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Karl Ernst von Baer (1792-1876) and Evolution

SABINE BRAUCKMANN*

Science Centre, Tartu University Library, Tartu, Estonia.

ABSTRACT The research program of Karl Ernst von Baer (1792-1876) intended to enhance the comparative approach of animal classification by demonstrating vertebrate affinities (homology). Baer visualized his ideas on development and evolution with an unpublished figure of a branching tree. To buttress his reflections on how species-specific embryogenesis produces a branching tree, he worked out a cladogram-like chart, depicting the ontogeny and phylogeny of vertebrate embryos. For Baer, changes in development were responsible for changes in phenotype. I will offer a new interpretation of Baer's ideas about evolution showing that he believed in the transformation of species and announced such views publicly.

KEY WORDS: *von Baer, history of developmental biology, evo-devo, hourglass model*

Introduction

As a contribution to the developing history of evo-devo, I present here a previously unknown and quite prescient view about development and evolution advanced by Karl Ernst von Baer (1792-1876) in the early 19th century. When scrutinizing the research problems that were disregarded by neo-Darwinism (Gilbert *et al.,* 1996; Hall, 1999; Raff, 2000; Wagner, 2000; Amundson, 2002; Arthur, 2002; Love & Raff, 2003; Minelli & Fusco, 2008), *Entwickelungsgeschichte* (developmental history) provides an important and up to now neglected topic. Baer's reflections about developmental history (Baer, 1819, 1823, 1827, 1828) offer a most appropriate point of departure, particularly since his ideas are referred to and propagated among scientists dealing with the genetic connection between evolution and development (see most recent research on phylotypic stage, hourglass model), despite debates about the validity of his research programme (Ballard, 1976; Kluge & Strauss, 1985; Richardson & Keuck, 2002; Poe, 2006).

Baer's law of individual development and, in particular, its third proposition (embryos of different species progressively diverge from one another during ontogeny) was newly explored when developmental biologists started to reason about the phylotypic stage and zootype, and formulated the hourglass model (Seidel, 1960; Sander, 1983, 2002; Slack *et al.,* 1993; Duboule, 1994; Richardson *et al.,* 1998; Galis & Metz, 2001; Bolker, 2001; Binida-Edmonds etal, 2003; Hazkani-Covo *et al.,* 2005; Domazet-Lošo & Tautz, 2010; Prud'homme & Gompel, 2010). The phylotypic stage is the period during ontogeny when general characters shared by all members of the phylum become evident; that means, embryos converge to relative similarity from very disparate beginnings, diverging again afterwards (Hall, 1997). The morphogenetic equivalent is the zootype, identifying a spatial pattern of conserved *Hox* gene expression, which to an extent rehabilitates Geoffroy St. Hilaire's notion of archetype (Slack *et al.,* 1993). The overall theory was provided by the developmental hourglass model (Richardson *et al.,* 1998; Duboule, 1994) which predicts a developmental stage of a maximum degree of similarity among the members of the phylum (Kalinka *et al.,* 2010). In extending these morphological concepts to the molecular level, recent studies that utilized different methods of gene expression data (Domazet-Lošo & Tautz, 2010) and phylostratigraphy (Prud'homme & Gompel, 2010) have demonstrated how the "waist" in the hourglass arises and to which extent ontogeny and phylogeny are linked at a molecular level. All these scientists refer to Baerian comparative embryology, either regarding their results as supporting Baer's guiding principles of developmental history (Domazet-Lošo & Tautz, 2010), or stating the basic correctness of Baer's, Darwin's and Haeckel's earlier studies (Kalinka *et al.,* 2010).

They could have also referred to Baerian ideas to connect evolutionary and developmental processes along their time axes. However, research on Baer has placed him for some time inside the anti-Darwinian camp not paying attention to the full body of his works (Baer, 1819, 1823, 1827, 1828, 1834, 1859, 1864). Due to this oversight Baer was misplaced (so to speak), partly due to Haeckel's not entirely accurate view of Baerian scholarship and some misinterpretation of Huxley's approach towards archetypes.

