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Discovery of rare lecture notes from 1866 provides exceptional insights into the conceptualization and visualization of paleontology by Ernst Haeckel

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Abstract

Here we report on a recently discovered student script of a lecture on paleontology given by Ernst Haeckel (1834–1919). The script dates to the summer semester of 1866, comprises 63 pages, and provides an overview of fossil invertebrate and mainly fossil vertebrate taxonomy and anatomy. It can be assumed that Russian student Nikolai Nikolajevitch Miklucho-Maclay (1846–1888), who later became a famous ethnologist, did not follow up on the lecture, but took the content directly from the lecture and from the blackboard in his notes. Hence, the drawings by Miklucho allow direct insight into Haeckel's visualization of paleontology in the 1860s. We place the transcript in the historical context of understanding paleontology in the second half of the 19th century and address the break between zoology and embryology on the one hand and paleontology on the other, which is typical for Germany, partly persisting to this date. For that, we illustrate Haeckel's integration of paleontology as part of a holistic triad, with fossil research gradually taking a back seat to zoology and embryology over the decades.

Keywords

Embryology, illustration, paleontology, Vertebrata, zoology

Interpreting Paleontology: from prehistory to Ernst Haeckel

The existence of creation myths in all cultures known to us proves that, as soon as they became aware of their own existence, humans thought about their origins and beyond that about the origin of the world and considered themselves a part of it (Campbell 1959–1968, Lévi-Strauss 2008). When considering the history of paleontology, it is noteworthy how the dimension of time was assessed in the various theories and whether variability, change, or evolution were considered (Gould

1990, Hölder 1989, Werneburg 2021). These questions also concerned humans with regard to their constitution and mental abilities (van Schaik and Michel 2016, Maier 2021), after their "integration" into the so-called kingdom of nature in terms of biological systematics (Linné 1758). While archeology subsequently turned to antiquity and to the cultures of the unwritten so-called prehistoric period and also developed related theories (Bernbeck 1997), the interpretation of fossil finds turned out to be much more difficult (Thenius and Vávra 1996). In order to clarify the connection between fossil and extant species, the actual age of the earth had to be determined against the background of the debate about the constancy or variability of species (Gould 1990). Both touched on the Christian idea of creation (Scheuchzer 1726, Tschudi 1837, Reif and Lux 1987). Georges Cuvier (1769–1832), for example, tried with his so-called 'catastrophe theory' to reconcile the stated existence of fossils of different ages with the Christian doctrine by postulating the respective re-creation of species after previous extinctions caused by catastrophes, including the Flood (Cuvier 1825).

Despite his scholarly authority, Cuvier met with opposition from the scholarly world (May 1919). Jean-Baptiste de Lamarck (1744–1829) and Étienne Geoffroy Saint-Hilaire (1772–1844), as well as Jacques Boucher de Perthes (1788–1868), who based his finds on the simultaneous existence of humans and extinct animals (Cohen and Hublin 1989). A purely scientific explanation was made possible by including Charles Darwin's (1809–1882) theory on the origin of species (Darwin 1859), which, based on English geology, suggested a hitherto unimaginably great age of the Earth and a correspondingly long period of existence preceded by life (Lyell 1830–1833, Hoßfeld et al. 2021).

In Germany, like Thomas H. Huxley (1825–1895) in England, the Jena zoologist Ernst Haeckel (1834–1919, Fig. 1A–B) in particular tried to advance his research in the Darwinian sense and to integrate it into his edifice of ideas (Hoßfeld et al. 2019, Levit and Hoßfeld 2019). Haeckel's contributions to the justification and establishment of biological anthropology, evolutionary morphology, and evolutionary embryology were in part formative in the 19th century and exerted a central influence on the development of subjects such as paleontology or systematics (Werneburg 2019). We here report on a recently discovered transcript of Haeckel's paleontology lectures from the summer semester of 1866 and provide a historical contextualization.

Paleontology and its conceptions have been part of Haeckel's construct of ideas since the beginning of his work in Jena (Fig. 1C), whereby the so-called "*threefold parallelism between the embryological, the systematic, and the paleontological development of organisms*"[1] (Haeckel 1864: 29) was first mentioned in his Stettin lecture in 1863 (Haeckel 1864). About 30 years later, in his last major zoological work, the "Systematische Phylogenie" (1895), the concept of comprehensive paleontology was no longer that important in Haeckel's work, but rather prehistoric anthropology with human phylogenetic arguments came to the fore (Hoßfeld 2016).

The paleontology lecture from 1866 and Miklucho-Maclay

The notes on a paleontology lecture given by Ernst Haeckel in the summer semester of 1866 in Jena, Germany, stem from the archive of the Russian Geographical Society (RGO, St. Petersburg, inventory-number: 6/1/9) and belong to the estate of famous ethnographer Nikolai Nikolajevitch Miklucho-Maclay (1846–1888). The transcript of these lecture notes (Werneburg et al. 2022) and notes on two other lectures (Hoßfeld et al. 2022a,b) were recently edited and published.

With Haeckel and his circle of students, zoology in Jena (Fig. 2A) became the "*Mecca to which all zoologists made pilgrimages*" and it became a "*stronghold of Darwinism*" (Uschmann 1959)[2]. The Russian explorer Nikolai Nikolayevich Miklucho-Maclay also belonged to this illustrious company. He came to Jena in October 1865 and studied at the medical faculty until 1868, but later refused to take the state exam (Levit 2019: 87). In Jena, the nineteen-year-old met Haeckel and Gegenbaur, who aroused his enthusiasm for zoology. Among others, he attended the lecturs on comparative anatomy by Gegenbaur (Hoßfeld et al. 2022a), the zoology lectures by Haeckel (Hoßfeld et al. 2022b), as well as the lectures on paleontology discussed herein (held as "*General Paleontology with Special Consideration of Vertebrates*"[3]), which Haeckel offered for two hours per week in the summer semester of 1866 and which was attended by 44 students.

As detailed in Table 1, the lecture appears a bit disorganized with abrupt topical changes, and we provide different interpretations on that issue (Appendix 1). One reason could have been the Austro-Prussian war (June 14th to July 22nd, 1866), which finally even reached Thuringian territory (Fontane 1871). Haeckel did not adopt party for Prussia (Uschmann 1983), which, however, was very successful in the war. Hence, the Jena professor might have been a bit distracted from preparing the lecture in these months and might have relied on topics that he had prepared for other lectures long before, such as the zoology lecture (Hoßfeld et al. 2022b). Also, the Russian student Miklucho-Maclay apparently did not work on his own notes after the lecture was given. It is to say that Austria had a difficult political relationship with Russia at the time provoking a potential suspence in the Jena institute.

Nevertheless, Haeckel was soon impressed by Miklucho-Maclay (Fig. 2C) and, in a letter to his parents

[1] Our translation from: "dreifache Parallele zwischen der embryologischen, der systematischen und der palaeontologischen Entwickelung der Organismen"

[2] Our translation from: "Mekka, wohin alle Zoologen pilgerten" […] "Hochburg des Darwinismus"

[3] Our translation from: "Allgemeine Paläontologie mit besonderer Berücksichtigung der Wirbeltiere"

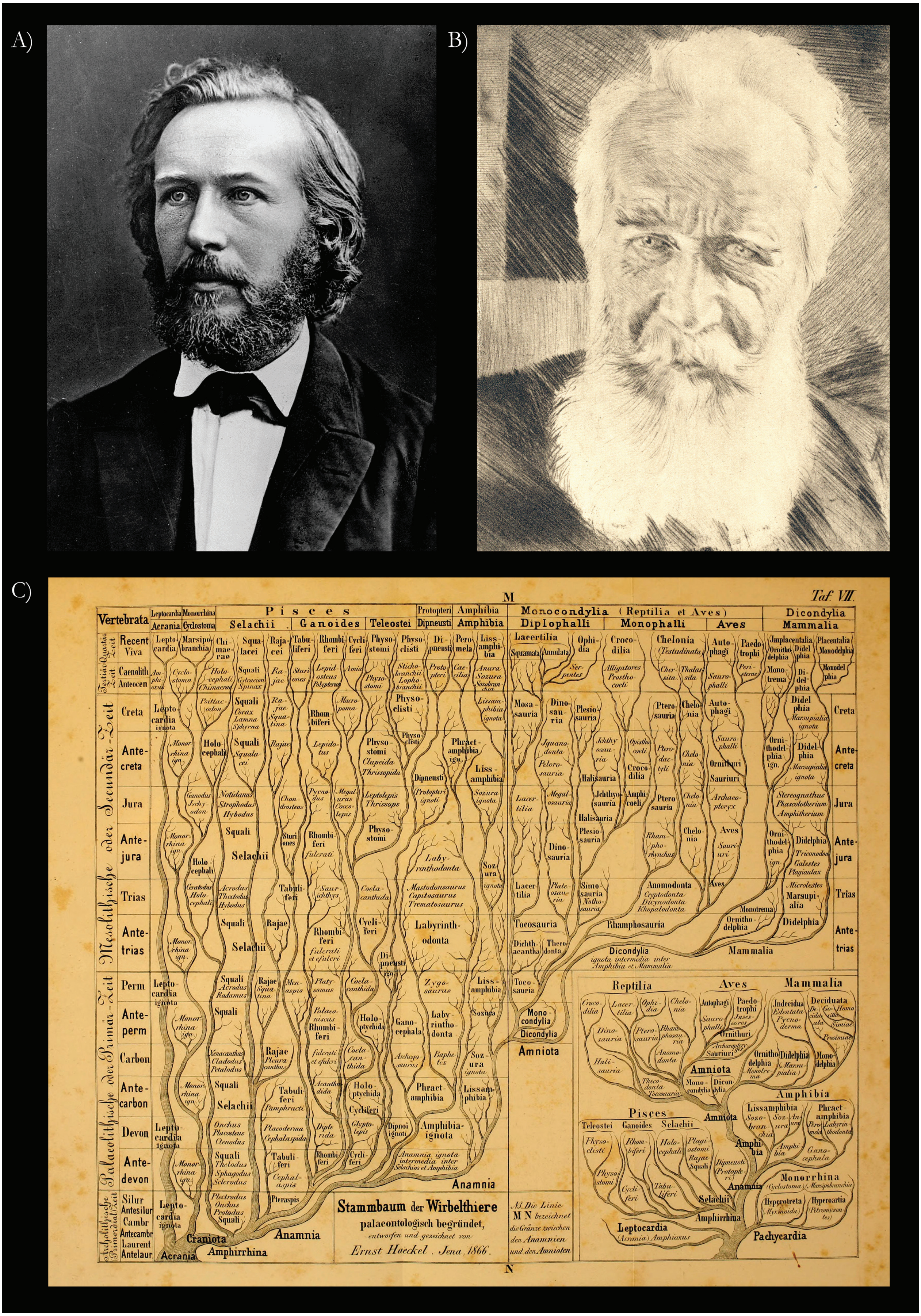

Figure 1. Haeckel and Paleontology. **A)** Ernst Haeckel at Christmas 1860, **B)** and in 1913 (edging by Karl Bauer, from: W. Haeckel 1914). **C)** '"Phylogenetic tree of vertebrates based on paleontological evidence" [„Stammbaum der Wirbeltiere palaeontologisch begründet"] (Haeckel 1866, plate VII).

