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ORIGINAL ARTICLE

The concept of the 'organic individual' in Haeckel's writings

Olivier Rieppel[1]

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Abstract
Biological individuality was a hotly debated concept in nineteenth-century German biology, both in botany and in zoology. Much discussion centered on a comparison of higher plants with colonial organisms that are subject to polymorphism and exhibit division of labor among their parts. Building on the work of Matthias Jakob Schleiden, Johannes Müller, Rudolf Leuckart, and especially the botanist Alexander Braun, Haeckel in his writings continued to refine his theory of relative individuality. Haeckel recognized three kinds of individuality: physiological, morphological, and genealogical, the latter two hierarchically structured. These distinctions allowed him to embed in his theory of relative (biological) individuality the threefold parallelism of ontogeny, phylogeny, and classification. For Haeckel, this threefold parallelism provided the strongest proof for Darwin's theory of descent with modification.

Keywords Individuality · Ontogeny · Phylogeny · Classification · Ernst Haeckel

Introduction

Classically, and in philosophy, the concept of individuality is anchored in Leibniz's principle of the 'Indiscernibility of Identicals', which states that numerically identical entities share exactly the same properties. This is a purely logical conception of individuality that is of little, if any use to biologists, as it results in a *logical* contradiction if the individual so conceptualized is allowed to change through time. Logical relations, just as mathematical ones, are timeless. According to Leibniz's principle, an individual is a numerically (self-)identical entity characterized by some essential intrinsic property—call the latter '*p*'. If an individual is subject to change, '*p*' becomes a transient property: An individual could be '*p*' at one time, 'not-*p*' at another, later time. But in the timeless language of logic, this means that an individual is both '*p*' and 'not-*p*' (*P* & ~*P*), which the law of non-contradiction says is false. In contrast, the biological world is fundamentally one of change, which is why biological individuality cannot be captured by purely logical relations. Instead, other relations such as wholeness, boundedness, integration, interaction, continuity, and propagation have been invoked to capture the biological individual (Nyhart and Lidgard 2017a: 4).

The concept of the biological individual was a much-debated issue in nineteenth-century German biology (Nyhart and Lidgard 2011, 2017b). Haeckel wrote exuberantly on plant and animal individuality, so much so that one scholar attested him 'a kind of mania for puzzle solving' (Richards 2008: 134). It has been argued that Haeckel's treatment of organic individuals was influenced by two of his erstwhile teachers, the botanist Alexander Braun and the physiologist Johannes Müller (Rinard 1981), but other authors influenced Haeckel as well, most notably the botanist Matthias Jakob Schleiden and the zoologist Rudolf Leuckart (Nyhart and Lidgard 2011, 2017b). Alexander Braun in particular was a frequent visitor at Haeckel's parents' house in Berlin. The professor Alexander Braun and the newly enrolled student Ernst Haeckel forged a close personal friendship as they roamed the parks and outskirts of Berlin on their joint botanizing excursions (Bölsche 1900 [1906: 52]). Haeckel attended Müller's course at the University of Berlin in the summer of 1854, after which he traveled, at the end of August 1854, to Helgoland, accompanied by a friend. The

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✉ Olivier Rieppel
orieppel@fieldmuseum.org

[1] Integrative Research Center, Science and Education, The Field Museum, 1400 S. Lake Shore Drive, Chicago, IL 60605-2496, USA

idea was to collect seaweeds and enjoy the sun on the beach. Unexpectedly, Johannes Müller turned up and immediately invited Haeckel and his friend to accompany him on his fishing excursions. The marvelous, also mysterious invertebrate sea creatures that Müller was able to collect, demonstrate and explain 'irrevocably altered the course of Haeckel's research interest, from botany to invertebrate zoology' (Richards 2008: 40). What had captured Haeckel's botanical interest most were Braun's expositions on the alteration of generations in plants, a phenomenon that Müller hit upon as well when commenting on his haul of marine invertebrates. It so happened that in 1851, Leuckart had published a seminal and widely read monograph on polymorphism and the alteration of generations in colonial invertebrates, Braun having been his colleague at the University of Giessen in the academic year 1850–1851 (Nyhart and Lidgard 2011: 397). Matthias Schleiden finally secured himself a permanent place in the pantheon of the history of biology as the co-founder of the Schleiden–Schwann cell theory. The cell as the fundamental building block of organic life forms immediately evoked a discussion of biological individuality: Was the cell the fundamental biological individual, or was it the multicellular organism such as a human person that represents the individual, or could it be both? Could biological individuality be expressed at different levels of complexity?