Here I will present a new piece of evidence for why he is part of the history of embryology and evolutionary reasoning. Based on an unpublished hand-drawing uncovered in the Baer Collection of the University of Giessen, and some forensic analysis of a table by

***Address correspondence to:** Sabine Brauckmann. Science Centre, Tartu University Library, Struve 1, 50091 Tartu, Estonia. e-mail: sabine.brauckmann@ut.ee

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Fig. 1. Portrait of Karl Ernst von Baer (1792-1876), *ca. 1834. Engraving by Friedrich Leonhard Lehmann (1787-c, 1840), after a drawing by Carl Wilhelm Hübner (1814-1879). Fond 570b, Photographic Collections, Tartu University Library, Estonia.*

Baer, I argue that he did indeed have a genuine evolutionary theory, and not merely a limited view of evolution. Evidence suggesting that Baer was an evolutionist sheds new light on current debates about the role of embryology in the formation of theories of species transformation. As I show, he conceived of species transformation in the image of a "branching tree" and, much as Darwin would later do, he built his argument from evidence in comparative embryology, biogeography, paleontology, and animal breeding. In the following paragraphs I will reconstruct Baerian reflections on developmental history, relying on this tree drawing of Baer.

The present analysis also hinges on a new interpretation of Baer's use of the word "type", which should not be taken to mean an "ideal archetype", as is still commonly assumed (Mikhailov, 2012). Because of its Platonic connotations Baer intentionally did not use archetype when defining type as the "positional relationship between the organic rudiments and organs" (Baer 1828: 208), which is empirically verifiable by any observer (Rieppel, 2006). The Platonic view on Baer actually goes back to an interpretation of Thomas H. Huxley's translation (Huxley, 1853; Eng, 1978; Lyons, 1995), which misconstrued Huxley's word "archetype" (Baer's *Grundform*) as a kind of metaphysical entity and therefore misplaced Baer's work into the anti-evolutionist category (Horder, 2006). According to Huxley, the concepts of general types and common plan (or archetypes) function as a tool for classifying animal form (Huxley, 1854, 1856: 306). To explain the transformation of major animal groups (evolution) Baer employed the concept of "(developmental) scheme". Indeed, scheme is the term he proposes to use instead of type: *"Basically I could have exchanged the expressions 'type' and 'scheme' for one common term"* (Baer, 1828: 257-258).[1]

The branching tree of developmental history

Around 1820 Baer intensified his studies of comparative embryology, applying the concept of general types, or (developmental) schemes to animal classification (Oppenheimer, 1953; di Gregorio, 1982; Lenoir, 1988). The general issue he addressed was "whether the developmental differences in individual animals and the structural diversity in the whole animal kingdom can be related to each other" (Baer, 1828: 202). In other words, he tackled the issue of whether there are ancestral relationships among the animal groups. Baer's point of departure was to refute the belief in the uni-directional mode of preformation, or recapitulation (Meyer, 1935; Holmes, 1947; Patterson, 1983), which he had already attacked in his dissertation (Baer, 1823), discussing mammalian fossils that were found in Prussia. In defining animal classes according to their actual structure he showed that embrogenesis of higher animals cannot include forms resembling a series of lower animals (Winsor, 1976).

By tracing the developmental stages of vertebrate and invertebrate embryos (Baer, 1819, 1828, 1834) he aimed to discover how and in what way the various organic forms emerged, whether they develop out of one another through reproduction and transformation (evolution), and how organic life came about. Using comparative embryology as his way into this question, he focused on how schemes control ontogeny and how these controlling mechanisms transform species over geological time.

