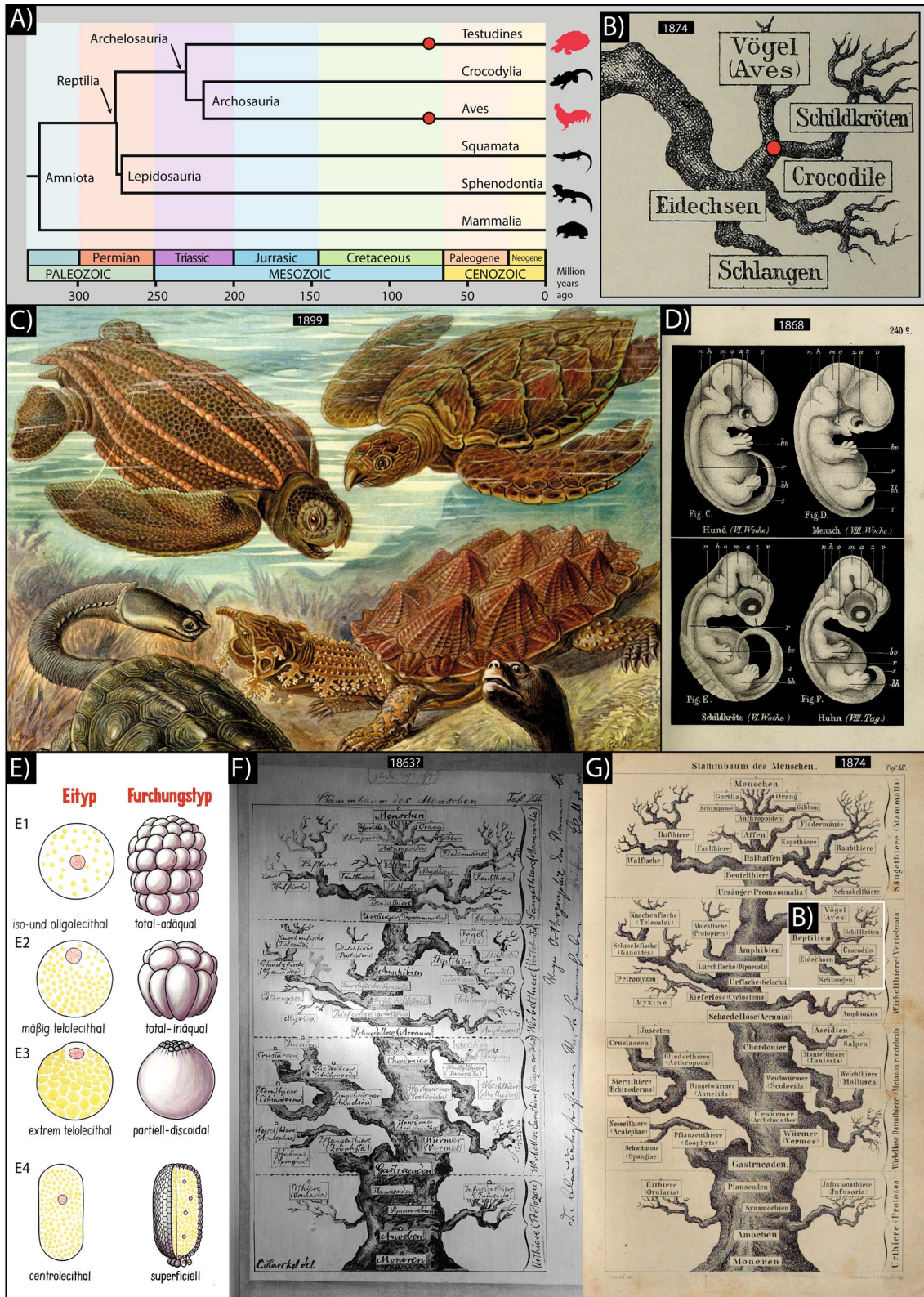


Fig. 1 (See legend on previous page.)

bellows are prepared with arsenic soap. As with *Emys*, the eyes are small and have a light brown iris.”⁴

In addition to his responsibility as a director of a scientific collection and to the aesthetic value of turtles (Haeckel, 1899), Haeckel emphasized these animals for his general and holistic research agenda to understand the morphology of organisms from an evolutionary point of view (Levit & Hoßfeld, 2019; Levit et al., 2014). Much of this understanding might have emerged from discussions with the vertebrate morphologist Carl Gegenbaur in Jena, who was rather reserved regarding phylogenetic hypotheses in his own writings (Gegenbaur, 1859, 1878; for further details, see Hoßfeld & Olsson, 2003; Maier, 1994; Rieppel, 2011).

Turtles as closest relatives of birds (1866 to 1868)

Along with Gaudry (1866) (Laurin, 2023; Tassy, 2006, 2011), Ernst Haeckel produced the first phylogenetic trees of organisms in his *Generelle Morphologie* in 1866 (Fig. 3A, B) (Dayrat, 2003; Haeckel, 1866; Hoßfeld, 2010; Hoßfeld et al., 2016, 2017). When doing so, he integrated an enormous amount of anatomical knowledge that was already present in the mid-nineteenth century (Hoßfeld et al., 2022a, 2022b; Werneburg et al., 2022a, 2022b; Zeller & Werneburg, 2024a, 2024b, 2024c). In the absence of analytical–numerical tools, such as phylogenetic systematics and cladistics (Hennig, 1950; Willmann, 2003), he attempted to sort organisms by morphological similarity, which was typical for this time. However, in the context of his Darwinian and monistic thinking, “Haeckel’s phylogeny was a linear series of main morphological stages along the line of descent of a given species” (Dayrat, 2003: p. 515). He arranged the

branches of his trees according to his conception of a trifold parallelism of embryology, paleontology, and comparative anatomy (Hoßfeld et al., 2021; Levit & Hoßfeld, 2019; Werneburg et al., 2022a, 2022b, 2022c).

Haeckel (1866, Vol. II, p. CXXXIII) grouped non-mammalian amniotes (his ‘Monocondylar’; Fig. 3A, B) into five ‘classes’ using his idiosyncratic nomenclature: ‘Tecosaurier’ (only extinct, stem-reptiles), ‘Hydrosaurier’ (including crocodiles), ‘Pachypoda’ (dinosaurs), Lepidosauria (tuatara, lizards, snakes), and ‘Rhamphosauria’ (animals with a beak). Among the latter, he recognized four groups with a stepwise reduction of teeth: Pterosauria (flying reptiles), ‘Anomodontia’, Chelonia (i.e., Testudinata; turtles), and Aves (birds). According to Haeckel (1866, Vol. II, p. CXXXVIII), the pterosaurs, which still had teeth, were likely an early offshoot from the ancestral tecosaurs (Fig. 3A). ‘Anomodontia’, which translates from Greek as animals with “teeth opposing the rule”, are mainly considered stem-mammals today (i.e., early Synapsida) (Angielczyk, 2009). They increasingly lost their teeth culminating in the so-called ‘Cryptodontia’ (‘hidden teeth animals’). Among those, the rhynchosaurs (i.e., *Rhynchosaurus articeps* OWEN 1842, from England), which are considered early archosauromorphs today, were placed as the closest relatives of turtles and birds.