In ancient Greek and Roman philosophy, individuality meant indivisibility; a nineteenth-century biologist's definition of individuality accordingly often invoked an entity that cannot be subdivided without it losing its nature. Greater sophistication was put to work by the botanist Anton Friedrich Spring in an award-winning essay on the nature of the genus, the species, and the variety (*Abart*) in biological, especially botanical systematics, submitted to the philosophical faculty of the Ludwig–Maximilian University of Munich in 1834 (Spring 1838). Heavily influenced by Schelling's romantic nature philosophy (see Richards 2002), Spring explained: 'Nature is to be compared to a tree, the stem branching into branches, those branching into twigs, the twigs branching into leaves' (Spring 1838: 5). What is the individual, what are the individuals, in such a hierarchically structured living system, or complex whole? Following up on that question, Spring introduced the concept of the 'natural-historical individual' (*naturhistorisches Individuum*: Spring 1838: 24): 'a natural object (*Naturkörper*)…which stands in a special and unique relation to time and space; or, in other words, the spatial and temporal relations of which differ from those of any other individual' (Spring 1838: 26).

Commenting on the complex life cycle (metamorphosis) manifest in butterflies and amphibians, Spring contrasted the natural–historical individual with the metaphysical individual: the caterpillar and the butterfly, the tadpole and the frog, respectively—they are discrete appearances in the course of a life cycle, 'a succession in shape and function, each stage a positive entity that is spatio-temporally constrained, and that cannot be subdivided without its proper nature being destroyed'. Spring (1838: 35) called such stages of a life-cycle metaphysical individuals, whereas the life cycle of a butterfly or of a frog as a whole represents a natural–historical individual. Behind that distinction lurk important implications. Cut a caterpillar, or a tadpole, into two, and they will perish. In that sense, they represent individuals. At the same time, they are distinct in appearance (morphology) and in function (physiology) from the butterfly and the frog, respectively. This says that the caterpillar differs from the butterfly and the tadpole differs from the frog in intrinsic properties of morphology and physiology. The metaphysical individual is thus individuated by intrinsic properties. Conversely, the butterfly and the frog likewise differ from the caterpillar and the tadpole, respectively, in their intrinsic properties. The natural–historical individual that comprises the entire life cycle is thus individuated not by intrinsic properties transiently manifest in its stages, but by the unique spatiotemporal relations that tie its parts together. Caterpillar and butterfly, tadpole and frog, they represent stages (parts) of a life cycle that is individuated through spatiotemporal continuity. The natural–historical individual *sensu* Spring is thus a relational concept that is not built on intrinsic properties.

Turning to a plant, or a zoophyte, Spring noted that they can propagate by budding and that parts can be cut off from the whole without the whole being destroyed as an entity in the process. The plant and the zoophyte hence cannot represent metaphysical individuals, but they do represent natural–historical individuals, Spring concluded (1838: 36). This is because the plant or zoophyte is individuated by a unifying inner force which governs its growth and development according to type and yet demarcates it from all other products of nature (Spring 1838: 37). As a contrast to his conclusion, Spring (1838: 37) cited Erasmus Darwin and Augustin Pyramide de Candolle, who both considered plants to represent aggregates of individuals.