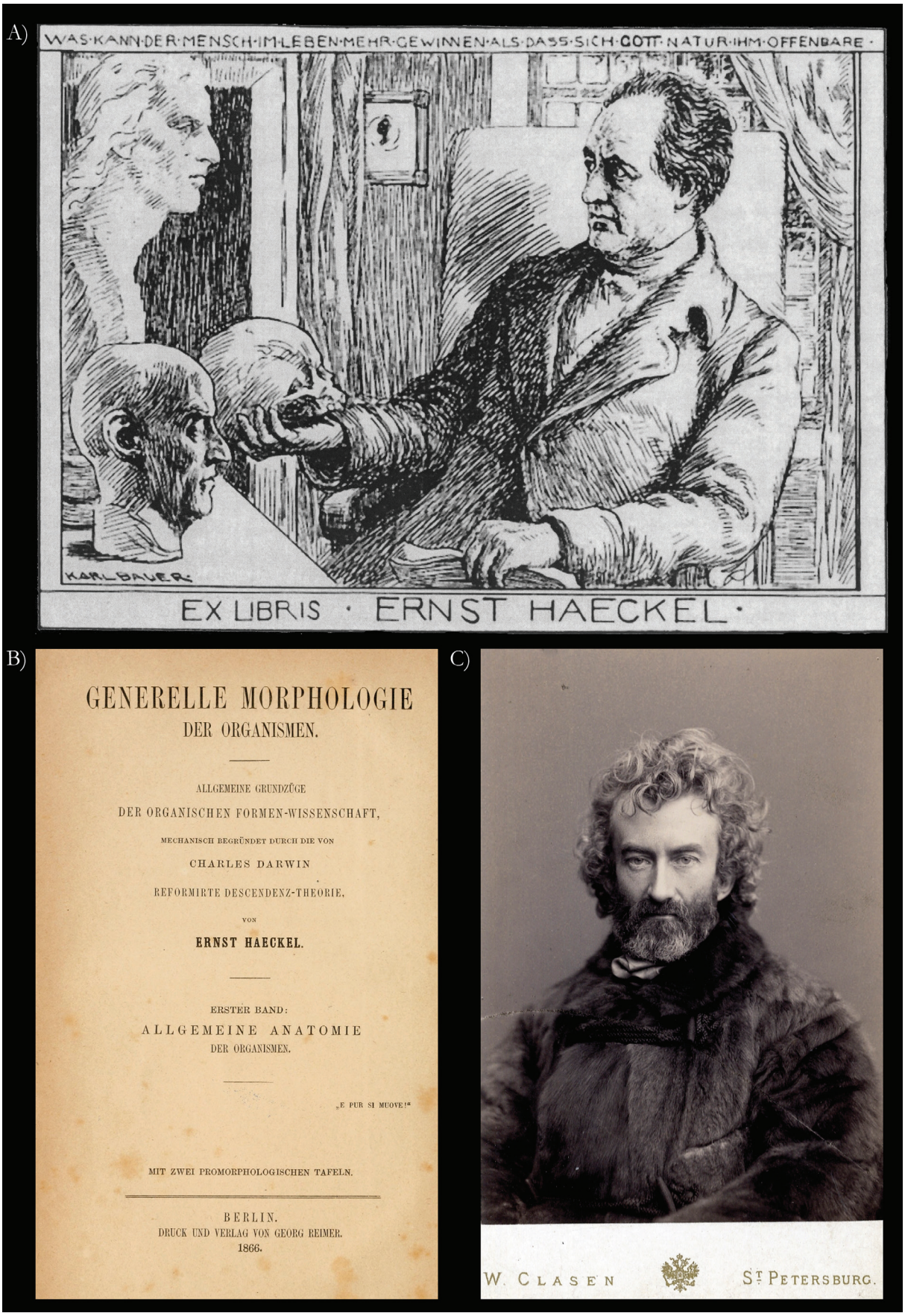

Figure 2. Goethe, Haeckel, and Mikucho-Mayclay. **A** A drawing with Johann Wolfgang von Goethe and the skull of his former companion, the poet and historian Friedrich von Schiller (1759–1805), Ex Libris Ernst Haeckel (private collection of Uwe Hoßfeld), quote by Goethe: "Was kann der Mensch im Leben mehr gewinnen, als daß sich Gott Natur ihm offenbare" ("What more can man gain in life than God Nature reveals himself to him"). **B** Cover page of "Generelle Morphologie der Organismen", Vol. 1 (1866), **C** Micklucho-Maclay in the winter 1886 in St. Petersburg (Russian Geographical Society archive: RGO 6/3/20).

Table 1. Overview of the essential content of the paleontology script discussed herein. Words with normal letters correspond to underlined words in the script. Our summaries or logical additions are shown in italics. f = front page, b = back pack. For further specific notes on the structure of the manuscript see Appendix 1.

Script-Page	**Content**
Cover, 1f	*Cover pages* "Paleontology Prof. E. Haeckel summer semester 1866"
2f	The new conception of paleontology, process of fossilization
2b	*Overview of the geological ages and formations*, diatoms and sponges
3f	Radiolarians, *Origin of Organisms, Overview of Plants*: Thalo- and cormophyta
3b	Siphoneae, oelenterates, Anthozoa
4f	Anthozoa, echinoderms
4b	Crinoids
5f	*Brief commentary on the vertebrates*: Teleosts, ganoids, selachians, cyclostomes, *then introduction to the invertebrates*: Tunicata, Bryozoa, Centrifugines, brachiopods, Lamellibranchi, Cephalophora, Cephalopoda
5b	Cephalophores, cephalopods, tetrabranch, Nautilus, ammonite
6f	Cephalopods, Dibranchia
6f	Primary period, *1.* Silurian system
6b	2. Devonian system
7f	*3.* Coal system (*Carboniferous*), *4.* Permian system
7b	Permian System: The Rotliegend
8f, 8b	*Mesozoic Period*: 1. Triassic
8b, 9f, 9b	*2.* Jurassic
9b, 10f, 10b	*3.* Cretaceous
10b, 11f, 11b	Tertiary period – *ends on incompletely written page with final dash*
12f	Vertebrates, non-appropriate classification of fish according to Agassiz according to scales, conodonts
12b	Classification of fish according to Johannes Müller (natural system), eye anatomy
13f, 13b, 14f	*Gills, scale formation, taxonomy,* I. Selachians, *jaw suspension, tooth plates*
14b, 15f, 15b	II. Ganoids, *tail anatomy, taxonomy*
15b, 16f	Cyclifera, *taxonomy*
16f, 16b	III. Teleosts
17f, 17b, 18f, 18b	Amphibians
18b, 19f, 19b, 20f, 20b	Reptiles, *taxonomy – ends on incompletely written page with the heading* "*Aves*"
21f, 21b	[medical issues]
22f, 22b, 23f, 23b	*History of Biology and Zoology*: Aristotle, Galen, Pliny, Albertus Magnus, Watson, Buffon, Cuvier (Typis, Classe, Ordo, Fam), Lyell, Darwin
24f	C.E. von Baer, Meckel, School of Natural Philosophy, Lamarck, E.G. Saint-Hilaire, Lorenz Oken, Johannes Müller
24b	Charles Darwin, *Outline of the Disciplines of Zoology*, Literature
25f	*Summary*: *Overview of the animal kingdom and explanation of the groups,* journals
25b	Rhizopoda, Infusoria, Porifera, Coelenterata
26f	Hydromedusa, Ctenophora, crinoids, Asterida, sea urchins – Echynodermata, Vermes, Arthropoda, Mollusca
26b, 27f, 27b	1. General part, *classification of nature into organic and inorganic kingdoms, commitment to materialism, reference to monism, explanation of the elements, substances and forms in the kingdoms*
28f	Main axis of the body, colony formation, tissues, cells, nutrition, digestion, reproduction
28b	Elementary organism, budding, irritability, movement, protogenes, amoebas, vacuoles
29f	Systematic ["Spezielle"] zoology, transition of cells to tissues, types of tissues, *1.* Nervous tissues
29b	2. muscle tissue, 3. connective tissue, 4. epithels
30f	Glands, lung, general organology, basic forms of the nervous system
30b	Pharyngeal ring, ventral cord, spinal cord, sympathetic nerves, sense organs, 1. sense of hearing
31f	*Sense of hearing*, 2. The eye
31b	*Eye*, organs of movement

dated February 10, 1866, he described him as a "*special, very talented and hopeful*"[4] student (Uschmann 1983: 86). In another letter dated March 22, 1866, he counted him among his "dearest students"[5] (Uschmann 1959: 66). From 1866 to 1868 Miklucho-Maclay worked as Haeckel's assistant and published several zoological works during his time in Jena (Miklucho-Maclay 1867, 1868a, b, 1870; Maclay 1974). On the island of Lanzarote he studied sponges and cartilaginous fish. The results of this work were later published (Miklucho-Maclay 1870;

[4] Our translation from: "speziellen, sehr talent- und hoffnungsvollen"

[5] Our translation from: "liebsten Schülern"

Fischer 1955: 16). His work relates, for example, to the swim bladder rudiment in cartilaginous fish (Uschmann 1959: 66–67). These studies were "*very speculative and apt to disturb long-established anatomists*"[6] (Schneider 1997: 5). Haeckel later described his young colleague Miklucho to T. H. Huxley as a "*talented young Russian from Kyiv*"[7], who was a Darwinist. During his time in Jena, he used the double name "Miklucho-Maclay" for the first time (Uschmann 1959: 66–67). Miklucho-Maclay was in Jena for the last time in 1869/1870, when he wrote his monograph on the comparative neurology of vertebrates (Miklucho-Maclay 1870).