Because fossil evidence was scarce at the time (Werneburg et al., 2022a, 2022b, 2022c), Haeckel (1866) acknowledged the preliminary nature of his phylogenies and highlighted that they were ‘fluent working hypotheses’ instead of ‘perfect cladograms’ in the current understanding. In the summarizing subfigure of his vertebrate tree⁵ (Haeckel, 1866: plate VII; our Fig. 3B), Haeckel showed birds more “distant” from lepidosaurs

(See figure on next page.)

Fig. 2 Turtle + bird (both always highlighted in a red rectangle) and other vertebrates in the famous embryonic plates published by Haeckel. **A** Plate IV (left) and V (right) of *Anthropogenie* (Haeckel, 1874) [note: here are reproduced the unchanged plates, as Plate VI and VII, of the 3rd edition (Haeckel, 1877), because a better scan was available]. **B** Detail of A, showing the oldest turtle and chicken embryos [here reproduced from the version of the 1st edition, (Haeckel, 1874)]. **C** Plates VI to IX (from left to right) of the 4th edition of *Anthropogenie* (Haeckel, 1891) with nine more species included. Fish and salamander (see A) are no longer listed. The European pond turtle (*Emys orbicularis*) is replaced by a marine turtle [“*Chelone*”, likely *Chelonia* (“*viridis*”) *mydas*, (Parker, 1880)]. In addition to the chicken, the ostrich (*Struthio camelus*) is added as a second bird species. Below the embryonic columns, “(1874)” is added by us when the images already appeared in the first edition (**A–B**) of the book. **D** The plates shown in C were reproduced – as plates VIII, IX, XII, and XIII – in the 5th edition of *Anthropogenie* (Haeckel, 1903). Between them, the here shown plates X (left) and XI (right) were added based on new publications in embryology (e.g., Dendy, 1899; Keibel, 1897; Semon, 1897). Herein, also a soft-shelled turtle (“*Trionyx*”, likely *Apalone spinifera*) and the flightless bird kiwi (*Apteryx*) were added. **E** Also published in the 5th edition of *Anthropogenie* (Haeckel, 1903), early developmental, i.e. post-cleavage (see Fig. 1D) “Sandalion”-stages, were added, which highlight the greater similarity of the turtle to a lizard (*Lacerta*) than of both reptiles to a bird (chicken)

⁴ Our translation from: „Beifolgend empfangen Sie die Schildkröte mit der Bitte, für deren Fortkommen gütigst Sorge tragen zu wollen. Der Balg ist mit Arsenikseife präpariert. Die Augen sind, wie bei *Emys*, klein und besitzen eine hellbraune Iris.“

⁵ Full title inside the tree figure: „Stammbaum der Wirbeltiere palaeontologisch begründet, entworfen und gezeichnet von Ernst Haeckel, Jena, 1866“; translated by us as: „Phylogenetic tree of vertebrates based on palaeontology, designed and drawn by Ernst Haeckel, Jena, 1866“



Fig. 2 (See legend on previous page.)

(See figure on next page.)

Fig. 3 Reptiles in Haeckel's trees of life 1/2. **A-B** Section with amniotes taken from the vertebrate tree of *Generelle Morphologie*, Haeckel (1866: plate VI). B shows a simplified version of the tree in A, note the different branch splitting and the position of "Rhamphosauria" (i.e., *Ramphorhynchus*?) in B, see text for details. **C** Reptile and bird section of the vertebrate tree from the 1st edition of *Natürliche Schöpfungsgeschichte*, Haeckel (1868), plate VI). Numerations: 40: Proreptilia, 52: Cynodontia, 53: Cryptodontia, 54: Rhamphorhynchii, 55: Pterodactyli, 56: turtles, 57: Tocornithes, 58: intermedial form between reptiles and birds. Note the questionmarks for turtle and bird origins (i.e., they are no longer present in D). **D** Reptile and bird section of the vertebrate tree from the 2nd edition of *Natürliche Schöpfungsgeschichte*, Haeckel (1870): plate XII [here a better scan of the same, unchanged tree from the 3rd edition (Haeckel, 1872) is reproduced]. Numerations 38: Proamnians (common stem form of all amniotes) 39: Promammalia, 40: Proreptilia, 41: Thecodonta, 45: teleosaurians (Amphicoela), 46: steneosaurians (Opisthocoela), 47: aligatorids (Prostocoela), 48: carnivore dinosaurs (Harpagosauria), 49: herbivore dinosaurs (Thecosauria), 50: Mosasauria, 51: Ophidia (stem-snakes), 52: Cynodontia, 53: Cryptodontia, 54: Rhamphorhynchii, 55: Pterodactyli, 56: turtles, 57: Tocornithes, 58: intermedial form between reptiles and birds. **E** "Phylogenetic tree of the sauropsids (reptiles and birds)" from the 7th edition of *Natürliche Schöpfungsgeschichte* (Haeckel, 1879). Birds originate from dinosaurs and turtles are sister to crocodiles. Note the anomalous relation to mammals and the position of Rhynchocephalia (tuatara-group) basal to "Pelycosauria". Turtles and birds are highlighted in all subfigures

(tuatara, lizards, and snakes) and grouped turtles with "Anomodontia"⁶. As with phylogenetic trees in general, the labeling of branches was also "fluent" in Haeckel's publications with larger taxon names appearing between various branches in the drawings. As far as we can tell, Haeckel did not outline any methodology for this approach but rather expressed uncertainties.

A close relationship of turtles and birds is hypothesized in the famous tree on man (and other extant taxa) published by Haeckel (1874) in *Anthropogenie* (Fig. 1B, G). He never changed the branch arrangements of this figure in the later editions of this book (Haeckel, 1910a), which were, of course, mainly focusing on general and global human origins as the "crown of evolution" and did not urgently require revisions of the interrelationship within a side-branch such as that of reptiles. It will be shown below that Haeckel changed his opinion about turtle origins already before 1874, but, certainly, the respective tree was already drafted (Fig. 1F) years before, maybe already in 1863, inspired by a tree of the Indo-European languages from the same year (Schleicher, 1863).

The list of taxa with reduced dentition illustrates that Haeckel (1866) considered the stepwise reduction of teeth ('cryptodontology') and the associated formation of keratinized beaks ('rhamphodontology') to be the most important characteristics to establish the classification of many land vertebrates (i.e., noteworthy without the beaked mammalian monotreme, the platypus). He also stated that other characters would unite them without going into detail. For a potential association of turtles and birds, Haeckel only mentioned some footprint trace fossils of both groups that had been found in Triassic sandstone, but he admitted that these were quite "uncertain" findings.

⁶ "Rhamphosauria" now appeared as the sister group to turtles (Chelonia), but "Rhamphosauria" might be a misspelling for *Rhynchosaurus*, which was sister of turtles + birds in his written argumentation. It is unlikely that he meant the pterosaur *Ramphorhynchus*, which was erected in 1846, because the clade Pterosauria is shown as a separate branch.