Aggregates versus individuals: Schleiden, Braun, and Nägeli

Matthias Jakob Schleiden was a confrontational man, with strong opinions as to how natural sciences should be pursued. The goal of science for him was knowledge of the pure and unvarnished truth, unadorned with idle speculation (Schleiden 1842: xv). Observation, free from preconceptions and predispositions, is the first, but not the sufficient step toward that goal. The objects and results of observation need to be conceptualized, compared, and contextualized in light of the prevailing scientific knowledge and along a path of strictly logical argumentation: 'Botany is an empirical science and yet consists of two quite different components; not just of the facts revealed to the senses by nature, but also of how the human intellect, in grasping and ordering those facts…transforms this aggregate of facts into a truly scientific system' (Schleiden 1842: 9)—a system governed by natural laws and hence subject to an all-pervading causality. Schleiden emphasized his 'wholehearted commitment' to Kant's philosophy and consequently to a mathematical foundation for nature philosophy (Schleiden 1842: 6). Given such an austere approach to the world of plants, Schleiden proclaimed in his seminal paper on the cellular foundation of plant growth: 'every somewhat more highly differentiated plant [than unicellular ones] is an aggregate of totally individualized and self-contained individuals, namely the cells' (Schleiden 1838: 137). In that sense, the cell lives a double life: 'its own individual life belonging exclusively to its own development, and another mediated life to the extent that it has become an integrative part of a plant' (Schleiden 1838: 138). Viewed from such a perspective, the tree corresponds completely to a hydrozoan colony (*Polypenstamm*), and there is as little justification for a botanist to consider the tree an individual, as there is for a zoologist who calls a gorgonia an individual (Schleiden 1838: 171). It is true, Schleiden conceded, that among higher animals the individuality of particular organisms becomes ever more evident but at the bottom of the animal scale, as in hydrozoans, the same vegetative principles govern the organism as they do at the top of the plant scale, i.e., in trees (Schleiden 1838: 171).

In his 1842–43 textbook on botany, Schleiden broadened his perspective somewhat (Nyhart and Lidgard 2017b: 142), although only under certain qualifications: 'In botany we obtain individuals from a scientific point of view: the cell, and from an empirical point of view: the plant' (Schleiden 1843: 4). The scientific point of view obtains from the integration of the two paths of scientific inquiry: observation and reflection. The empirical point of view obtains from sensuous perception. The scientific point of view is clearly superior to the empirical point of view, the cell thus the true individual in the world of plants. To consider the plant as an individual creates special problems, as any plant is visibly composed of parts: A tree comprises the stem, branches, twigs, and leaves—and of course the roots. Schleiden proposed to deal with plant individuality in terms of a nested hierarchy of complex wholes. He thus stipulated plants of first order (the cell), plants of second order 'that comprise a union of first-order ones, and third-order plants that similarly unite second-order ones into composites' (Nyhart and Lidgard 2017b: 142). For most of his readers, this hierarchy translated into the cell (first-order plant), shoot (second-order plant), and the whole plant (third-order plan). One of those readers was Alexander Braun (1853: 50), who called the third-order plant a 'stock', in analogy to invertebrate colonies such as a *Polypenstock*: 'The word 'stock' is used here and elsewhere in the sense of…the totally organically connected structure composed of a number of partially independent links or members' (Braun 1851 [1853: 21]).

Alexander Braun represents quite a contrast to the sober naturalist Matthias Schleiden, as he pursued a romanticist–idealistic approach to botany that implied a distinctly teleological world view: Braun's 'philosophic efforts in the domain of morphology…carry out Goethe's half-explained conceptions to their remotest consequences, and express in purer form the idealism which lies at the foundation of the older nature-philosophy' (Sachs 1890 [1906: 172]). Such intellectual background is certainly revealed in Braun's 1851 (1853) treatise on phenomena of rejuvenation in plants, where the idea of rejuvenation was identified as an extension of Goethe's concept of metamorphosis (Sachs 1890 [1906: 174]). In the opening pages of that treatise, Braun (1851 [1853: 6]) offered some general comments on the nature of individuality:

> The term reached by the *Individual*, is not the last term of development for the greater complex of the whole [of which the individual is a part], nay the individual itself indicates this totality in its dependence. The individual existences of Nature are links in the development of that Kingdom of Nature to which they belong, and in the widest sense, links in the development of the totality of natural life…constantly renewing living Nature in her individual members, and thus bearing up and carrying her onwards to her final purpose.