The contact between him and Haeckel finally ended in 1871. In a letter to Carl von Siebold (1904–1885) on February 14, 1877, Haeckel made disparaging remarks about Miklucho-Maclay (Uschmann 1959: 66). It is assumed that Haeckel's hierarchization of the people, including the Papuans, was not acceptable to the ethnologist Miklucho-Maclay and that contact was therefore broken off (Levit 2019: 87; Levit and Hoßfeld 2020). There would be a certain irony in a rift between teacher and student that came about in this way. Miklucho-Maclay's precise and largely unbiased observation and documentation was also a result of his former teacher's didactic decisions (Werneburg in press). Haeckel himself had announced to his zoology students that his goal was not "*to acquaint* [*them*] *with the innumerable multitude of individual animal forms and their differences, but to show* [*the students*] *a way* [...] *themselves to find one's way* [*in the whole discipline*]" (Uschmann 1959: 41)[8]. In 1868 he boasted of his teaching style, which was intended to encourage students to think independently and do practical work: "*I regard it as the essential task of the practical scientific institutes at the universities to give the students a thorough education through practical exercises, which can never be attained through theoretical instruction alone; and to fill in the essential gaps, which the latter always has to leave, through his own observation and investigation*"[9] (ibid.: 62). Miklucho-Maclay had dealt with the theory and in the next step, 'through his own observation and investigation', he tried to close the knowledge gaps that still existed. When following the path of scientific knowledge taught in Jena, he simply did not come to the result that his former teacher had wished for to further base his hierarchization of people (Levit and Hoßfeld 2020). It was not until 1923 that Miklucho-Maclay's diaries of the main voyages to New Guinea were published in the Soviet Union (Tumarkin 1982: 6, Miklucho-Maclay 1990).

Other reports on paleontology lectures given by Ernst Haeckel

Haeckel addressed paleontological issues already in his zoology lectures in order to provide evidence for Darwin's theories. The excerpt of the zoology lectures in the winter semester of 1863/64 provides an overview on the following topics: "*Paleontological development, paleontology in general, petrification, deposition, layer sequence, Cuvier versus Lyell* ([*lecture hour*] *3*)*. Overview of the periods and formations, three large sections, example of paleontological development: Vertebrates* (*4*)*. General results of paleontology and evidences for Darwin, geographical distribution, consequences of Darwin's lore, descent of man from apes, summary on Darwin* (*5*)"[10] (Uschmann 1959: 43).

Uschmann (1959: 45) also noted that Haeckel gave a lecture on paleontology as early as 1863, but that it was not listed in the university's course catalog. Furthermore, in the summer of 1864 he read the "*Natural History of Living and Fossil Mammals*"[11] (ibid.: 45). These paleontology lectures began first with a "*survey of the history of paleontology*", followed by its "*reform by Lyell and Darwin*" (ibid.: 45–46). Haeckel then discussed the "*petrification process*", the "*determination of the sequence of geological layers*", and the "*importance of petrefacts* [*i.e., fossils*] *for the determination of geological layers*"[12] (ibid.: 46). The remaining part of the lecture, from the 5th to the 26th lecture hour in 1863, and from the 6th to the 45th lecture hour in1868, would then have taken up "*the discussion of the individual* [*geological*] *formations*"[13] (ibid.: 46). The comparison of this information with the Miklucho-Maclay transcript now provides comprehensive information about that paleontology lectures given in 1866. Although the 1866-lecture was not included in

6 Our translation from: "sehr spekulativ und dazu angetan, alteingesessene Anatomen aufzustören"

7 Our translation from: "talentvollen jungen Russen aus Kiew"

8 Our translation from: "[s]ie mit der zahllosen Menge der einzelnen tierischen Formen und ihren Differenzen bekannt zu machen, sondern [i]hnen einen Weg zu zeigen, [...] sich [im Gesamtgebiet] zurechtzufinden"

9 Our translation from: "Ich betrachte es vielmehr als die wesentliche Aufgabe der praktisch-naturwissenschaftlichen Institute an den Universitäten, den Studierenden durch praktische Übungen die gründliche Durchbildung zu geben, welche durch den theoretischen Unterricht allein niemals erlangt werden kann; und durch eigene Anschauung und Untersuchung die wesentlichen Lücken aufzufüllen, welche der letztere immer lassen muß."

10 Our translation from: "Paläontologische Entwicklung, Paläontologie überhaupt, Petrifikation, Ablagerung, Schichtenfolge, Cuvier gegen Lyell (3). Übersicht der Perioden und Formationen, drei große Abschnitte, Beispiel der paläontologischen Entwicklung: Wirbeltiere (4). Allgemeine Resultate der Paläontologie und Beweise für Darwin, geographische Verbreitung, Konsequenzen der Darwinschen Lehre, Abstammung des Menschen vom Affen, Resumé über Darwin (5)"

11 Our translation from: "Naturgeschichte der lebenden und fossilen Säugetiere"

12 Our translation from: "Vorgang der Versteinerung […] Bestimmung der Schichtfolgen […] Bedeutung der Petrefakten für die Schichten-Bestimmung"

13 Our translation from: "die Besprechung der einzelnen Formationen"

Uschmann's (1959) elaboration, it seems to resemble that one from 1863 in regard to the distribution of specific lecture hours.

Compared to other lectures in which Haeckel spoke about paleontology (Uschmann 1959), Miklucho-Maclay's notes appear less extensive. The introductory chapters on the history of paleontology and the influences of Lyell and Darwin listed by Uschmann (1959) are missing completely. While there is a section on the history of biology, it remains much more general and certainly not specifically limited to the subject of paleontology. In Uschmann's (1959) listing, the petrification process and the determination of the sequence of strata follow immediately afterwards. This order corresponds to the beginning of the transcript. Apparently, Miklucho-Maclay missed the first date of the lecture and therefore only started his notebook on Script Page 2v. He probably left space at the beginning of the notebook, because he wanted to add notes from a fellow student but later did not do so. Did he later write these blank pages on an additional cover sheet (Script Page 1v), even though this had already been done on the front page of the notebook?

There are other similarities that are reminiscent of other comments by Uschmann (1959). For example, most of the script that filled 'the remainder of the lecture' occupies the 'discussion of each formation' mentioned above (Table 1). It seems possible that Haeckel did not usually include an excursus on the history of biology and histology in his paleontology lectures and that Miklucho-Maclay used his notebook for other purposes at this point.

Also of interest is the note on the 1863/64 zoology lecture (Uschmann 1959): "*Example of Paleontological Evolution: Vertebrates*".[14] Up to the 23rd lectures hour Haeckel had treated the formations and had already spoken several times about fish. The excursus that follows about the different ideas on how the systematics of fish can be set up and what anatomical differences exist in the taxonomic groups fits into this concept. The explanation of the fish leads, via the amphibians, to the reptiles, where the aforementioned break occurs in the subject of birds (which phylogenetically belong to the reptiles). It is quite possible that these Script Pages, from 12v to 20r, are some version of what Haeckel called "*Example of Paleontological Evolution: Vertebrates*" in his zoology lectures mentioned above.

Paleontology in the holistic world view of Ernst Haeckel

In the period discussed here around Haeckel's reception of paleontology, Karl Alfred von Zittel (1839–1904) (Zittel 1895, 1899) "*founded a paleontology that was not merely empirical, but also theoretical* (*through Darwin's theory of descent*)"[15] (Tamborini 2015: 188). Also, an endowed professorship for geology and paleontology was founded at the University of Jena, which was first occupied by Johannes Walther (1860–1937) beginning in 1894 (Müller 2015: 59). In principle, however, it must be stated that in Germany for a long time there was a strong separation between paleontological research on the one side and zoological and embryological research on the other side. This situation continues in many areas to this day.

Darwin's theory of common descent was acknowledged by the German paleontologists, but not exercised with rigor (Hölder 1976), as was the case with the recent biological research objects of the biologists (Levit et al. 2013, Werneburg 2021). A major reason may initially have been the respective material basis and the corresponding questions of both disciplines. The paleontologists were well aware of the fragmentary type of data in their science and the focus was therefore primarily on biostratigraphic investigations using extinct organisms (Fraas 1910, Quenstedt 1846–1884). These 'index and facies fossils' provided information about the paleo-environment with trophic relationships and ecological conditions or about the relative position of different layers of the earth (Ziegler 1992). For this purpose, taxonomy, i.e. the determination of organisms according to a static classification system, was the basic tool of the paleontologists, who – and in Germany up to the present day – mostly brought along a basic geological education. What Carl von Linné (1707–1778) had created for the flora and fauna in his *Systema naturæ* (Linné 1758), namely a consistent taxonomy, was primarily carried out by Friedrich August von Quenstedt (1809–1889) for extinct organisms (Quenstedt 1867). In geological research, for example, questions about oil prospection based on the occurrence of certain fossil microorganisms are still more decisive than the phylogenetic relationships between these organisms. Zoology and embryology differ significantly from paleontology in the types of research material available. A recent organism can be examined in all anatomical components. Although more difficult to organize (Hopwood 2007, Werneburg 2009), there were also sufficient embryos to perform ontogenetic comparisons. Especially through those, questions about the homology of individual organs and the relationships of organisms could be answered more easily and thus the conceptual structure of the Darwinian theory of descent gained an empirical basis.