Haeckel (1866) stated that, although fossil evidence was missing, embryological data would clearly prove that birds are derived from reptiles. The original discovery on the shared meroblastic cleavage mode (Fig. 1E3) had been provided by his friend Gegenbaur (1861). In a letter dated October 28th (Bach, 2024), Gegenbaur who wrote to Haeckel, 1860: "I am happy to do without snakes and lizards, the eggs of a turtle have completely confirmed what I found for birds and selachians [i.e., sharks and allies; see Werneburg et al., (2024a, 2024b)], and I now want to finish the work."⁷

In his book *Natürliche Schöpfungsgeschichte*, Haeckel (1868) summarized (p. 457): "The class of birds (Aves) is, as already noted, so closely related to the reptiles by its internal structure and embryonic development that it undoubtedly took its true origin from a branch of this class. As you can see on figure C-F, p. 242 [reproduced in our Fig. 1C], the embryos of birds can hardly be distinguished from those of turtles and other reptiles [note: he did not show other reptiles] at a time when they already appear very different from the embryos of mammals [see also our Fig. 2], as yolk furrowing is partial in birds and reptiles [see our Fig. 1E3], but not in mammals [see our Fig. 1E1]."⁸ As a side note, Haeckel always insisted in adding this important figure to the book, as documented in a letter to his publisher Georg Reimer (1804–1885), dated March 26th, 1868 (Bach, 2024).

⁷ Our translation from: „Auf Schlangen und Eidechsen verzichte ich gerne, die Eier einer Schildkröte haben das was ich für Vögel u. Selachier fand völlig bestätigt, u[nd] ich will nun die Arbeit abschliessen.“

⁸ Our translation from: „Die Klasse der Vögel (Aves) ist, wie schon bemerkt, durch ihren inneren Bau und durch ihre embryonale Entwicklung den Reptilien so nahe verwandt, daß sie zweifelsohne aus einem Zweige dieser Klasse ihren wirklichen Ursprung genommen hat. Wie Ihnen allein schon ein Blick auf Fig. C-F, S. 242 zeigt, sind die Embryonen der Vögel zu einer Zeit, in der sie bereits sehr wesentlich von den Embryonen der Säugethiere verschieden erscheinen, von denen der Schildkröten und anderer Reptilien noch kaum zu unterscheiden. Die Dotterfurchung ist bei den Vögeln und Reptilien partiell, bei den Säugethieren dagegen nicht.“

purposely drew the marine turtles—which he considered ancestral (see below)—above the other turtles as “flying animals”, like birds, just underwater (Fig. 1C)?⁹ It is noteworthy that Haeckel did not consider ecological factors (Watts et al., 2019) that may have influenced parallel morphological adaptations through evolution. His focus was exclusively on the structural homogeneity in the sense of his evolutionary ‘triad of systematics, embryology, and paleontology’ (Haeckel, 1864; Werneburg et al., 2022a, 2022b, 2022c), which prevented a comprehensive discussion on the parallel evolution of form-function complexes (Bock & Wahlert, 1965). In particular, he was very careful about declaring convergences in evolution (Bernroider, 1999; Dayrat, 2003; Levit & Hoßfeld, 2019). This is because, as a morphologist, he was well aware of the minute, highly specific anatomical differences among taxa.

The stiffening of a bird’s body is related, among others, to the strong forces experienced during flight. Although birds have great neck mobility, they cannot retract their necks inside the body as turtles do. Additionally, birds have large eyes for distance vision and voluminous brains, partly for sensory processing, resulting in compact and highly modified brain cases in their skulls. Concerning beaks, it has been demonstrated that the keratinous anlagen of rhamphothecae are ancestral to all land vertebrates (Louchart & Viriot, 2011), including amniotes, and have often evolved in parallel. Therefore, a tetrapod taxonomy using this characteristic no longer seems optimal.

Birds and turtles are separated (1870 to 1879/89)

It must be highlighted that Haeckel was always aware of current developments in phylogenetics as is suggested, for example, by his comprehensive correspondence with Charles Darwin and other leading biologists (Darwin Correspondence Project, 2022; Uschmann, 1984; Bach, 2024), and by all the literature discussed in his books. In the first edition of *Natürliche Schöpfungsgeschichte*, Haeckel (1868: 458) briefly mentioned Huxley’s hypothesis on a dinosaur origin of birds: “Huxley places [the theropod *Compsognathus*] with the dinosaurs, and believes that these are the closest relatives of the tocornithes [i.e., the progenitors of birds]”.¹⁰ In the phylogeny that he published in this book, Haeckel (1868) stayed with his original hypothesis of turtle-bird-relationship (see Fig. 1B–G), but added question marks to both taxa

(Fig. 3C; No. 56 and 57/58) to highlight the uncertainty of their phylogenetic positions.

In the 2nd edition of the book, Haeckel (1870) modified this tree illustration and placed turtles closer to crocodiles (his plate XII; our Fig. 3D). The birds (his No. 58) now belonged to “Tocornithes” (No. 57),¹¹ but were still close to “Cryptodontia” (No. 53) and, subsequently, to Cynodontia (No. 52). All together, they formed the sister group to the carnivorous and herbivorous Dinosauria (No. 48–49).

As arguments for a close bird-to-reptile relationship, he repeated the shared embryonic characters and also mentioned blood cell anatomy, feather development, and jaw bone composition. However, with increasing access to embryonic material of many vertebrate species (Bininda-Emonds et al., 2002, 2003; Keibel, 1897; Werneburg & Sánchez-Villagra, 2009; Werneburg et al., 2016), Haeckel obviously recognized further differences between birds and turtles in embryology. Whereas Haeckel highlighted similarities between birds (chicken) and turtles (European pond turtle) in his earlier works (Haeckel, 1866, 1868; Figs. 1D, 2A, B), he later added more bird (ostrich, kiwi) and turtle (a marine and a soft shell turtle) species to his famous embryo plates to highlight the closer similarity of turtles to other reptiles than to birds (Haeckel, 1891, 1903) (Fig. 2C, D). This also included early developmental, post-cleavage stages [i.e., “sandalion” stages; (Haeckel, 1910b)], in which the differences become obvious (Fig. 2E) (Haeckel, 1903).

Regarding the phylogenetic position of the “noteworthy turtles”, Haeckel (1870, p. 530) was still uncertain and wrote that “[t]hese strange animals first appear in the Jurassic. By some characters, they approach the Amphibia, by others the crocodiles, by particular characters even the birds—as such, their true position in the phylogenetic tree is difficult to define. Most obvious is the incredible similarity that their embryos still share with birds in the later stages of ontogeny (Fig. 1D)”.¹²

In the 7th edition of the *Natürliche Schöpfungsgeschichte*, Haeckel (1879) provided for the first time a very detailed phylogenetic tree of reptiles (p. 549; our Fig. 3E; see also the 8th edition, Haeckel, 1889), in which birds are deeply nested inside Dinosauria, and Pterosauria

⁹ Note that this picture was published after Haeckel reconsidered reptilian phylogeny. In his later works, he clearly separated turtles from birds.

¹⁰ Our translation from: „Huxley stellt diesen letzteren [den theropoden *Compsognathus*] zu den Dinosauriern, und glaubt, daß diese die nächsten Verwandten der Tocornithen [der Stammväter der Vögel] seien“

¹¹ „57. Vogelschleicher (Tocornithes): Zwischenformen zwischen Reptilien und Vögeln“ translates as “57. bird-reptiles—intermedial forms between reptiles and birds”.