As noted by Nyhart and Lidgard (2017b: 143), 'for Brown, individuals could be comprehended only when seen as members of a higher-level temporal entity, the species', which ultimately of course results in a multilevel nested hierarchy of individuals, or complex wholes, with the cell as the most elementary unit (Braun 1851 [1853: 121, 155]). In contrast to Spring (1838), Braun attested reality to every level of inclusiveness of this hierarchy; 'for [Spring's] assertion that merely the individual is real to have any meaning, the species, genera, families, classes and kingdoms, must be regarded as individuals of a higher order…just as Nature, as a whole…is to be regarded as an individual…' (Braun 1851 [1853: 322]). In support of his views, Braun turned to the phenomenon of alteration of generations, 'which exhibits the remarkable case of the individual, in the higher sense (the biological individual) breaking up into a limited or unlimited series of subordinate (morphological) individuals, which sometimes are developed in permanent connection, as compound family-stocks, as in the 'stock' formation of the zoophytes and plants…' (Braun 1851 [1853: 322f]).

Braun returned to the issue of plant individuality in a later monograph published in 1853, opening the tract with a distinction of the 'subordinate developmental cycle of the individual, as opposed to the superordinated developmental cycle of the species' to which the individual belongs

(Braun 1853: 24). The species consequently has the same superordinated life cycle of juvenescence, adolescence, and senescence as the subordinated individuals which constitute its parts. Individuality is bestowed upon such a hierarchical system of individuals not through some criterion of indivisibility (citing Nägeli in this context: see below), but by the goal-directed inner force that propels and constrains the development of the constituent parts of this hierarchy at every level of inclusiveness. Such a conception of nature finally led Braun to the 'doctrine of the relative individuality', which he backed up with a reference to Schleiden's distinction of first-, second-, and third-order plants (Braun 1853: 50). Citing Leuckart's 1851 treatise on polymorphism and division of labor in colonial invertebrates (Nyhart and Lidgard 2011), Braun emphasized the many parallels of relative individuality that prevail in the plant and animal kingdoms: The comparison of a plant with a coral colony (*Korallenstock*) revealed in his eyes 'an analogy of essential importance' (Braun 1853: 59). Closing his monograph on relative individuality in plants, Braun (1853: 105) drew an analogy with human individuals partaking in a family, a state, or a *Volk*, which again display polymorphism and division of labor: 'is it not the case that a human individual can become a mere organ' serving the group of which it is a part (Braun 1853: 105)?

Another highly regarded botanist of the time, cited by both Braun and Haeckel, was the Swiss-born Carl Wilhelm von Nägeli, who in 1856 published a short paper on individuality in nature, with special emphasis on plants. As in his view all life is tied to individuals, 'everything in nature must be individual…a conglomerate is composite only in the sense that it is composed of individual parts (*Teilindividuen*)' (Nägeli 1856: 211). He, again, found plants to be organized in terms of a nested hierarchy of complex wholes, for which reason he found it impossible to partition a plant into parts that are characterized by essential properties while at the same time represent an independent and self-contained living entity: 'we therefore have to distinguish morphological from physiological individuals' (Nägeli 1856: 186). In morphological terms, a plant is a hierarchically organized system of individuals of different degrees: the cell, the organs, the buds, the twigs carrying leaves, the whole tree—they all are morphological individuals at different levels of complexity. A physiological individual, in contrast, is simply an entity capable of an independent and self-contained life (Nägeli 1856: 187). Braun (1853: 47) had already drawn the distinction of a physiological versus a morphological perspective on plant individuality, noting that the 'two ways of seeing' partition the plant differently (except in the lowermost, unicellular plants). In his review of the history of botany, Julius Sachs (1890 [1906: 178]) concluded that 'the morphological consideration of the individual plant…breaks up the whole from above downwards, and the physiological…extends it in the upward direction'.