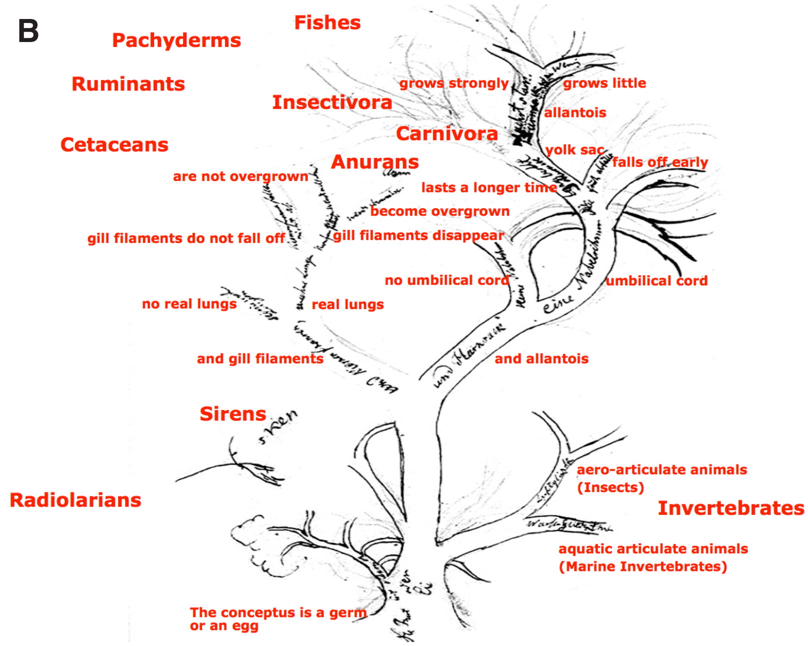
In the process of working out the relationship between ontogeny and species transformation, he drew a branching tree diagram (Fig. 2A; translated into English in Fig. 2B) illustrating how he thought about the evolutionary relationship among animals, including the relationship between the invertebrate and vertebrate forms, all of which grow from the same trunk. This tree diagram makes it astonishingly clear that not only did he have an evolutionary conception of animals, but that he based his understanding of these evolutionary relationships mainly on evidence from embryology. The different branches correspond to embryological differences, with the germinal vesicle or egg being the common first stage.

Lest we conclude that by not publishing the diagram, Baer was not truly committed to an evolutionary theory, I note that the published table in *Entwickelungsgeschichte der Thiere* is in fact a written version of this very same branching tree diagram (Fig. 3A). If the "tree" is turned on its side, with the trunk to the left, there is a close match between this tree diagram and the published chart. In order to make this connection clear, I have redrawn the tree using the information from the chart, substituting brackets with lines, but otherwise without changing any of the content of Baer's table. In this cladogram-like drawing the close correspondence between the unpublished tree image and the published chart is evident (Fig.3B) (see also Patterson, 1983; Kluge & Strauss, 1985).

A table of developmental progress and a cladogram of species transformation

In Baer's view, development is regulated by the same mechanism in all animals (Baer, 1834: 497-502), starting with the primary separation of the embryo into germ layers (gastrulation), followed by histological differentation (cellular specification) and the species-specific phenotype of the adult animal. In his study of Batrachian development Baer traced the mechanism of cleavage and concluded: "The norms proposed here for the divisions contain, I believe, a theory of transformations, so that if one can measure the reciprocal power of each of these rules, one is in a

[1] "Im Grunde hätte ich also die Ausdrücke Typus und Schema mit einem gemeinsamen vertauschen können." (pp. 257-258) (translated by author)



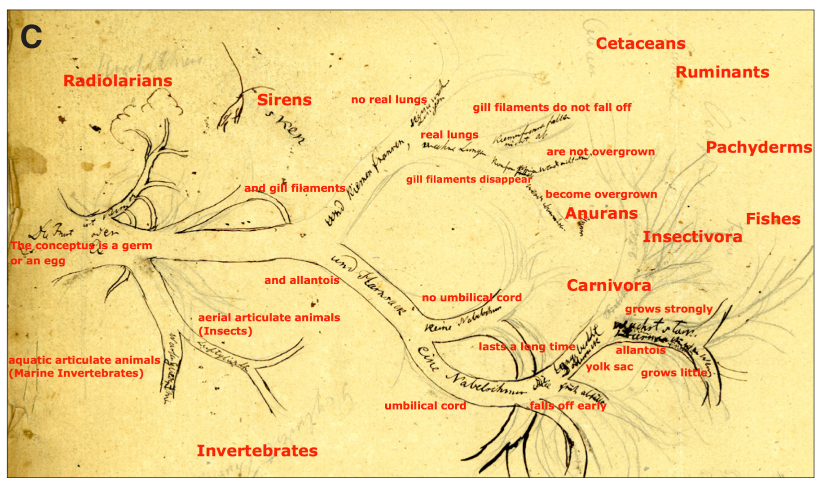


Fig. 2. Baerian tree of Developmental History. (A) *Hand drawing by Karl Ernst von Baer, ca. 1826 (Giessen, Universitätsbibliothek, Special Collections, Nachlass Baer, Schriften vol. 22, Blatt/Sheet 16; reprinted with permission from Special Collections, University Library Giessen, Germany).* **(B)** *The same as (A), with an English translation of Baer's hand-writing (by author).* **(C)** *The same as (B), but rotated to the right.*