¹² Our translation from: „Sie nähern sich durch einige Charaktere den Amphibien, durch andere den Krokodilen, und durch gewisse Eigenthümlichkeiten sogar den Vögeln, so daß ihr wahrer Platz im Stammbaum der Reptilien äußerst schwierig zu bestimmen ist. Höchst auffallend ist die außerordentliche Aehnlichkeit, welche ihre Embry[on]en selbst noch in späteren Stadien der Ontogenesis mit den Vögeln zeigen.“

are the sister taxon to the latter, similar to our current understanding (Weishampel et al., 2004), and turtles are close to crocodiles. The non-avian and non-chelonian “beaked animals” are distributed among the tree as being on the stem line of Pterosauria (‘Rhamphorhynchi’) and, as in current understanding, along the mammalian stem (“Cryptodonta” and Cynodonta [i.e., Anomodontia]). For the latter opinion, Haeckel respectfully referred to the US-American paleontologist Edward Drinker Cope (1840–1897), who filled many gaps in vertebrate paleontology (Kammerer et al., 2014; Kemp, 2005). Regarding the “still uncertain” position of turtles, Haeckel (1879) again referred to the bird-like embryology (always referring to and insisting on his suggestive embryo figure; our Fig. 1D) and considered (p. 550) a phylogenetic position “likely deep down in the root [of reptiles]”¹³ Haeckel did not provide a rationale, in the modern sense, to justify this grouping.

Endless confusions most beautiful (1895 to 1898)

Six years after the 8th edition of *Natürliche Schöpfungsgeschichte* (Haeckel, 1889) (Fig. 3A–C), a very detailed treatment of vertebrate phylogeny was provided in *Systematische Phylogenie*, volume 3 (Haeckel, 1895), which took the latest developments of systematic vertebrate zoology and, in particular, of paleontology into account (see also Hoßfeld et al., 2021; Werneburg et al., 2022a, 2022b, 2022c).

In this book, Haeckel (1895) separated Mammalia from its synapsid ancestors (Fig. 4B, C) and put those (“Theriodontia” and ‘Anomodontia’), together with turtles, into the taxon “Proterosauria” (with “Pareosauria”/“Pareotricha”) (Fig. 4C). Inside “Proterosauria”, turtles were again close to the ‘Anomodontia’-subgroups, though with a question mark added (Fig. 4C). A major criterion to group them was, again, the almost or the complete loss of teeth, but he added the fusion of the vomer (“Zwischenkiefer”), four or five fused sacral vertebrae, and similarities of limb anatomy (pp. 308, 315). Moreover, Haeckel (p. 318) suggested that the leatherback turtles (Dermochelyidae) with their “rudimentary” shell would be ancestral and nicely link to the anomodont condition (p. 317, fig. § 293 on p. 323).¹⁴ The dicynodont *Cistecephalus* would be closest to turtles (p. 316). Although Pterosauria were again closer to Dinosauria, the position of birds in close relation to dinosaurs was no longer questioned, although the exact position was not clear to Haeckel, and he considered – at one point – even a “paraphyly” of birds (see his “§ 328. Stammbaum der Draconen” on p. 373).

A detailed historical evaluation of Haeckel’s considerations on reptilian phylogeny was out of the scope of this article. It should be noted, however, that only three years after *Systematische Phylogenie*, volume 3 (Haeckel, 1895), a largely revised, extended, and now two-volumed 9th edition of *Natürliche Schöpfungsgeschichte* was published (Haeckel, 1898). Therein, Haeckel again made comprehensive rearrangements of the reptilian phylogeny, which might document a certain confusion of the author about this topic. In his figure on p. 621, he divided Amniota into Mammalia, Reptilia, and Aves. In his figure on p. 649 of the same publication (our Fig. 4D), turtles were still together with Anomodontia, but birds were grouped inside Reptilia, outside of Pterosauria and Dinosauria, and both of these taxa, along with Crocodilia, formed the ‘Mesosauria’. In the text, Haeckel acknowledged new discoveries in paleontology by Edward Drinker Cope and Othniel Charles Marsh (1831–1899). The discoveries presented in the course of the famous disputes (“Bone Wars”) between those paleontologists (Jaffe, 2000) might have inspired and forced Haeckel to rethink some relationships in his phylogenetic tree.

To our knowledge, Haeckel did not further discuss turtle origin or anatomy beyond the discussed books. The *Systematische Phylogenie* from 1895 must be understood as Haeckel’s scientific testament, in which he united all the insights on phylogenetic systematics and general morphology that he conceived throughout his career (Hoßfeld, 2010; Richards, 2008). After the turn of the twentieth century, aged 66, Haeckel merely concentrated on the dissemination of his political and religious ideas and did not produce any further primary scientific literature (Hoßfeld, 2010; Hoßfeld & Breidbach, 2005).

Conclusions

The phylogenetic origin of turtles remains controversial until today. Compared to his Jena colleague, Carl Gegenbaur, Ernst Haeckel did not focus much on turtles in his own research, but the uncertain origin of turtles bothered him when creating his trees of life.

Our observations show that Haeckel understood his phylogenies as “fluent working hypotheses”, which experienced many rearrangements throughout his long career. Haeckel witnessed an enormous multiplication of knowledge in biology and particularly in paleontology in the second half of the nineteenth century and tried to integrate most new insights. He copiously cited the primary literature in his books and also acknowledged the uncertainties in phylogeny and the origin of taxa such as turtles and birds.

His works show that he carefully observed great variation in the ontogeny of birds as well as turtles and other reptiles. This was also possible by increased availability

¹³ Our translation from: „Wahrscheinlich liegt er tief unten an der Wurzel.“

¹⁴ Compare to our “footnote 1”.