After reading Darwin's epoch-making work in its first German translation by the Heidelberg zoologist Heinrich G. Bronn in 1860 (Darwin 1860), Haeckel spontaneously and early on acknowledged this still very controversial theory and rated it as "*the first, serious, scientific attempt to explain all phenomena of organic nature from a grand, unified point of view and to replace the incomprehensible miracle with the comprehensible law of na-*

[14] Our translation from: "Beispiel der paläontologischen Entwicklung: Wirbeltiere"

[15] Our translation from: "Begründung einer nicht bloß empirischen, sondern auch theoretisch (durch Darwins Deszendenztheorie) angeleiteten Paläontologie"

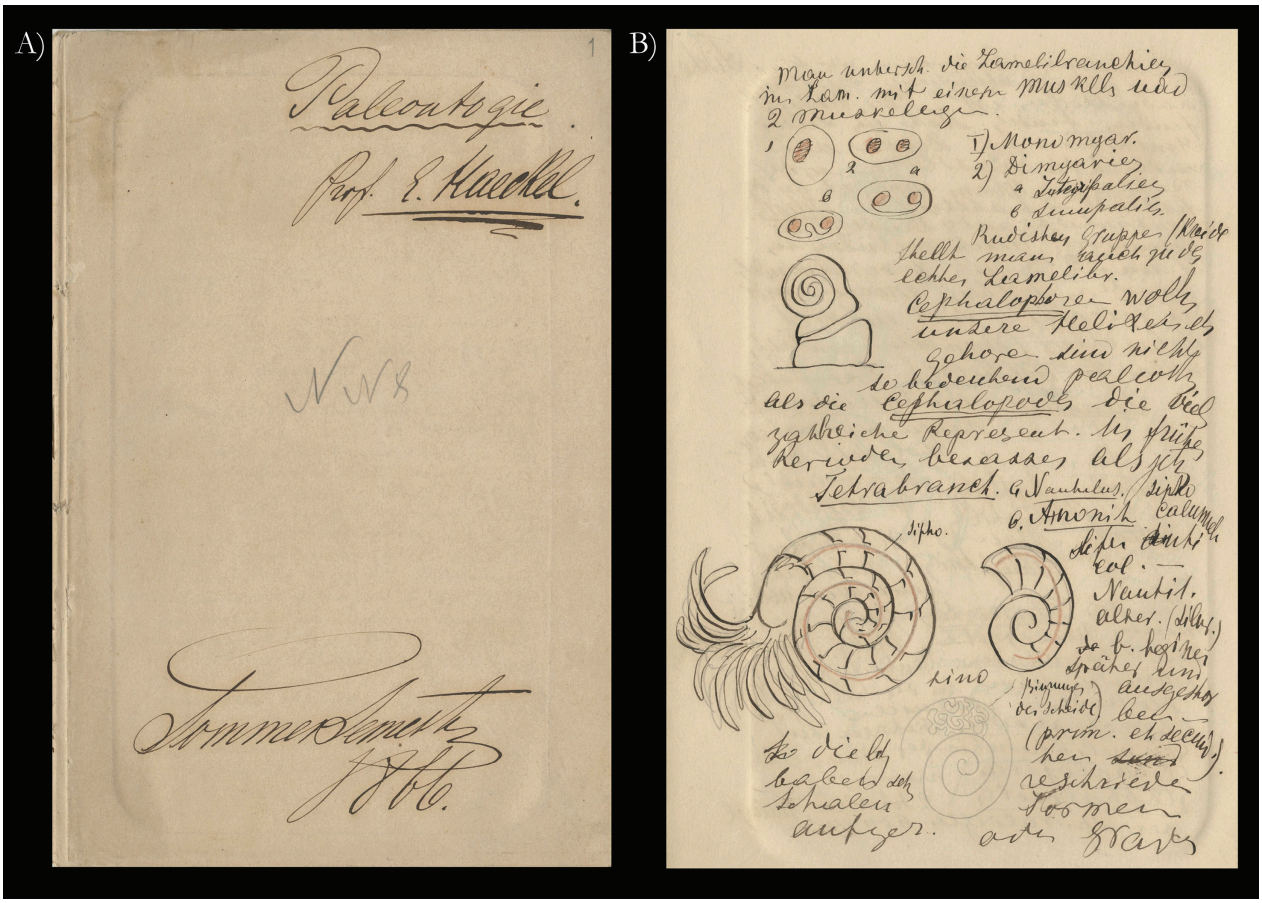

Figure 3. Images from the discovered manuscript of the paleontology lecture from summer semester 1866. **A** Title page (Script Page 1f); **B** example page with notes on mollusk diversity and anatomy (Script Page 5b).

ture"[16] (Haeckel 1864: 232). With the decision in favor of Darwin, Haeckel also fixed his future research program. The successful Darwin lectures in the winter semester of 1862/63 at Jena University were followed by his highly acclaimed and sensational Stettin lecture on September 19, 1863, entitled "*On Darwin's Theory of Evolution*"[17]. Unlike Bronn, who in his German Darwin translation had omitted Darwin's last sentence "*Light will be thrown on the origin of man and his history*", Haeckel from now on used every opportunity to propagate these ideas, which were revolutionary at the time. Haeckel was aware, however, that his advocacy of Darwin's ideas could not proceed without controversy and scientifically conducted debates. In this context he wrote: "*If, despite this and many*

[16] Our translation from: "den ersten, ernstlichen, wissenschaftlichen Versuch[,] alle Erscheinungen der organischen Natur aus einem großartigen, einheitlichen Gesichtspunkte zu erklären und an die Stelle des unbegreiflichen Wunders das begreifliche Naturgesetz zu bringen"

[17] Our translation from: "Ueber die Entwickelungstheorie Darwin's"

Figure 4. Images related to vertebrate paleontology from the lecture manuscripts of Miklucho-Mayclay. From the zoology lecture of winter semester 1865/66 (Hoßfeld et al. 2022a, p. 152–153): **A** categories of fossil amniotes (transcript: "Reptilia fossilia / I. Thecodontes / *Paleosaurus* /*Proterosaurus* / II. Anomodonta / ~~*Cyo*~~ *Dicynodon* / III. Mosasauria / *Mosasaurus* / *Geosaurus* / IV. Pterosauria *Rhamphorhynchus Pterodactylus* V. Enaliosaurus. / Va. Simosauria / Nothosauria / Vb. *Ichthyosaurus* / *Plesiosaurus* / Dinosaurus / *Iguanodon* / *Megalosaurus*") with drawings of a partial skeleton of a pterosaur and a silhouette of a plesiosaur. Note the student's decoration at the bottom of the page; **B** "*Archeopter*[*yx*]", note that this is not a skeleton of *Archaeopteryx lithographica* von Meyer 1861, but a pterosaur skeleton (*Pterodactylus antiquus* Soemmering 1812). Both species are found in Solnhofener Plattenkalk, Eichstätt, Germany. – From the paleontology lecture of summer semester 1866 (Werneburg et al. 2022): **C** silhouettes of an ichthyosaur and an plesiosaur with following comment (Script Page 19b): "Wahrscheinlich besassen die Thiere ein[e] [[D]a[-] rmspiral[-]clappe] ([Sch[l]uss ? nach d[er] Beschaffen[-]heit der C[o]prolyten)." = "They likely had a spiraled valve in their gut (based on the shape of the coproliths)."; **D** tooth of a herbivore dinosaur (Script Page 20f); **E** typological categorization (Script Page 23b) (transcript: "Typus (Orbes Embrens?) = type / Classe = class / Ordo = order / Fam[ilie] = family / G[attung] = genus / Ind[ividuum] = specimen" with following comment: "Die Typen sind v[on]einander gänzlich unabhängig. Diese Typen k[önnen] miteinander nicht verglichen werden." = "The types are completely independent from each other. These types cannot be compared with each other.")


A)
Reptilien Fossilien.
I Thecodonten
Pelorosaurus
Pterodactylus
II Anomodonten
Cetiosaurus
Plesiosaurus
III Mosasaurier
Megalosaurus
IV Pterosaurier
Rhamphorhynch.
Pterodactylus
V Enaliosaurier
Ichthyosaurus
Plesiosaurus
VI Dinosaurier
Iguanodon
Megalosaurus
B)
Archeopter
C)
Plesiosaur.
D)
E)
Typus (Orbes Embranch.)
Classe
Ordo
Fam.
S.
Gen.

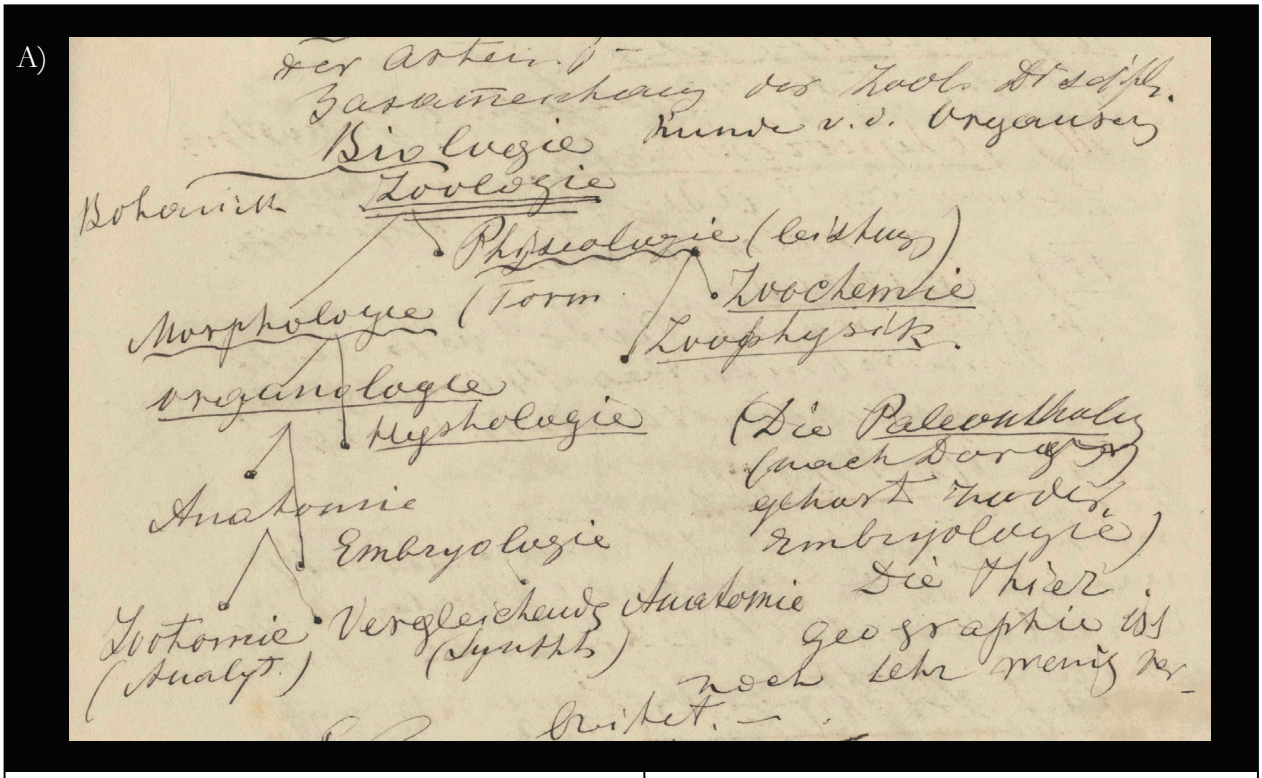

Figure 5. Conceptualization of paleontology as a sub-discipline of embryology. **A** Image from the paleontology lecture notes (Script Page 24b); **B** German transkript of A; **C** English translation of the German transcript.