position to construct the whole process *a priori*." (Baer, 1834: 502). When starting his studies of developmental history and animal systematics, he first utilized the (new) botanical system that classified plants on the basis of their embryonic stages, resulting in divisions between Acotyledons, Monocotyledons, and Dicotyledons (Baer, 1828: 225, 242-243; de Candolle, 1813; Farber, 1976). An advantage of using embryonic stages was that the species-specific schemes of development were more visible than in adult organisms. In the next step he inferred that the individual development of a specific animal form is determined by two relations, (1) by the formation of the animal body triggered by progressive histological (cellular) and morphological differentiation (Baer, 1828: 153-159), and simultaneously (2) by transformation of a more general form to a more specific one (Baer, 1828: 231). That means, the developmental scheme, residing inside the embryo (later he located it inside the nucleus, Baer, 1847) results in a specific segregation that, conversely, results in a specific phenotype. Baer argued that all developmental schemes procede from an initially hollow sphere (*Bläschenform*, or blastula) and include a vesicular form, wherein differences appear between internal and external layers, and that the specific form is determined by the growth and differentiation of the germ layers (Baer, 1828).

In the tree drawing the roots start from the ovum, a primordial form that is common to all animals. Then it branches, or differentiates into species-specific organs, using the classificatory value of components such as the gills, lungs, or placenta. In tracing the developmental trajectories of moving germ layers changing into organs (*Bildungsbögen*, see Baer 1828, table III, fig. 4; Brauckmann, 2011) he classified species according to whether branchial gills, lungs, allantois and/or umbilical cord emerges during ontogeny. Then he looked closely for what particular shapes the organs are transformed into, how long they persist, or how fast they develop. For example, at the beginning, the vertebrate developmental scheme produces nothing else than a vertebrate with a *chorda dorsalis* (notochord), ventral (gut) and dorsal (neural) tube, gill slits, gills and heart. Then the embryo differentiates; in some embryos gill filaments grow out, but no allantois; in others, the gills merge and an allantois develops. Animals with an outgrowing allantois form either an umbilical cord (mammals), or do not possess an umbilical cord (birds, reptiles). The umbilical cord of mammals