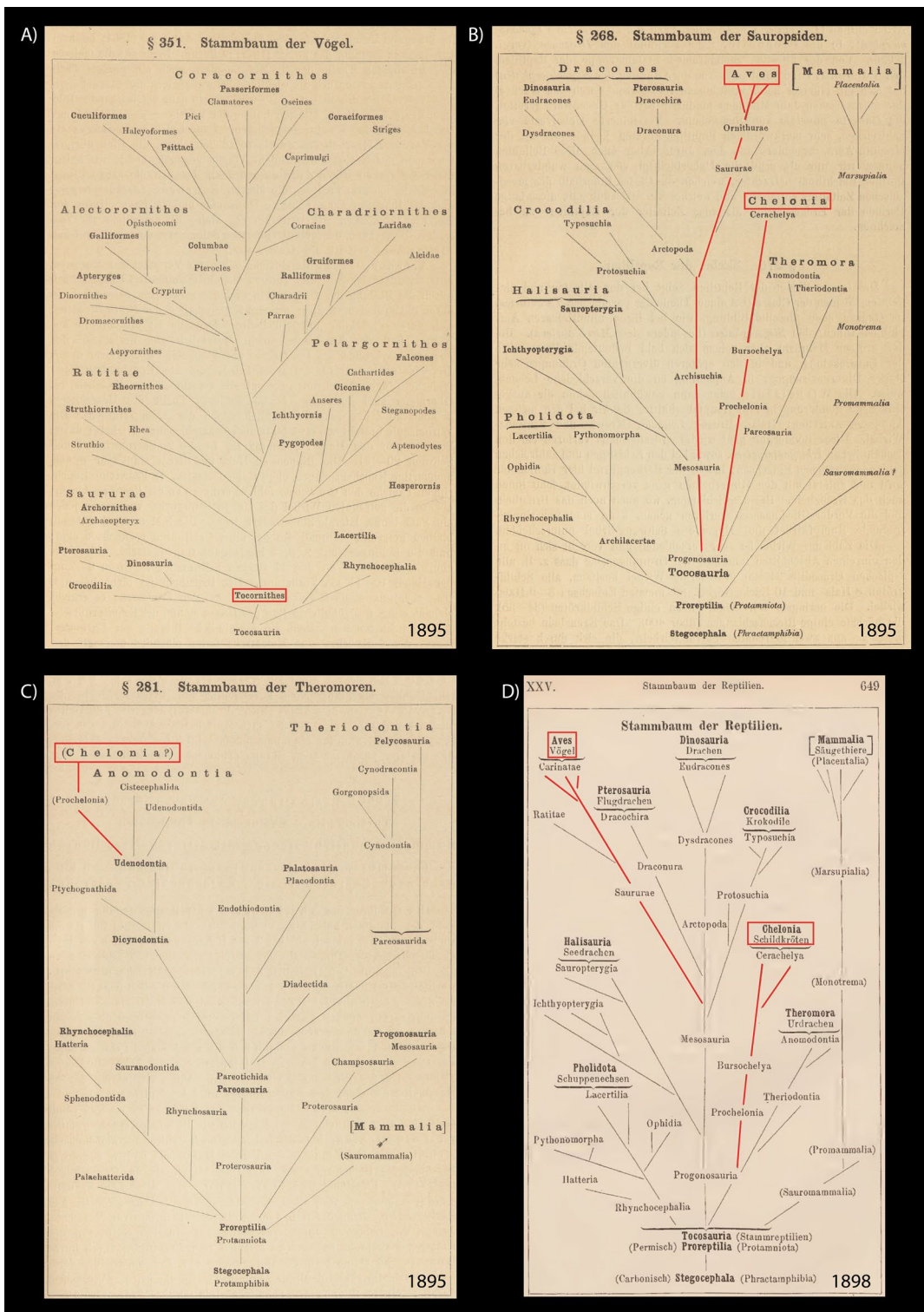


Fig. 4 Reptiles in Haeckel's trees of life 2/2. The phylogenetic trees of birds (A), sauroside (B), and 'theromorphans' (C) as illustrated in the *Systematische Phylogenie* (Haeckel, 1895). Note the question mark on turtle origin in C. D "Phylogenetic tree of reptiles" as illustrated in the 9th edition of *Natürliche Schöpfungsgeschichte* (Haeckel, 1898). Turtle and bird lineages are highlighted

and publications of embryonic material at the end of the nineteenth century. As a scientist, Haeckel behaved correctly and honestly, taking his personal abilities and disabilities into account. In this regard, the almost 30-year old debate on Haeckel's "scientific frauds" in embryology (Pennisi, 1997; but see also Richards, 2008, 2009; Richardson & Keuck, 2002) might be worth reconsidering.

Modern molecular studies suggest that turtles are closely related to extant archosaurs, which include crocodiles and birds, and these three taxa form the clade Archelosauria (Field et al., 2014). The exact point in the evolution of stem archosaurs where turtles emerged is still uncertain. It should be mentioned that several more recent morphological studies grouped turtles with lepidosauromorphs (deBraga & Rieppel, 1997; Hill, 2005) or close to the origin of then diapsid clade (Gauthier et al., 1988; Werneburg & Sánchez-Villagra, 2009). A recent paleontological paper found turtles close to archosaurs (Simões et al., 2022). It is possible that, one day, Haeckel's idea of a rhynchosaur relationship of turtles may be revisited. When considering new fossil finds, phylogenetic analyses will continue to challenge the tree of life.

To maintain objectivity in phylogenetic reconstructions, it is important to include specific morphological observations. Haeckel's neglect of convergent evolutionary traits is a reasonable limitation of his research. Convergences need to be addressed to better understand the complexity of tissue interactions and phylogenetic inferences. This will contribute to improve our understanding of biological forms and highlight the importance of morphology in discussions of evolutionary processes.

In the 7th and 8th edition of *Natürliche Schöpfungsgeschichte*, Haeckel (1879, 1889) was closest to our current understanding of amniote phylogeny. Obviously, this understanding was also influenced by the ideas and discoveries of Edward Drinker Cope. With the new paleontological discoveries through the „Bone Wars“ in the Angloamerican community, triggered by Cope and Marsh, the central European scientist, Haeckel, became inspired and confused about reptilian phylogeny as documented in his *Systematische Phylogenie der Wirbeltiere* (1895) and the 9th edition of *Natürliche Schöpfungsgeschichte* (1898), respectively. With developments in our understanding of amniote phylogeny in recent decades—with the positions of turtles and many fossil land vertebrates being rearranged on the vertebrate tree of life (e.g., Buffa & Laurin, 2024; deBraga & Rieppel, 1997; Ford & Benson, 2020; Gauthier et al., 1988; Laurin & Reisz, 1995; Rieppel, 2008; Wang et al., 2013)—one may more respectfully approach Haeckel's scientific attempts to unite embryology, paleontology, and comparative anatomy in a holistic manner

(Maier & Werneburg, 2014) at the rise of phylogenetic research.

Acknowledgements

We wish to thank the editors for the organization of this special issue based on the Turtle Evolution Symposium held in Fribourg, Switzerland, in 2024. We wish to thank Michael Laurin (Paris), one anonymous reviewer, and the editor, Walter G. Joyce (Fribourg), for useful suggestions to the manuscript. Furthermore, we thank Wolfgang Maier (Tübingen) for discussion.

Author contributions

Conceptualization: IW, UH. Wrote paper: IW. Final evaluation and editing of the manuscript: IW, UH.

Funding

Open Access funding enabled and organized by Projekt DEAL. DFG-grant WE 5440/6–1 to I.W.

Availability of data and materials

No datasets were generated or analyzed during the current study.

Declarations

Ethics approval and consent to participate

Not applicable.

Competing interests

The authors declare no competing interests.