other misgivings, I try to introduce you to the struggle that has unleashed by the Darwinian evolutionary theory, it is mainly because of the grand dimensions of this struggle has already accepted. The whole large army of zoologists and botanists, paleontologists and geologists, physiologists and philosophers is already split into two opposing factions: on the flag of the progressive Darwinists are the words: ›Development and progress!‹ From the camp of the conservative opponents of Darwin they shout: ›Creation and Species!‹ The chasm that separates both parties is growing daily, daily new weapons are brought in for and against from all sides; daily more circles are seized by the powerful movement; those who are far away [*from the topic*] *are also drawn into their swirl* [...]"[18] (ibid.: 18).

[18] Our translation from: "Wenn ich trotzdem, dieser und vieler anderer Bedenken ungeachtet, Sie in den Kampf, der durch die Darwinsch'sche Entwickelungs-Theorie entbrannt ist, hineinzuführen versuche, so geschieht es hauptsächlich wegen der großartigen Dimensionen, die dieser Kampf bereits angenommen hat. Bereits ist das ganze große Heerlager der Zoologen und Botaniker, der Palaeontologen und Geologen, der Physiologen und Philosophen in zwei schroff gegenüberstehende Parteien gespalten: auf der Fahne der progressiven Darwinisten stehen die Worte: ‚Entwickelung und Fortschritt!' Aus dem Lager der conservativen Gegner Darwin's tönt der Ruf: ‚Schöpfung und Species!' Täglich wächst die Kluft, die beide Parteien trennt, täglich werden neue Waffen

After the relatively precise presentation of Darwin's thoughts and a historical outline of the history of the idea of evolution, Haeckel then came to the conclusion that man, too, does not appear "*as an armed Minerva from the head of Jupiter*"[19] or "*as an adult, sin-free Adam from the hand of the Creator*"[20] (ibid.: 27). This claim was supported by contemporary discoveries in geology and archaeology, as well as in comparative linguistics; but he was not yet able to cite fossil finds. Haeckel acknowledged the "*threefold parallelism between the embryological, the systematic, and the paleontological development of organisms*" as the strongest proof "*for the truth of the theory of evolution*"[21] (ibid.: 29), a construction that later became decisive for the interdisciplinary genesis of certain bioscientific disciplines. In the threefold parallelism and in Haeckel's thinking, paleontology was an integral part from the very beginning.

In 1866, his two-volume book "*Generelle Morphologie der Organismen*" (Vol. I. Principal Anatomy of Organisms; Vol. II. General Development History) (Fig. 2B) was published. The work was subtitled as "*General principles of the science of organic form, mechanically based on the theory of descent as reformed by Charles Darwin*"[22], with the first volume dedicated to his friend and colleague Carl Gegenbaur (1826–1903), the second volume dedicated to the "*Founders of the Theory of Descendancy*"[23], Darwin, Goethe (1749–1832), and Lamarck. The book represents the central key for Haeckel's later entire life's work. The aim of "*Generelle Morphologie der Organismen*" was to apply Darwin's theory to the entire field of biology (initially especially to morphology) and to present a comprehensive kingdom of animals and plants from these points of view. In addition to all criticism on this work and in addition to the naming of new research directions and the introduction of new biological terms (ecology, chorology, etc.), there are also initial thoughts on the relationship between ontogeny and phylogeny (the later 'biogenetic law'; Hoßfeld et al. 2016, Olsson et al. 2017, Levit et al. 2022) with an attempt to arrange the major existing taxonomic groups in a genealogical-phylogenetic (and not in a typological-idealistic) system. The second volume of the book can also be viewed as the first attempt to justify an 'evolutionary morphology and embryology', with the 21st chapter on "*The Concept and Task of Phylogeny*"[24] also containing Haeckel's central core theses with regard to paleontology. At the beginning of his book, he had already tried to correctly classify paleontology in the scientific structure of the time and he noticed: "*If we call the sum of all organisms which derive their common origin from one and the same simplest, spontaneously arisen ancestral form an organic phylum or phylon, we may accordingly call paleontology the evolutionary history of phyla or phylogeny. To be sure, paleontology hardly exists as a science in this sense; and only after Darwin had re-established the theory of descent did some paleontologists begin in recent years to apply the genealogical standard here and there to the progressing series in fossil record and to recognize their real blood relationship in the similarity in form of the species that appeared one after the other. But we cannot doubt that this seed, which has just germinated, will quickly develop into a mighty tree, the crown of which will soon absorb and overshadow a whole series of other scientific disciplines*"[25] (Haeckel 1866, 1: 58–59).

In contrast to the individual (i.e., biontic) history of development (ontogeny), statements on the individual development of the organism in the context of the paleontological or phyletic history of life in general are more difficult according to Haeckel: "[*In paleontology,*] *there is nowhere a coherent chain of facts that the lucky observer can simply take up and present in this way as he sees it* [...]. *The evolutionary history of paleontology* [...] *remains an utterly fragmentary and torn patchwork, if it confines itself to the mere facts, which paleontology furnishes us, and if it does not supplement them with the all-important triple parallelism* [...]"[26] (ibid., 2:306–7).

für und wider von allen Seiten herbeigeschleppt; täglich werden weitere Kreise von der gewaltigen Bewegung ergriffen; auch Fernstehende werden in ihren Strudel hineingezogen […]"

19 Our translation from: "als eine gewappnete Minerva aus dem Haupte des Jupiter"

20 Our translation from: "als ein erwachsener sündenfreier Adam aus der Hand des Schöpfers"

21 Our translation from: "der Wahrheit der Entwickelungstheorie […] dreifache Parallele zwischen der embryologischen, der systematischen und der palaeontologischen Entwickelung der Organismen"

22 Our translation from: "Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformierte Descendenz-Theorie"

23 Our translation from: "Den Begründern der Descendenztheorie"

24 Our translation from: "Begriff und Aufgabe der Phylogenie"

25 Our translation from: "Wenn wir die Summe aller Organismen, welche von einer und derselben einfachsten, spontan entstandenen Stammform ihren gemeinschaftlichen Ursprung ableiten, als einen organischen Stamm oder Phylon bezeichnen, so können wir demnach die Palaeontologie die Entwicklungsgeschichte der Stämme oder Phylogenie nennen. Allerdings existirt die Palaeontologie in diesem Sinne noch kaum als Wissenschaft; und erst nachdem durch Darwin die Abstammungslehre neu begründet war, haben in den letzten Jahren einige Palaeontologen angefangen, hier und da den genealogischen Maßstab an die palaeontologischen Entwickelungsreihen anzulegen, und in der Formen-Aehnlichkeit der nach einander auftretenden Arten ihre wirkliche Blutsverwandtschaft zu erkennen. Wir können aber nicht daran zweifeln, daß dieser kaum erst emporgekeimte Samen sich rasch zu einem gewaltigen Baume entwickeln wird, dessen Krone bald eine ganze Reihe von anderen wissenschaftlichen Disciplinen in ihren Schatten aufnehmen und überdecken wird" (Haeckel 1866, 1: 58–59).

26 Our translation from: "Hier liegt nirgends eine zusammenhängende Kette von Thatsachen vor, welche der glückliche Beobachter einfach aufzunehmen und so darzustellen hat, wie er sie sieht […]. Die paläontologische Entwickelungsgeschichte […] bleibt ein

Thus, paleontology was the crucial pillar in his trinity: "*If we consider comparatively all the circumstances which make empirical paleontology such a highly fragmentary piece of work, we can place them in two series, one of which has its cause in the nature of the organisms that others have in the nature of the circumstances under which their remains can be obtained in the Neptunian layers of earth deposited from the water*"[27] (ibid.: 309). However, two pages later he summarized his view again: "*All these circumstances taken together prove to us that the body of paleontological material or the so-called 'geological record of creation' is in the highest degree incomplete and fragmentary, and that we are left with only a few scant indications, but nowhere a complete and coherent series of developments. Of the very many fossil species of organisms we know of only a single specimen or a few highly imperfect fragments, e.g. a single tooth or a few bones. We cannot form a reasonably complete picture of the entire distribution and development of any fossil species in prehistoric times*"[28] (ibid.: 311).

Haeckel repeated his criticism on paleontological material: "*For the correct understanding of phylogeny, one of the first and most necessary prerequisites is the correct and full knowledge of the extraordinarily high degree of incompleteness and fragmentary nature that the entire empirical material of paleontology possesses*" (ibid.: 308).[29]

Two years after the "*Generelle Morphologie*", Haeckel (1868) published his "*Natural History of Creation*"[30] (Hoßfeld 2010). Already in the 'third lecture' of this book, he addressed the history of paleontology by acknowledging Cuvier's merits in detail and again addressing the gaps in the fossil record: "[…] *but there are still a number of difficulties for paleontology, which are rooted in the nature of organisms themselves. Above all, it must be emphasized here that as a rule only hard and solid body parts of the organisms reach the bottom of the sea and fresh waters and can be trapped and petrified here in mud. It is therefore especially the bones and teeth of vertebrates, the calcareous shells of molluscs and asteroids, the chitinous skeletons of arthropods, the calcareous skeletons of corals, and also the woody, solid parts of plants that are capable of such fossilization. The soft and tender parts, on the other hand, which form by far the largest part of the body in most organisms, only seldom get into the mud under such favorable conditions that they petrify, or that their external form is clearly imprinted in the hardening mud. Now consider that whole large classes of organisms, such as the medusae, the naked mollusks, which have no shell, a large part of the arthropods, almost all worms, and even the lowest vertebrates do not have any solid and hard body parts capable of fossilization*"[31] (ibid.: 309–310).