A

B

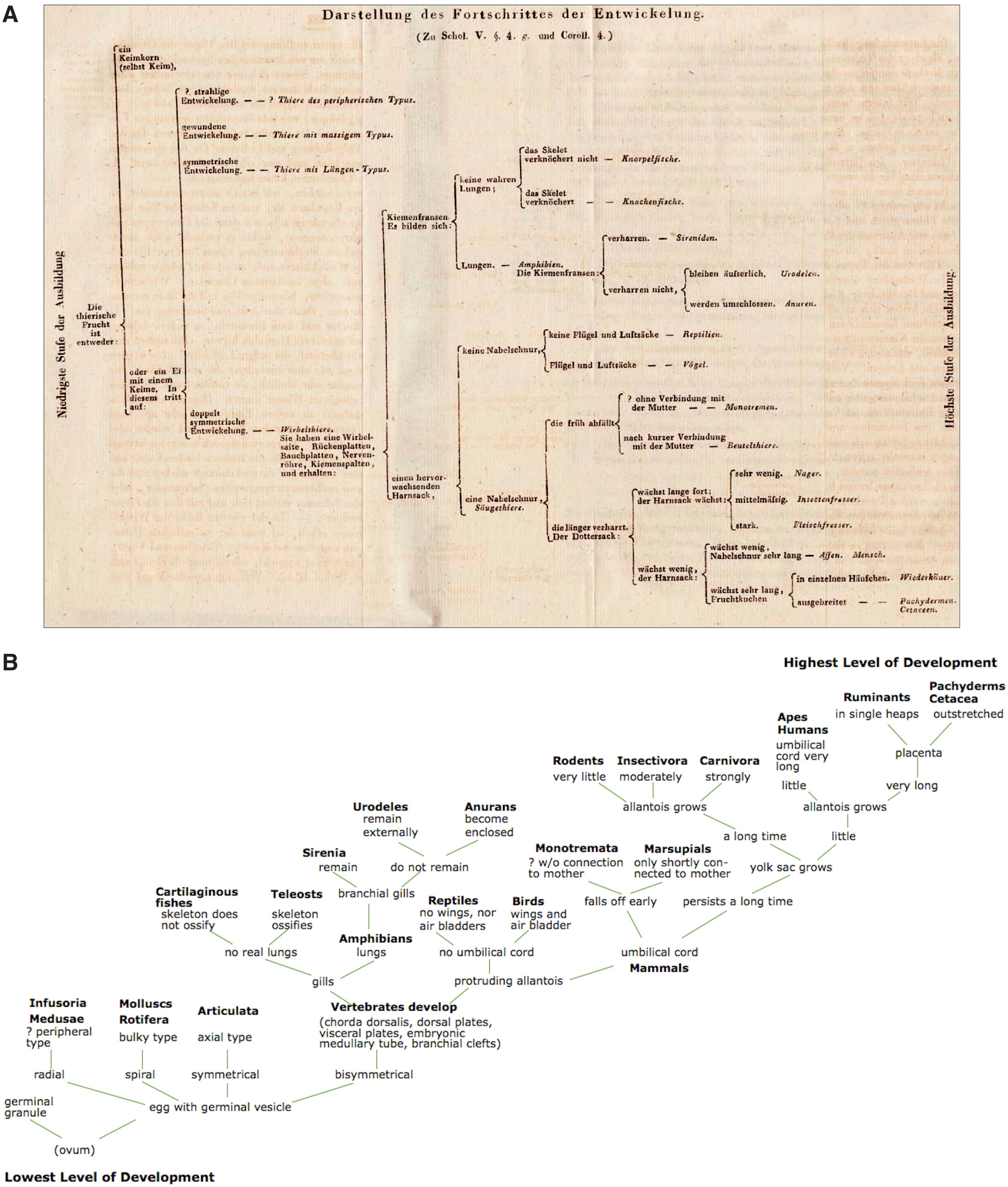


Fig. 3. Scheme of the progress of development in vertebrates. (A) *From Karl Ernst von Baer 1828.* Entwickelungsgeschichte der Thiere, *vol. I, p. 225.* **(B)** *The same information as in (A), but without the brackets and an English translation of Baer's words (by author).*

either falls off early (marsupials), nourishes the embryo a long time (placental mammals), and/or forms a yolk sac. Despite that, in these species the umbilical cord can be either a short stalk or a long cord. The most fundamental difference in vertebrates that do not acquire external gills is that a simple navel forms in some animals (reptiles, birds), and that in others (apes, humans) the umbilical cord moves out (Baer 1828). The hand-drawing discontinues at this stage whereas the table continues in considering, for example, the longitudinal growth of the allantois, and in placing humans and apes beneath pigs, cows and hoofed animals, due to the complex patterns of their placenta. Baerian reflection flouted conventional Cuverian wisdom when positioning cows and pigs at the top of the tree, elevating both due their stomach perfection in comparison to apes and humans (Elwick, 2007).

Baer himself was not entirely satisfied with his table as a way to depict evolution as it attempts to model processes that happen in the 4-dimensions of space and time onto the 2-dimensional flatness of paper. He openly conceded that there does not exist any 2-dimensional depiction that sufficiently represents organic relationships, whether ontogenetic or phylogenetic.