Received: 12 September 2024 Accepted: 6 February 2025

Published online: 27 March 2025

References

- Abel, P., & Werneburg, I. (2021). Morphology of the temporal skull region in tetrapods: research history, functional explanations, and a new comprehensive classification scheme. *Biological Reviews*, 96(5), 2229–2257. <https://doi.org/10.1111/brv.12751>
- Angielczyk, K. D. (2009). *Dimetrodon* is not a dinosaur: using tree thinking to understand the ancient relatives of mammals and their evolution. *Evolution Education and Outreach*. <https://doi.org/10.1007/s12052-009-0117-4>
- Bach, T. (2024, ed.). Ernst Haeckel (1834–1919): Briefedition. <https://haeckel-briefwechsel-projekt.uni-jena.de> (Last Accessed: 22 08 2024).
- Bernroider, G. (1999). On Form, Mind and Matter (with special reference to *Crystal Souls* by Ernst Haeckel, translated by A Mackay). *Journal for the Science*, 185, 198.
- Bininda-Emonds, O. R. P., Jeffery, J. E., Coates, M. I., & Richardson, M. K. (2002). From Haeckel to event-pairing: The evolution of developmental sequences. *Theory in Biosciences*, 121, 297–320.
- Bininda-Emonds, O. R. P., Jeffery, J. E., & Richardson, M. K. (2003). Is sequence heterochrony an important evolutionary mechanism in mammals? *Journal of Mammalian Evolution*, 10(4), 335–361.
- Bock, W. J., & Wählert, G. V. (1965). Adaptation and the form-function complex. *Evolution*, 19(3), 269–299. <https://doi.org/10.1111/j.1558-5646.1965.tb01720.x>
- Buffa, V., & Laurin, M. (2024). Paleozoic Origin of Major Reptile Groups. In J. Ulrich (Ed.), *Volume 1 General Biology, Archosauria, Chelonia* (pp. 75–86). Berlin: De Gruyter.
- Darwin Correspondence Project (2022). <https://www.darwinproject.ac.uk/>. University of Cambridge [Accessed: 27 08 2024]
- Dayrat, B. (2003). The roots of phylogeny: How did Haeckel build his trees? *Systematic Biology*, 52(4), 515–527. <https://doi.org/10.1080/10635150390218277>
- deBraga, M., & Rieppel, O. (1997). Reptile phylogeny and the interrelationships of turtles. *Zoological Journal of the Linnean Society*, 120, 281–354.

- Dendy, A. (1899). Outlines of the development of the tuatara *Sphenodon (Hatteria) punctatus*. *Quarterly Journal of Microscopical Science*. <https://doi.org/10.1242/jcs.s2-42.165.1>
- Field, D. J., Gauthier, J. A., King, B. L., Pisani, D., Lyson, T. R., & Peterson, K. J. (2014). Toward concision in reptile phylogeny: miRNAs support an archosaur, not lepidosaur, affinity for turtles. *Evolution & Development*, 16(4), 189–196. <https://doi.org/10.1111/ede.12081>
- Fischer, M. S., Brehm, G., & Hoßfeld, U. (2008). *Das Phyletische Museum in Jena*. Gera: Druckhaus Gera.
- Ford, D. P., & Benson, R. B. (2020). The phylogeny of early amniotes and the affinities of Parareptilia and Varanopidae. *Nature Ecology & Evolution*, 4(1), 57–65. <https://doi.org/10.1038/s41559-019-1047-3>
- Gaudry, A. (1866). *Considérations générales sur les animaux fossiles de Pikermi*. Paris: F. Savy.
- Gauthier, J., Kluge, A. G., & Rowe, T. (1988). Amniote phylogeny and the importance of fossils. *Cladistics*, 4, 105–209.
- Gegenbaur, C. (1878). *Grundriss der vergleichenden Anatomie (2nd edition)*. Leipzig: Engelmann.
- Gegenbaur, C. (1859). *Grundzüge der vergleichenden Anatomie*. Leipzig: Verlag von Wilhelm Engelmann.
- Gegenbaur, C. (1861). Über den Bau und die Entwicklung der Wirbeltiereier mit partieller Dotterteilung. *Reicherts und Dubois-Reymonds Archiv Für Anatomie, Physiologie und Wissenschaftliche Medizin, Gesammelte Abhandlungen*, 2(33), 491–529.
- Gegenbaur, C. (1865). *Untersuchungen zur vergleichenden Anatomie der Wirbeltiere (Heft 2): 1 Schultergürtel der Wirbeltiere / 2 Brustflosse der Fische*. Leipzig: Wilhelm Engelmann.
- Gegenbaur, C. (1898). *Vergleichende Anatomie der Wirbeltiere mit Berücksichtigung der Wirbellosen (Vol. 1)*. Leipzig: Wilhelm Engelmann.
- Gregory, W. K. (1946). Pareiasaurs versus placodonts as near ancestors to the turtles. *Bulletin of the American Museum of Natural History*, 86(6), 277–326.
- Haeckel, E. (1864). Über die Entwicklungstheorie Darwins. (Vortrag auf der 38. Versammlung Deutscher Naturforscher und Ärzte in Stettin am 19.9.1863). - Amtlicher Bericht, Stettin 1863.
- Haeckel, E. (1879). *Natürliche Schöpfungsgeschichte. Siebente, umgearbeitete und vermehrte Auflage (7. ed.)*. Berlin: Georg Reimer. <http://www.zum.de/stueber/haeckel/naturliche/naturliche.html>
- Haeckel, E. (1889). *Natürliche Schöpfungsgeschichte. Achte, umgearbeitete und vermehrte Auflage (8. ed.)*. Berlin: Georg Reimer. <http://www.zum.de/stueber/haeckel/naturliche/naturliche.html>
- Haeckel, E. (1898). *Natürliche Schöpfungsgeschichte. Neunte umgearbeitete und vermehrte Auflage (2 volumes) (9. ed.)*. Berlin: Georg Reimer. <http://www.zum.de/stueber/haeckel/naturliche/naturliche.html>
- Haeckel, E. (1866). *Generelle Morphologie der Organismen*. Berlin: Georg Reimer.
- Haeckel, E. (1868). *Natürliche Schöpfungsgeschichte (1st ed.)*. Berlin: Georg Reimer.
- Haeckel, E. (1870). *Natürliche Schöpfungsgeschichte. Zweite, verbesserte und vermehrte Auflage (2nd ed.)*. Berlin: Georg Reimer.
- Haeckel, E. (1872). *Natürliche Schöpfungsgeschichte. Dritte, verbesserte Auflage (2nd ed.)*. Berlin: Georg Reimer.
- Haeckel, E. (1874). *Anthropogenie oder Entwicklungsgeschichte des Menschen. Gemeinverständliche wissenschaftliche Vorträge über die Grundzüge der menschlichen Keimes- und Stammes-Geschichte*. W. Engelmann: Leipzig.