Central to all paleontological interpretations was the emphasis on the importance of his "*threefold parallelism*".

Haeckel's conception of paleontology in its philosophical embedding

Despite these differences, Haeckel recognized and reiterated the appreciation Darwin (1859) gave to paleontology for the chain of evidence for the theory of evolu-

vollständig lückenhaftes und zerrissenes Flickwerk, wenn sie sich auf die bloßen Thatsachen beschränkt, welche die Paläontologie uns liefert, und wenn sie nicht zu deren Ergänzung den äußerst wichtigen dreifachen Parallelismus benutzt […]"

[27] Our translation from: "Wenn wir die sämmtlichen Umstände, welche die empirische Paläontologie zu einem so höchst fragmentarischen Stückwerk machen, vergleichend erwägen, so können wir sie in zwei Reihen bringen, von denen die einen ihre Ursache in der Beschaffenheit der Organismen, die anderen in der Beschaffenheit der Umstände haben, unter denen ihre Reste in den neptunischen, aus dem Wasser abgelagerten Erdschichten erhalten werden können"

[28] Our translation from: "Alle diese Umstände zusammengenommen beweisen uns, daß die Gesammtheit des paläontologischen Materials oder die sogenannte ‚geologische Schöpfungs-Urkunde' im allerhöchsten Maaße unvollständig und lückenhaft ist, und daß sie uns für die zusammenhängende phyletische Entwickelungsgeschichte nur einzelne dürftige Andeutungen, nirgends aber eine vollständige und zusammenhängende Entwickelungsreihe liefert. Von den sehr vielen fossilen Organismen-Arten kennen wir nur ein einziges Exemplar oder einige wenige höchst unvollkommene Bruchstücke, z. B. einen einzelnen Zahn oder ein paar Knochen. Von keiner einzigen fossilen Art können wir uns ein einigermaaßen vollständiges Bild ihrer gesammten Verbreitung und Entwickelung in der Vorzeit entwerfen"

[29] Our translation from: "Für das richtige Verständniss der Phylogenie ist eine der ersten und nothwendigsten Vorbedingungen die richtige und volle Erkenntniss von dem außerordentlich hohen Grade der Unvollständigkeit und Lückenhaftigkeit, den das gesammte empirische Material der Paläontologie besitzt"

[30] Our translation from: "Natürliche Schöpfungsgeschichte"

[31] Our translation from: " […] kommen aber noch eine Reihe von Schwierigkeiten für die Paläontologie hinzu, welche in der Natur der Organismen selbst begründet sind. Vor allen ist hier hervorzuheben, daß in der Regel nur harte und feste Körpertheile der Organismen auf den Boden des Meeres und der süßen Gewässer gelangen und hier in Schlamm eingeschlossen und versteinert werden können. Es sind also namentlich die Knochen und Zähne der Wirbelthiere, die Kalkschalen der Weichthiere und Sternthiere, die Chitinskelete der Gliederthiere, die Kalkskelete der Corallen, ferner die holzigen, festen Theile der Pflanzen, die einer solchen Versteinerung fähig sind. Die weichen und zarten Theile dagegen, welche bei den allermeisten Organismen den bei weitem größten Theil des Körpers bilden, gelangen nur selten unter so günstigen Verhältnissen in den Schlamm, daß sie versteinern, oder daß ihre äußere Form deutlich in dem erhärtenden Schlamme sich abdrückt. Nun bedenken Sie, daß ganze große Klassen von Organismen, wie z. B. die Medusen, die nackten Mollusken, welche keine Schale haben, ein großer Theil der Gliederthiere, fast alle Würmer und selbst die niedersten Wirbelthiere gar keine festen und harten, versteinerungsfähigen Körpertheile besitzen"

tion. The triad of paleontology, zoology, and embryology also shaped the first writings of Haeckel (1866, 1868; cf. Fig. 6). The arguments on paleontology, however, took on a more theoretical dimension, since in the middle of the 19th century only relatively few usable fossils were available, as Haeckel repeatedly emphasized. In fact, even Darwin (1859) lacked paleontological evidence for his theory. Only Franz Hilgendorf (1839–1904), a doctoral student of Friedrich August Quenstedt in Tübingen, Germany (Hölder 1983), with a detailed stratigraphy, created a first phylogenetic system on fossil organisms, namely freshwater snails (Hilgendorf 1863, 1867), and provided the required facts, so that Darwin later (after some hesitation: see Rasser 2013) included these findings in a new edition of his "*Origin of Species*" (Reif 1983a, Werneburg 2021).

Otherwise, from the biologists' point of view, paleontology remained rather erratic: fossils mainly provided only fragments of former organisms and the so important soft tissue and early ontogenetic stages, which together make a significant contribution to clarifying homologies (Remane 1952), are virtually non-existent in fossils. Accordingly, the importance of paleontology for Haeckel dwindled sharply in the coming decades and the triad of paleontology, zoology, and embryology receded into the background as an unfulfillable ideal.

The propagation of a phylogenetic perspective within a 'palaeo*biological*' research program by Othenio Abel (1875–1946) and the author's polemics against the traditional working methods and questions of paleontology (Abel 1914, 1915, 1918) caused a further distancing of biology and paleontology in the beginning of the 20th century (Schlesinger 1918, Khittel 2005). Abel's "*law of inertia*" [Trägheitgesetz] clearly placed him in the neo-Lamarckian camp, a departure from Darwinian biology (Rieppel 2012).

Haeckel's most important anthropological work is his "*Anthropogeny or Evolutionary History of Man*"[32] from 1874, consisting of four parts (historical, ontogenetic, phylogenetic, organogenetic part). Here he dealt in great detail with questions of human descent and general zoology taking into account ontogeny and organogenesis, etc., but did not represent any essentially new positions with regard to human phylogeny compared to the statements made in the 1860s (Haeckel 1874: 481–496). Also, with regard to his statements and listed tables and graphics on paleontology, there is nothing essentially new, especially since the focus here is on the comparative-anatomical and ontogenetic documents within the phylogeny of humans. Human fossil finds were still rare at the end of the 19th century, which is why he largely excluded the paleontological aspects in this work.

Haeckel's remark that individual human fossils are not absolutely necessary to substantiate our descent from the primates and that a "*comprehensive knowledge of comparative anatomy and ontogeny*" [33] (Haeckel 1895: 618) would be completely sufficient should – in this context – not be seen as an arrogance of the Jena professor towards paleontology in general. Rather, this statement underscores Haeckel's high scientific standards for a professionally managed morphology, which primarily refers to the anatomically more meaningful zoological and embryological facts.

Almost 30 years after the publication of his "*Generelle Morphologie der Organismen*" (1866), in the work "*Systematic Phylogeny*"[34] (Haeckel 1894–1896), Haeckel finally discussed in the eighth chapter of the third part "*Systematic Phylogeny of Vertebrates* (*Vertebrata*)"[35] again in detail the "*Systematic Phylogeny of Man*"[36], partly now with stronger consideration of paleontology and morphology. According to Haeckel, however, the paleontology of primates offered only very sparse data, which could be explained by the "*arboreal way of life of the apes and prosimians, and by the unfavorable conditions that make their preservation in the fossil state more difficult*" [37] (ibid.: 616–617). Of the (skull) fragments found, he attributed a certain "*high value*" to some, such as the *Homo* ("*Pithecanthropus*") *erectus* of Java (found in 1894), "*which is indeed the so eagerly sought 'missing link' in the chain and seems to correspond to the transitional forms. Also the similar Neanderthal and Spy diluvial skulls, with very low forehead and strongly projecting orbital arch, probably belong in that chain*"[38] (ibid.: 617).

Despite these individual positive statements, he did not assign such a central role to paleontology as he did in 1863 in the theoretical discussion about the threefold parallelism. One would like to think that a certain reduction in the meaningfulness that paleontology – in comparison to zoology – can provide for the great questions of evolution due to its fragmentary nature developed. Thinking more holistically, he remarked: "*We can only partially recognize the great importance that laypeople or one-sidedly trained specialists in science place on the detection of such 'fossil humans' and 'transitional forms from apes to humans'. Those who have extensive knowledge of comparative anatomy and ontogeny, as well as of paleontology, and who are capable of an impartial*

[32] Our translation from: "Anthropogenie oder Entwickelungsgeschichte des Menschen"

[33] Our translation from: "umfassende Kenntnis der vergleichenden Anatomie und Ontogenie"

[34] Our translation from: "Systematische Phylogenie"

[35] Our translation from: "Systematische Phylogenie der Wirbeltiere (Vertebrata)"

[36] Our translation from: "Systematische Phylogenie des Menschen"

[37] Our translation from: "aboralen Lebensweise der Affen und Halbaffen, und aus den ungünstigen Verhältnissen, welche ihre Erhaltung in fossilem Zustande erschweren"

[38] Our translation from: "hohen Werth […] welches in der That dem so eifrig gesuchten 'fehlenden Gliede' in der Kette der Uebergangsformen zu entsprechen scheint. Auch die ähnlichen diluvialen Schädel von Neanderthal und Spy, mit sehr niedriger Stirn und stark vorspringendem Orbital-Bogen, gehören wahrscheinlich in jene Kette hinein"

comparison *of phenomena, do not need those fossil documents in order to recognize the 'descent of man from the ape' as a* historical fact*. For us, the same already appears as a* fully empirically founded *hypothesis, regardless of whether later paleontological discoveries will still find 'intermediate forms' or not*"[39] (ibid.: 618, emphasis as in the original).

A major shortcoming in Haeckel's reception of paleontology was the expectation of a higher development, a "perfection" of the organisms over time: "*The paleontological perfection or the phylogenetic progress is of these three parallel progressive development series* (*like this also applies of the three parallel differentiation rows*) *the most original and therefore most important one. When we showed previously that progress is a necessary consequence of the interaction of adaptation and heredity, this applied first only to phylogenetic perfection, which shows itself in the gradually progressive development of species and tribes, i.e. in the fact that the transmutation of species not only leads to the production of new species, but also to more perfect species as a whole, and that consequently the tribes as a whole are constantly improving themselves. All paleontology provides a continuous chain of evidence for this*"[40] (ibid.: 264–265).