Species and evolution

In a public lecture delivered in 1834, Baer concluded that species are as transitory as individuals: *"We may also conclude [.] that the complete extinction of very many types is certain and that the emergence – not simultaneous but gradual – of many types is equally certain. [.] scientific observation, in its first infantile view, also believes that organic bodies have some constant quality, but soon recognizes that individuals are only transitory and only live on through reproduction. If science seeks the aid of history of all ages, it will recognize that species or procreative series are also transitory"* (Baer, 1864: 60-61).[2] When species are not permanent, the question Baer asked himself was whether the different forms we recognize as varieties have developed from one another through a process of gradual transformation, but appear to be different to us because we, as ephemeral animals, cannot comprehend the scope of their developmental modifications. He elaborated on this question by citing selective cases from animal breeding, biogeography and paleontology. For instance, he noted that the guinea pig was introduced to Europe from South America in the 16th century and over merely three centuries the species changed its color, reproductive cycle and the bones of its skull. Baer agreed that there was evolution (or transformation), although he is not willing yet to admit that all animals have developed by evolving from one another. He repeated this statement in another lecture about the issue 'where do we come from', read at the Russian Academy of Sciences in St. Petersburg in March 1859 (Baer, 1859). A month later he gave a printed version to Thomas H. Huxley and Richard Owen whom he visited in London.

In the posthumously published treatise "On Darwin's Doctrine" (Baer, 1876) Baer reviewed at length Darwin's theory of evolution, elaborated his objections by citing examples from paleontology, animal and plant geography, and breeding experiments, and finally concluded the discussion of all the points in which he agreed with Darwin as follows: *"We have just expressed that a full proof of a general transmutation is not yet given, but we must declare that a gradual occurrence of higher animal forms [.] cannot be thought of in another fashion than by transmutation, [.] we are convinced to find a defence against many objections that were raised towards Darwinism and transmutation, by the steady acceptance of an evolution in the progress of organic life. [.] To deny a transmutation natural science is not entitled to; for, to a lesser degree we still see its existence."* (Baer 1876: 463, 473).[3]

The notion that evolution occurs through changes in development was a view of evolution that preceded Darwin (Bowler 1975, Ragan 2009) and has been reinvigorated (with genetic mechanisms) by

Fig. 4. Photo of the portrait of Karl Ernst von Baer (1792-1876), ca. 1873. *Drawing by Julie Wilhelmine Hagen-Schwartz (1824-1902). Until 1899 the original drawing belonged to the Albertus University of Königsberg in Prussia. Fond 3408-3c. Photographic Collections, Tartu University Library.*

[2] "Wir müssen hieraus schließen, [..] daß der völlige Untergang sehr vieler Typen gewiß und das nicht gleichzeitige, sondern allmählige Auftreten derselben ebenso gewiß ist. [..] so glaubt auch die wissenschaftliche Beobachtung bei der ersten kindischen Ansicht, die organischen Körper hätten etwas Bleibendes, sieht dann bald, daß die Individuen vorübergehend sind und nur durch die Zeugung fortleben; wenn sie die Geschichte aller Zeiten zu Hülfe nimmt, erkennt sie, daß auch die Arten oder Zeugungsreihen vorübergehend sind." (translated by author)

[3] "Wir haben soeben geäußert, daß ein voller Beweis einer allgemeinen Transmutation noch lange nicht gegeben ist, aber wir müssen erklären, daß ein allmäliges Auftreten der höheren Thierformen [..] gar nicht anders gedacht werden kann, als durch Transformation [..] allein wir glauben in der festen Anerkennung einer Entwickelung im Fortgange des organischen Lebens eine Abwehr vieler Einwürfe, die man dem Darwinismus und der Transmutation überhaupt gemacht hat, zu finden. [..] Eine Transmutation überhaupt zu leugnen scheint mir die Naturwissenschaft nicht berechtigt; in geringerem Maße sehen wir sie noch jetzt bestehen." (translated by author)

evolutionary developmental biology (Gilbert *et al.,* 1996; Müller, 2001; Wagner, 2001). To claim that Baer was against evolution is to hold to a limited and, I should like to submit, a scientifically outmoded view of evolution. Rather, Baer thought that changes in developmental history were responsible for changes in the phenotype. He even drew a diagram of the branches that such developmental trajectories would have taken to produce several of the vertebrate classes. In his discussion of Darwin's evolutionary theory Baer stated that he did not doubt evolution, although he avoids the word "evolution" in his works. Further, he questioned the lack of empirical evidence for the theory of natural selection and did not believe that recapitulation was sufficient to account for evolutionary change (Baer, 1876).