- Haeckel, E. (1877). *Anthropogenie oder Entwicklungsgeschichte des Menschen (3rd ed.)*. Leipzig: W. Engelmann.
- Haeckel, E. (1891). *Anthropogenie oder Entwicklungsgeschichte des Menschen*. Leipzig: W. Engelmann.
- Haeckel, E. (1895). *Systematische Phylogenie Entwurf eines Natürlichen Systems der Organismen auf Grund ihrer Stammesgeschichte Dritter Teil: Systematische Phylogenie der Wirbeltiere (Vertebrata)*. Berlin: Verlag von Georg Reimer.
- Haeckel, E. (1899). *Kunstformen der Natur*. Berlin: Verlag des Bibliographisches Instituts.
- Haeckel, E. (1903). *Anthropogenie oder Entwicklungsgeschichte des Menschen (5th ed.)*. Leipzig: W. Engelmann.
- Haeckel, E. (1910a). *Anthropogenie oder Entwicklungsgeschichte des Menschen*. Leipzig: W. Engelmann.
- Haeckel, E. (1910b). *Sandalion. Eine offene Antwort auf die Fälschungs-Anklagen der Jesuiten*. Frankfurt am Main: Neuer Frankfurter Verlag.
- Hennig, W. (1950). *Grundzüge einer Theorie der phylogenetischen Systematik*. Berlin: Deutscher Zentralverlag.
- Hill, R. V. (2005). Integration of morphological data sets for phylogenetic analysis of Amniota: The importance of integumentary characters and increased taxonomic sampling. *Systematic Biology*, 54(4), 530–547.
- Hoßfeld, U. (2010). *Ernst Haeckel*. Freiburg im Breisgau: orange press.
- Hoßfeld, U., & Breidbach, O. (2005). *Ernst Haeckels Politisierung der Biologie*. Erfurt: Druckerei Sömmerda GmbH.
- Hoßfeld, U., Fröber, R., Fischer, M. S., Levit, G. S., Thieme, T., & Matveeva, M. (2022a). *Vorlesungen über Menschliche Anatomie von Carl Gegenbaur. Die Vorlesungsmitschrift von Nikolai Nikolajewitsch Miklucho-Maclay aus dem Wintersemester 1865/66*. Arnstadt: THK-Verlag.
- Hoßfeld, U., & Levit, G. S. (2016). "Tree of life" took root 150 years ago. *Nature*, 540(7631), 38.
- Hoßfeld, U., Levit, G. S., Fischer, M. S., Blankenburg, A., Thieme, T., Puchert, G., & Matveeva, M. (2022b). *Vorlesungen über Zoologie von Ernst Haeckel Die Vorlesungsmitschrift von Nikolai Nikolajewitsch Miklucho-Maclay aus dem Wintersemester 1865/66*. Arnstadt: THK-Verlag.
- Hoßfeld, U., & Olsson, L. (2003). The history of comparative anatomy in Jena - an overview. *Theory in Bioscience*, 122, 109–126.
- Hoßfeld, U., Pittelkow, J., & Levit, G. (2021). Paläontologie bei Ernst Haeckel. In D. Gurka (Ed.), *Time in the "third kingdom of nature": Prehistory of palaeontology and palaeoanthropology and its philosophical contexts*. Budapest: Gondolat Publishers.
- Hoßfeld, U., Watts, E., & Levit, G. S. (2017). The first darwinian phylogenetic tree of plants. *Trends in Plant Science*, 22(2), 99–102. <https://doi.org/10.1016/j.tplants.2016.12.002>
- Jaffe, M. (2000). *The gilded dinosaur: the fossil war between E. D. cope and O. C. marsh and the rise of american science*. New York: Crown Publishing Group.
- Kammerer, C. F., Angielczyk, K. D., & Fröbisch, J. (2014). *Early Evolutionary History of the Synapsida*. Heidelberg: Springer.
- Keibel, F. (1897). *Studien zur Entwicklungsgeschichte der Wirbeltiere*. Jena: Gustav Fischer.
- Kemp, T. S. (2005). *The Origin and Evolution of Mammals*. Cambridge: University Press.
- Knorre, D. v. (1983). *Die zoologisch-paläontologischen Sammlungen des Phyletischen Museums*. Jena: Friedrich-Schiller-Universität.
- Krahl, A., & Werneburg, I. (2023). Deep-time invention and hydrodynamic convergences through amniote flipper evolution. *Anatomical Record-Advances in Integrative Anatomy and Evolutionary Biology*, 306(6), 1323–1355. <https://doi.org/10.1002/ar.25119>
- Laurin, M. (2023). *The Advent of PhyloCode: The Continuing Evolution of Biological Nomenclature*. Boca Raton: CRC Press.
- Laurin, M., & Reisz, R. R. (1995). A reevaluation of early amniote phylogeny. *Zoological Journal of the Linnean Society*, 113(2), 165–223.
- Levit, G. S., & Hoßfeld, U. (2019). Ernst Haeckel in the history of biology. *Current Biology*, 29, R1276–R1284.
- Levit, G. S., Hoßfeld, U., & Olsson, L. (2014). The Darwinian revolution in Germany: from evolutionary morphology to the modern synthesis. *Endeavour*, 38(3–4), 268–279. <https://doi.org/10.1016/j.endeavour.2014.10.010>
- Louchart, A., & Viriot, L. (2011). From snout to beak: The loss of teeth in birds. *Trends in Ecology & Evolution*, 26(12), 663–673. <https://doi.org/10.1016/j.tree.2011.09.004>
- Maier, W. (1994). Wirbeltiermorphologie im 19. Jahrhundert; erläutert an den Schriften von Carl Gegenbaur (1826–1903). In W. F. Gutmann, D. Mollenhauer, & D. Peters (Eds.), *Morphologie und Evolution - Symposien zum 175jährigen Jubiläum der Senckenbergischen Naturforschenden Gesellschaft* (pp. 41–53). Frankfurt am Main: Verlag Waldemar Kramer.
- Maier, W., & Werneburg, I. (2014). Einführung: Zur Methodik der organismischen Evolutionsbiologie. In W. Maier & I. Werneburg (Eds.), *Schlüsselergebnisse der organismischen Makroevolution* (pp. 11–17). Zürich: Scidinge Hall Verlag.
- Müller, J. (2003). Early loss and multiple return of the lower temporal arcade in diapsid reptiles. *Naturwissenschaften*, 90(10), 473–476. <https://doi.org/10.1007/s00114-003-0461-0>
- Parker, W. K. (1880). *Report on the development of the green turtle (Chelone viridis, Schneid.)*. London: Longmans.
- Pennisi, E. (1997). Haeckel's embryos: fraud rediscovered. *Science*, 277, 1435.