This conception of progressive higher development in evolution can also be seen in the example of the important vertebrate morphologist Ernst Gaupp (1865–1916), a contemporary of Haeckel, whose arguments were based more on an evolutionary ladder (*scala naturae*; Lullus 1512) than on Darwin's evolutionary branching concept. Thus, Gaupp viewed the lizards, monotremes, and marsupials 'in line' with placental mammals (Werneburg and Spiekman 2017), leading to misinterpretations of his otherwise very detailed observations (Gaupp 1891, 1900, 1913; see discussion, but also appreciation in Maier 2021: pp. 383–385).

Haeckel never openly supported teleology. He insisted that natural selection constitutes the crucial argument 'for the exclusive validity of mechanically acting causes in the whole field of biology', i.e., the ultimate evidence for the necessity of naturalistic-causal explanations, thereby whisking away all kinds of teleology (Haeckel 1866, Bd. I, p. 100). In other words, natural selection was for Haeckel not only an ultimate explanatory pattern of biological phenomena but the cornerstone of the new naturalistic worldview opposed to religious prejudices (Levit and Hossfeld 2021).

To ban teleology from the theory of biological evolution Haeckel introduced the term "dysteleology" as a doctrine of "goallessness" in evolution (Haeckel, 1866, Vol. II, p. 266ff). At the same time, the whole logic of his doctrine seems to suggest inevitable progress [German "Vervollkommnung"] towards "more perfect" organic creatures: "*The notion of progress is the key of Haeckel's evolutionary theory*" (Dayrat, 2003, p. 524). Haeckel's progressivism is, however, not about the intrinsic tendency towards perfection but follows from natural laws governing cosmic and organic evolution and the ontological structure of the universe. For Haeckel, "*there was no teleological providence in the universe, only a naturalistic law of progress*" (Di Gregorio, 2005, p. 189). The progress towards perfection followed from these laws such that gradual perfecting in biological evolution (teleosis, in Haeckel's terms) is the inevitable result of natural selection (Haeckel 1900, p. 272). The transition from inert to living matter is a necessary logical link in this worldview. In other words, Haeckel's concept of "Vervollkommnung" should be separated from classical teleology. Organisms evolve towards perfection, but not towards a certain goal, whereby perfection is not the goal of evolution but a byproduct of fundamental natural laws.

According to Haeckel, the entire paleontology would have to provide, a continuous chain of evidence' for the imaginary higher development of organisms. But it did not do that (yet). This disappointment can be traced in Haeckel's view of nature, which was still in its infancy about evolutionary changes around the turn of the century. While many highly specialized forms of organisms had dominated certain geological epochs, but became extinct as a result of drastic events in geological history, less specialized, i.e. generalistic species survived (Raff 1983), which contradicts the imagined 'mechanism of perfection over time'.

As described above, the documentation of the fossil record had a more geological background and neither paleontologists nor biologists in the second half of the 19th century were able to estimate the complexity of evolutionary changes. This required modern analysis techniques such as phylogenetic systematics (Hennig 1950, 1966),

[39] Our translation from: "Das große Gewicht, welches von Laien oder von einseitig gebildeten Special-Forschern auf den Nachweis solcher ‚fossiler Menschen' und ‚Uebergangs-Formen vom Affen zum Menschen' gelegt wird, können wir nur theilweise anerkennen. Derjenige, der umfassende Kenntnisse in der vergleichenden Anatomie und Ontogenie, sowie in der Palaeontologie besitzt, und der zu einer unbefangenen *Vergleichung* der Erscheinungen befähigt ist, bedarf nicht jener fossilen Documente, um die ‚Abstammung des Menschen vom Affen' als *historische Thatsache* anzuerkennen. Für uns erscheint dieselbe schon jetzt als *völlig empirisch begründete* Hypothese, gleichviel ob spätere palaeontologische Entdeckungen noch ‚Zwischenformen' auffinden werden oder nicht"

[40] Our translation from: "Die paläontologische Vervollkommnung oder der phylogenetische Fortschritt ist von diesen drei parallelen fortschreitenden Entwickelungs-Reihen (wie dies auch ebenso von den drei parallelen Differenzirungs-Reihen gilt) der ursprünglichste und daher wichtigste. Wenn wir vorher zeigten, daß der Fortschritt eine nothwendige Folge der Wechselwirkung von Anpassung und Vererbung sei, so galt dies zunächst nur von der phylogenetischen Vervollkommnung, welche sich in der allmählich fortschreitenden Entwickelung der Arten und Stämme zeigt, darin also, daß die Transmutation der Species nicht allein zur Erzeugung neuer, sondern im Ganzen auch vollkommnerer Arten führt, und daß mithin auch die Stämme im Ganzen sich beständig vervollkommnen. Die gesammte Paläontologie liefert hierfür eine fortlaufende Beweiskette"

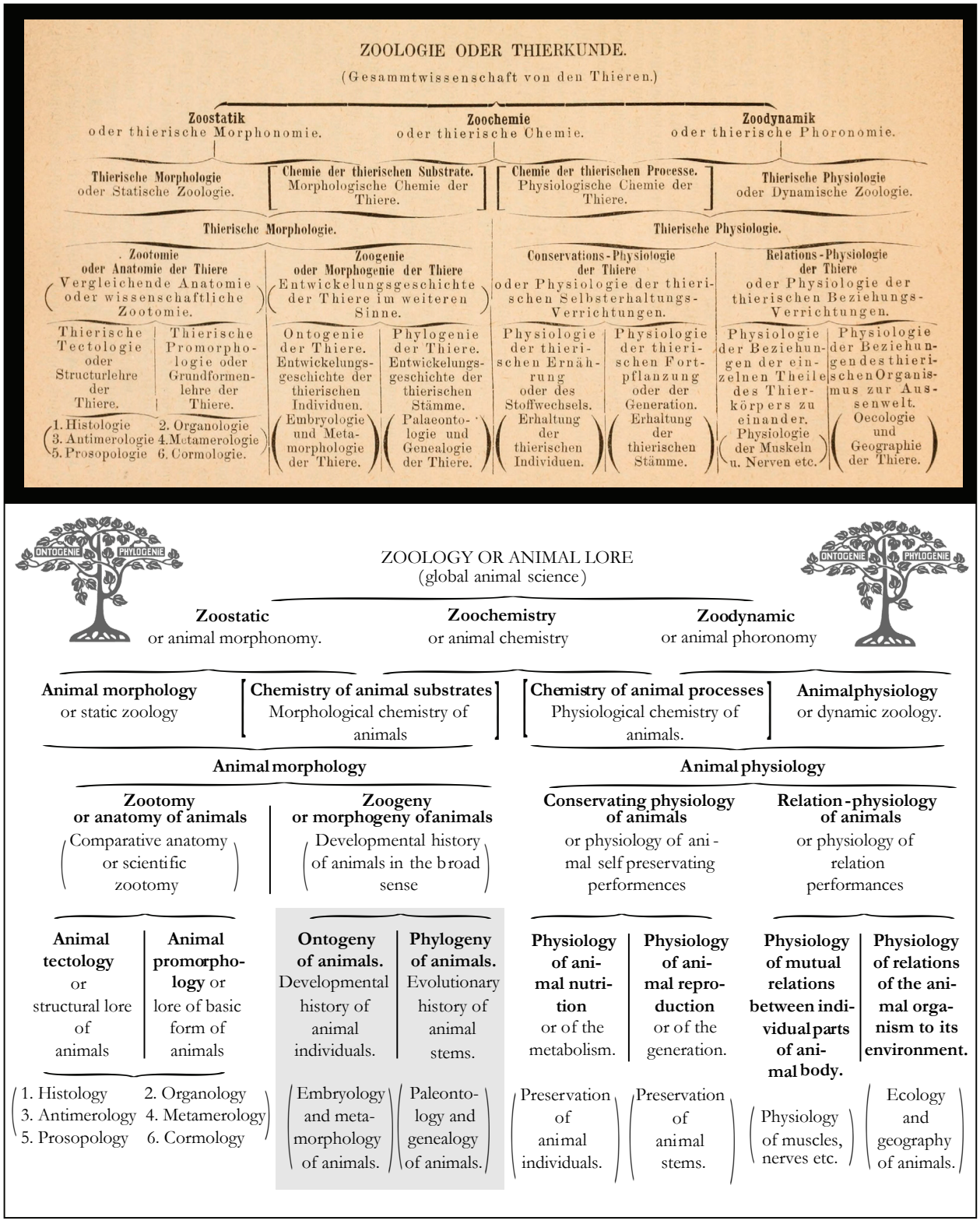

Figure 6. Conceptualization of "Zoology or Animal Lore" by Ernst Haeckel (1866: 238) and translation by us. The inlays "Ontogenie / Phylogenie" are from the pediment of Phyletisches Museum Jena, founded by Ernst Haeckel in 1907. Ontogeny/Embryology and Phylogeny/Paleontology are highlighted. Note that, different to the lecture presentation (Fig. 5), both are equally ranking as a sub discipline of "zoogeny".

cladistics (Wägele 2001), or various statistical methods (Hammer and Harper 2005), which could only be used effectively by computer methods more than a century later. In this way, 'fluctuating' complexes of forms are quantified and interpreted in space and time. Numerical tree reconstructions can now place even the previously daunting fragments of the fossil record in a phylogenetic context and secondarily test hypotheses about the homology of certain traits (de Pinna 1991). The geology also serves, in a new synthesis, for the temporal calibration of

reconstructed evolutionary splitting events. New global fossil deposits provide numerous 'transitional forms' of the once patchy fossil record, and morphological inferences often have to be reconsidered.

The dominance of the zoologist and embryologist Haeckel in the development of German paleontology should not be underestimated. Haeckel's books were widely read and their content influenced the perception and estimation of the fossil record, at least among German biologists. In the anglo-american part of the world, comparative anatomy was initially based on the research of osteologist Sir Richard Owen (1804–1892), primarily on skeletal or hard-tissue material, which also inspired extensive integration of fossils into research (Agassiz et al.; Rupke 1983, 1985, 1993, 1994). For this reason, zoology and paleontology in England and America tended to develop as a unit, while the dominance of phylogenetics and embryology prevented this unity in Germany (Reif 1983b, 1986, 1999).