This does not make him an anti-evolutionist, but shows that Baer did demand for firmer grounding in biological evidence from the evolutionary biologists of his times. Moreover, he was not the only scientist of his times who questioned the experimental record of natural selection. In the 19th century natural selection was not yet consistent with any theory of heredity (Gayon, 1998; Amundson, 2005). For example, even for Huxley (Huxley, 1860) natural selection played no role whatsoever in producing change (Schwartz, 2005). The main problem of the pros and cons of natural selection was sparked off by a fateful blend of historical narrative and addiction to one's own preconception (that means believing that 19th century embryologists believed in the typological dogma as formulated by the New Synthesis in the 20th century).

Coda

The recent spate of scholarship on the German biologist Ernst Haeckel, known for enunciating the biogenetic law (Richardson & Keuck, 2002; Richards, 2008; Gliboff, 2009) and the gastraea theory (Brauckmann & Gilbert, 2004) has revived discussion of earlier biologists who influenced Haeckel, such as the embryologist Karl Ernst von Baer (Raikov, 1968; Gould, 1977; Brauckmann, 2008). Baer has received attention because Haeckel synthesized Darwin's theory with Baer's developmental history in order to create his modern theory of recapitulation. Baer himself had strongly opposed earlier recapitulation ideas such as preformation (Baer, 1819, 1823, 1827; Richards, 1992) arguing that the embryo did not recapitulate lower stages of development in a hypothesized "scale of being", but instead developed from a more general to a more specific form. Because he rejected preformation, Baer is seen either as opposed to transmutation theories or at best as having a limited concept of evolution, allowing only for minor changes within the general animal "type" (Farber, 1976; Richards, 1992). However, viewing Baer through the lens of Haeckel has left us with a distorted view of Baer's views about species transformation.

The critical question how it happened that Baer was accused of ideas and opinions he did not state is a crucial issue of the history of biology in general, and in particular how we (mis)use historical facts. In an essay review Wagner (2007) raises the matter of historical fact (or interpretation of scientific concepts and analyses of experimental data) when pointing our attention to the "Synthesis historiography" of Mayr as recalled by Amundson (Mayr, 1981; Winsor, 2006) which he wryly interprets as the "victory tale of the white knight of population thinking over the anti-evolutionary dragon of typology". A most critical part of this historiography is the question of essentialism in 19th century taxonomy as presented by Mayr and others for getting accepted their interpretation of historical fact (see Winsor (2006) for a detailed critique of the metahistory). At issue here is less the historical fact than the scholarly objectivity that was renounced for a historiography of one's own preferences. Questioning the worth of such a history, Wagner, with good reason, requests for "intellectual consumer protection" to keep the scientist safe against partial and personal historians' history (Wagner, 2007: 152). However, historical knowledge offers more to the scientist (and the historian) than gaining a better perspective on present conflicts and controversies. Sometimes, old and seemingly outdated concepts and theories still affect science nowadays, direct and regulate scientific knowledge, or (the worst case scenario) might result in unwanted conceptual confusion and misinterpretation. In his comparative study of induction and positional information, Horder makes a good point (Horder, 2001). His focus is on the question on how we make judgements and choices for a specific procedure or trail to follow when doing science. He answers with "learning from past history" for procuring "guiding principles regarding the likelihood of achieving the intended outcomes through today's scientific efforts" (Horder, 2001: 124).

If past history is recorded in an accurate, unbiased and objective way it will work. Moreover, it will help to demonstrate the significance of seemingly outdated concepts, research programmes and data to most recent work of developmental evolutionary biology. However, if not, we are engrossed by distorted views resulting too often either in hagiographic accounts of scientists' history, or in sentencing scientists of the past for rather awkward "grand theories" without having formulated any. Baerian developmental history is a striking example here. The only remedy that will prevent the conversion of such metahistory into canonical wisdom shaping and influencing scientists and historians in their work is to read the original publications and to stop referring to them with eyes and minds closed.

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