- Rathke, H. (1848). *Ueber die Entwicklung der Schildkröten*. Braunschweig: Druck und Verlag von Friedrich Vieweg und Sohn.
- Richards, R. J. (2008). *The Tragic Sense of Life. Ernst Haeckel and the Struggle over Evolutionary Thought*. Chicago: The University of Chicago Press.
- Richards, R. J. (2009). Haeckel's embryos: fraud not proven. *Biology and Philosophy*, 24, 147–154.
- Richardson, M. K., & Keuck, G. (2002). Haeckel's ABC of evolution and development. *Biological Reviews*, 77, 495–528.
- Rieppel, O. (2004). Kontroversen innerhalb der Tetrapoda - die Stellung der Schildkröten (Testudines). *Sitzungsberichte der Gesellschaft Naturforschender Freunde Zu Berlin*, 43, 201–221.
- Rieppel, O. (2008). The relationships of turtles within amniotes. In J. Wyneken, M. H. Godfrey, & V. Bels (Eds.), *Biology of Turtles* (pp. 345–353). Boca Raton: CRC Press.
- Rieppel, O. (2011). The Gegenbaur transformation: a paradigm change in comparative biology. *Systematics and Biodiversity*, 9(3), 177–190. <https://doi.org/10.1080/14772000.2011.602754>
- Schleicher, A. (1863). *Die Darwinsche Theorie und die Sprachwissenschaft*. Vienna: Böhlau.
- Schoch, R. R., & Sues, H.-D. (2015). A Middle Triassic stem-turtle and the evolution of the turtle body plan. *Nature*, 523(7562), 584–587.
- Semon, R. (1897). *Morphologie verschiedener Wirbeltiere (Text)*. Jena: Gustav Fischer.
- Simões, T. R., Kammerer, C. F., Caldwell, M. W., & Pierce, S. E. (2022). Successive climate crises in the deep past drove the early evolution and radiation of reptiles. *Science Advances*, 8(33), 1898. <https://doi.org/10.1126/sciadv.abq1898>
- Tassy, P. (2006). Albert Gaudry et l'émergence de la paléontologie darwinienne au xix^e siècle. *Annales De Paleontologie*, 92(1), 41–70. <https://doi.org/10.1016/j.annpal.2005.09.003>
- Tassy, P. (2011). Trees before and after Darwin. *Journal of Zoological Systematics and Evolutionary Research*, 49(2), 89–101. <https://doi.org/10.1111/j.1439-0469.2010.00585.x>
- Türkdoğan, O., Javanbakht, H., Mazanaeva, L., Meiri, S., Kornilev, Y., Tzoraz, E., Popgeorgiev, G., Shanas, U., & Escoriza, D. (2023). *Testudo graeca* Linnaeus 1758 (Eastern Subspecies Clades: *Testudo g. armeniaca*, *Testudo g. buxtoni*, *Testudo g. iberica*, *Testudo g. terrestris*, *Testudo g. zarudnyi*) – Armenian Tortoise Zagros Tortoise Anatolian Tortoise Levantine Tortoise Kerman Tortoise. *Chelonian Research Monographs*. <https://doi.org/10.3854/crm.5.120.eastern.graeca.v1.2023>
- Uschmann, G. (1959a). *Das Phyletische Museum*. Jena: Gustav Fischer Verlag.
- Uschmann, G. (1959b). *Uschmann: Geschichte der Zoologie und der zoologischen Anstalten in Jena 1779–1919*. Jena: Verlag von Gustav Fischer.
- Uschmann, G. (1984). *Ernst Haeckel Biographie in Briefen (zusammengestellt und erläutert von Georg Uschmann)*. Jena: Prisma Verlag.
- Wagner, G. (1997). Carl Gegenbaur (1826–1903) - Anatom, Zoologe, Begründer einer Schule der Vergleichenden Anatomie. *Medizinische Ausbildung*, 14(1), 65–81.
- Wang, Z., Pascual-Anaya, J., Zadissa, A., Li, W., Niimura, Y., Huang, Z., Li, C., White, S., Xiong, Z., Fang, D., Wang, B., Ming, Y., Chen, Y., Zheng, Y., Kuraku, S., Pignatelli, M., Herrero, J., Beal, K., Nozawa, M., & Irie, N. (2013). The draft genomes of soft-shell turtle and green sea turtle yield insights into the development and evolution of the turtle-specific body plan. *Nature Genetics*. <https://doi.org/10.1038/ng.2615>
- Watts, E., Hoßfeld, U., & Levit, G. S. (2019). Ecology and evolution: Haeckel's Darwinian Paradigm. *Trends in Ecology & Evolution*, 34(8), 681–683. <https://doi.org/10.1016/j.tree.2019.04.003>
- Weishampel, D. B., Dodson, P., & Osmolska, H. (2004). *The Dinosauria*. Berkeley: University of California Press.
- Werneburg, I. (2025, in press). Biomechanische Grundlagen der Schläfenevolution bei Landwirbeltieren. *Jahreshefte der Gesellschaft für Naturkunde in Württemberg*, 181.
- Werneburg, I. (2024). Terrestrialisation and the cranial architecture of tetrapods. *Fossil Record*, 27(3), 473.
- Werneburg, I., Hoßfeld, U., & Levit, G. S. (2022a). Discovery of rare lecture notes from 1866 provides exceptional insights into the conceptualization and visualization of paleontology by Ernst Haeckel. *Vertebrate Zoology*, 72, 577–597. <https://doi.org/10.3897/vz.72.e84983>
- Werneburg, I., Hoßfeld, U., & Levit, G. (2024a). Darwin, Haeckel, and the »Mikluskan gas organ theory«. *Developmental Dynamics*, 253(4), 370–389. <https://doi.org/10.1002/dvdy.661>
- Werneburg, I., Hoßfeld, U., Rehm, C. U., & Levit, G. S. (2022b). *Vorlesung über Paleontologie von Ernst Haeckel Die Vorlesungsmitschrift von Nikolai Nikolajewitsch Miklucho-Maclay aus dem Sommersemester 1866*. Tübingen: Scidinge Hall Verlag.
- Werneburg, I., Hoßfeld, U., Rehm, C. U., & Levit, G. S. (2022c). Vorlesungen und Konzeptionen zur Paläontologie bei Ernst Haeckel. In I. Werneburg, U. Hoßfeld, C. U. Rehm, & G. S. Levit (Eds.), *Vorlesung über Paleontologie von Ernst Haeckel Die Vorlesungsmitschrift von Nikolai Nikolajewitsch Miklucho-Maclay aus dem Sommersemester 1866* (pp. 6–36). Tübingen: Scidinge Hall Verlag.
- Werneburg, I., Krahl, A., & Zhang, Z. (2024b). Chelonia: Morphology of a Stiffened Body. In U. Joger (Ed.), *Reptilia General Biology, Archosauria* (pp. 201–233). Berlin: Walter de Gruyter GmbH.
- Werneburg, I., Laurin, M., Koyabu, D., & Sánchez-Villagra, M. (2016). Evolution of organogenesis and the origin of altriciality in mammals. *Evolution and Development*, 18, 229–244. <https://doi.org/10.1111/ede.12194>
- Werneburg, I., & Preuschoft, H. (2024). Evolution of the temporal skull openings in land vertebrates: A hypothetical framework on the basis of biomechanics. *Anatomical Record-Advances in Integrative Anatomy and Evolutionary Biology*, 307(4), 1559–1593. <https://doi.org/10.1002/ar.25371>
- Werneburg, I., & Sánchez-Villagra, M. R. (2009). Timing of organogenesis support basal position of turtles in the amniote tree of life. *BMC Evolutionary Biology*. <https://doi.org/10.1186/1471-2148-9-82>
- Werneburg, I., Wilson, L. A. B., Parr, W. C. H., & Joyce, W. G. (2015). Evolution of neck vertebral shape and neck retraction at the transition to modern turtles: An integrated geometric morphometric approach. *Systematic Biology*, 64(2), 187–204.
- Willmann, R. (2003). From Haeckel to Hennig: the early development of phylogenetics in German-speaking Europe. *Cladistics*, 19, 449–479.
- Zeller, U., & Werneburg, I. (2024a). Ein Leben für Forschung und Ideal: Johannes Müller im Spannungsfeld zwischen empirischer Universalität und idealistischem Vitalismus Einführung. In U. Zeller & I. Werneburg (Eds.), *Vorlesung über Vergleichende Anatomie von Johannes Müller - Die Vorlesungsmitschrift von Ernst Zeller aus dem Sommersemester 1851* (pp. 6–48). Tübingen: Scidinge Hall Verlag.
- Zeller, U., & Werneburg, I. (2024b). A life dedicated to research and ideal: Johannes Müller between empirical universality and idealistic vitalism mirrored in lecture notes from 1851. *Theory in Biosciences*, 143, 161–182.
- Zeller, U., & Werneburg, I. (2024c). *Vorlesung über Vergleichende Anatomie von Johannes Müller - Die Vorlesungsmitschrift von Ernst Zeller aus dem Sommersemester 1851*. Tübingen: Scidinge Hall Verlag.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.