Another reason may lie in Germany's natural-philosophical traditions. Although Haeckel also apparently distanced himself from it in his lectures and with his monistic program, typological thinking lived on through him, namely through his reference to Goethe and his language (with its corresponding terminology of processes in nature). Since Goethe, holism, monism, and typology have persisted in Germany, the latter representing an epistemology based on the construction of mathematically abstract generalizations. The accusation that is often made, for example, that Haeckel falsified illustrations (discussion by Richardson and Keuck 2001 and by Richards 2009), should, therefore, be viewed with caution, because these were not falsifications, but rather typologically constructed abstractions. Goethe's worldview, widely adopted by German natural scientists (see Levit and Meister 2006), also influenced the long-lasting separation between zoology/embryology and paleontology in Germany. The peculiar mixture of the fundamental philosophy of nature and the fascination that emanated from Darwin's system led to the promotion of phylogenetics by zoologists. This approach, however, was suspect for paleontologists because of its inconsistency with half philosophical, half scientific approaches (see Reif 1983a). This problem was only solved by the method of phylogenetic systematics, which was only recognized late in Germany (Hennig 1950, 1966).

Concluding remarks

Haeckel was a pure zoologist and embryologist. This can be seen in the structure of his paleontology lectures held in 1863 (Uschmann 1959) and 1866 (Miklucho's manuscript presented herein). Rather quickly, he went through the epochs of the earth's history in just a few hours, later throwing himself into taxonomy and general zoological topics. His scheme for the position of paleontology as a sub-discipline, i.e. as just an additional piece of evidence of zoology and embryology (keyword: recapitulation) (Script Page 24r; Figs 5–6), is symptomatic. This reveals his emphasis on this holistic triad, which he had originally described as an ideal in 1866, but later turn towards the detriment of paleontology.

In his lecture of 1868, a certain change was already evident (Uschmann 1959), which documents a greater increase in knowledge in paleontology as a whole (e.g., Quenstedt 1852, 1861, 1867; Reif 2000), but also Haeckel's personal development and the enrichment of his own knowledge. Because now, in the new structure of the paleontology lecture, the geological eras actually dominated over the taxonomic aspects (Uschmann 1959). It is not possible to reconstruct whether much that was new had actually changed in terms of content. Judging from Haeckel's later writings, however, he does not appear to have incorporated any particular innovations into the later paleontology lectures. As in the earlier lectures, the questions on the fossilization principle and on taphonomy, central points in geology (Ziegler 1992), are also only mentioned briefly at the beginning of his 1868 lecture on paleontology. Conceptually, little seems to have happened, otherwise the above-mentioned questions about stratigraphy, ecosystems, trophic communities, and the like would have come more to the fore.

The paleontology of the late 19th century was still strongly taxonomically oriented. Researchers wanted to bring order to the complexity. For the vertebrates, Haeckel referred to Louis Agassiz (1807–1873) and Johannes Müller (1801–1858) (Script Pages 12v and 12r) with the latter proposing an innovative classification system for fossil fishes. In a comparison of both systems, Haeckel showed the limitations of Agassiz' taxonomic approach compared to Müller's 'natural approach'. However, the method for a well-founded family tree of fishes was still missing, which only became possible through phylogenetic systematics, later cladistics, and molecular analyses in the second half of the 20th to the 21st century (Wägele 2005; Rieppel 2016).

The holistic concept of creating a triad of paleontology, zoology, and embryology is now a crucial approach in a holistic evolutionary morphological research program (Maier and Werneburg 2014). A focus on geological events in paleontology can shift the focus to questions of biomineralization (Seilacher and Gishlick 2015; Briggs 2017), but it also remains a holistic way of working. Haeckel's vision must, therefore, be recognized as great and groundbreaking and may even serve as an example of holistic research for zoologists, embryologists, and paleontologists today.

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Appendix 1

Specific notes on Haeckel's paleontology lecture given in 1866

Haeckel's teaching activity extended over a period of 96 semesters (summer semester 1861 to winter semester 1908/09). Within these 48 years, he could not read for only five semesters – often because of his travels (1866/67: Canary Islands, 1881/82: Ceylon, 1900/01: Insulinde, 1903/04: Rapallo, 1905/06: disease). There are only a few records of the content of the lectures given (Uschmann 1959: 40 ff., Hoßfeld et al. 2022a, b), so that now, with Miklucho-Maclay's lecture notes on paleontology, a complete transcript of this subject exists for the first time. The manuscript "*Paleontologie*" dates to the summer semester of 1866 and comprises 63 pages (Werneburg et al. 2022).

Miklucho-Maclay's skill at drawing is undeniably documented by the detailed and realistic drawings from his travels (see Hoßfeld et al. 2021b). He also demonstrated those skills in the notes from the student time in Jena. In his lectures, Haeckel used a wide range of media and forms of representation to illustrate his lectures. According to another student, the later important morphologist Max Fürbringer (1846–1920), who also attended the paleontology lecture in 1866, "on the walls of the auditorium hung instructional boards drawn by Haeckel himself, and in front of the benches were tables with animals and preparations" [41] (Uschmann 1959: 68).

In addition to their intrinsic aesthetic value, Miklucho-Maclay's notes also offer valuable insight into Haeckel's style of presentation, as they provide information about the minimum scope of the means of representation he used in his presentation. The illustrations range from schematic cross-sectional drawings on Script Page 3r, through more detailed sketches with crosshatching, as on Script Pages 4v and 30v, to a detailed profile of a human face on Script Page 24f (Werneburg et al. 2022).

The lecture transcript is characterized by a relatively good legibility as well as the numerous morphological and paleontological drawings (Figs 3–4), which for the first time allow a direct insight into the content and visualization of Haeckel's paleontology of those years. It can be assumed that Miklucho-Maclay did not follow up on the lecture, but rather took the content directly from the lecture and from the blackboard etc. into the notebook. Table 1 provides an overview on the contents of the whole script.

There are several thematic breaks and jumps in the script. On Script Page 20r, for example, there is a heading which indicates that the next lecture subject would have been birds (Aves). Shortly thereafter, however, on pages 21v and 21r, are two sheets that seem completely out of place in the rest of the notebook. The typeface is striking: it is most illegible at this point in the notebook. Also, on no other Script Page are the edges of the sheets as badly damaged as on these two pages. The transcript for these two pages is very incomplete and riddled with illegible words. The individual groups of words that could be deciphered reveal that these two pages are not transcripts of paleontology lectures, but rather deal with medical issues.

Script Page 22v does not continue with the content on birds, but rather an outline of the history of biology follows, concluded with a list of further reading.

The overview of some taxonomic groups that follows on Script Pages 25v to 26v appears like a strongly condensed summary of a lecture on systematic zoology.

The general part, lasting from Script Pages 26r to 27v, provides an overview of the structure of chemical elements and their connection to tissues.

On Script Page 29v, there is a separate heading for systematic zoology, under which the types of tissue are also listed. The following list also seems incomplete, since on Script Page 31r under the heading "*Movement organs*"[42] there is another subdivision of which only the first half "*a*) *Passive*" is available. The implied second heading "*b*) *Active*", which would be assumed to be on the following page, does not exist.

There are different possibilities to explain this apparent incompleteness. Besides the historical situation associated with the Austro-Prussian war, as discussed in the main text above, it is possible, for example, that Haeckel deliberately omitted the birds in the paleontology lecture and referred to the corresponding explanations in the zoology lecture. Not all of the subgroups of reptiles listed on Script Page 18r appear on the following pages either. The "Glyptodermata" (worm lizards, i.e. Amphisbaenia) and snakes are missing here. Haeckel's notes and transcripts on the zoology lectures are available (Hollstein 2019: 32, Hoßfeld et al. 2022b) and also contain passages that could imply such cross-references. It could also be that Haeckel calculated speaking time somewhat more freely and considered it necessary to clarify the origins of paleontology in a paleontology lecture with an outline of the history of zoology. This could be justified by the overview of the sub-disciplines of zoology on Script Page 24r. There he integrates paleontology into zoology as a subfield of embryology (Fig. 5; note the conceptual difference to Fig. 6).

It is also possible that Miklucho-Maclay used the same notebook for different purposes. It is noticeable that the breaks and jumps on the thematic level occur almost identically to changes in the typeface and the length of the sentences. The first third appears hectic and written in bullet points, while the section on the history of biology, for example, appears to have been written rather

[41] Our translation from: "hingen an den Wänden des Auditoriums von Haeckel selbst gezeichnete Unterrichtstafeln, und vor den Bänken standen Tische mit Tieren und Präparaten"

[42] Our translation from: "Bewegungsorgane"

slowly due to its smaller font size, the clean spelling, the long sentences, and the lower density of spelling errors. This may reflect Miklucho-Maclay's personal interest in humanities-related issues, as his later career suggests (Schneider 1997) or another style of giving lectures by Haeckel to approach these non-natural science related topics.

The overview of the structure of the transcript (Table 1) already gives a first insight into Haeckel's teaching style. An interesting finding is that the individual sub-chapters on the respective groups of organisms rarely provide detailed information about them. In this respect, Haeckel may be doing justice to his own didactic approach when he claims that he does not want to overwhelm the students with a multitude of details, but rather to give them an overview that they can use to delve deeper into the topic individually.

In the general part, there is also evidence that Haeckel was spreading approaches to monism in his lectures already in 1866, even before the publication of the "Generelle Morphologie der Organismen". Miklucho-Maclay noted Haeckel's opinion as follows (Script Page 26r): "*If we wish to divide the nature into kingdoms, we can only divide them into organic and inorganic kingdoms. Forces of life function and life phenomena, vitalists* (*Johannes Müller*)*, imponderable moments* (*soul, spirit etc.*)*. We cannot accept this, we will maintain the monistic point of view*."[43]

[43] Our translation from: "Wenn wir die Natur der Reiche theilen wollen, so können wir diese nur in organische und anorganische Reiche eintheilen. Lebensfunktions-Kräfte und Lebenserscheinungen, Vitalisten (Johannes Müller), Inponderable [unwägbare] Momente (Seele, Geist etc.). Diese können wir nicht annehmen, wir werden den monistischen Standpunkt beibehalten."