Johannes Müller may serve as one of the zoological physiologists who adopted a similar view of composite and multilevel animal individuality and who also influenced Haeckel (Rinard 1981). In his *Elements of Physiology*, he confirmed the 'truth of the proposition, that the fully developed plant is a multiple of plants—a compound system of individual organisms' (Müller 1843: 815). The same holds for hydrozoans: 'the young polype…of a compound polypiferous animal is at first a single individual…as this young creature appropriates to itself new matter and grows, it becomes transformed into a multiple system of individuals, like that presented by a full-grown plant' (Müller 1843: 815).

Haeckel's classification of Radiolaria

Leuckart's seminal study of 1851 (Nyhart and Lidgard 2011) focused on polymorphism and division of labor in colonial invertebrates, and on how these phenomena relate to the question of biological individuality. It is obvious that polymorphism casts the problem of individuality in light of morphology, whereas division of labor casts the problem of individuality in light of physiology. Haeckel's first major scientific contribution was his 572-page monograph of 1862 on Radiolaria, pelagic unicellular organisms (protists) he collected in the Strait of Messina (Sicily, Italy) from October 1859 through April 1860 (Haeckel 1862). He had learnt the method of pelagic plankton fishing from Johannes Müller when they had unexpectedly met in Helgoland in 1854, and it was again his teacher's Johannes Müller's 1858 monograph on Mediterranean radiolarians that provided him with a starting point for his own studies of these microscopic invertebrates of stunning delicacy and beauty (Müller 1858; Haeckel 1862: vi; Richards 2008: 64).

Despite their tiny size, radiolarians display an intriguing complexity in their structure. Internally, the cell is segregated into a central capsule containing the endoplasm and the surrounding ectoplasm (also known as calymma). The endoplasm is separated from the ectoplasm by a porous membrane. The central capsule contains the cell nucleus and other organelles, and it performs the functions of reproduction, respiration, and chemical synthesis. The ectoplasm contains cellular organelles along with algal symbionts, and it performs the functions of digestion and waste disposal. The ectoplasm extends into numerous pseudopodia which are actively capturing prey and removing waste. What makes radiolarians so esthetically appealing is their complex, radially symmetrical siliceous skeleton of stunning complexity and diversity. Some species of radiolarians form extended colonies that can reach macroscopic dimensions.

In radiolarians, there is again a division of labor to be observed between the central capsule (endoplasm; reproduction) and the ectoplasm (calymma; digestion), while some species display the ability to form extended colonies. Haeckel (1862: 117) compared such radiolarian colonies to hydrozoan colonies (*Poypenstöcke*) and embarked on a discussion of their organization from the perspective of biological individuality. He found that the individual radiolarians partaking in colony formation enter into an intimate peripheral plasmodic connection with one another through anastomosing pseudopodia, whereas the central capsules remain distinct and separate. Given such insights 'it must remain doubtful whether we should consider the social radiolarians [i.e., the radiolarian colony] as [a colony of] intimately connected individuals, or whether [such colonies] represent one individual which has multiplied an organ, i.e., the central capsule' (Haeckel 1862: 120). Continuing a discussion that wavered back and forth between these two interpretations, he drew a comparison with coelenterate colonies and tapeworms, concluding with respect to radiolarian colonies: 'from a morphological point of view the central capsules are best interpreted as distinct individuals of a social colony of polyzoans, whereas from a physiological point of view they are best interpreted as multiple organs of a solitary individual' (Haeckel 1862: 122). He continued to explain that the distinction of individual organism and organ in nature, especially in plants, is fuzzy, sharp boundaries between the two hence a result of human abstraction, but recognized the systemic (classificatory) need to reach a decision. Giving morphology precedence over physiology, he opted for the first alternative, i.e., that a radiolarian colony is a colony of multiple individuals (Haeckel 1862: 123). He consequently classified the Radiolaria in two main lineages, the simple ones (*Radiolaria solitaria*) and the composite ones (*Radiolaria polyzoa*): 'This classification can be upheld even if those radiolarians with multiple central capsules are not recognized as a multiplicity of individuals, but instead as an individual with multiple organs; an interpretation which, as we have shown above, has its merits as well' (Haeckel 1862: 219).

Haeckel's theory of relative individuality

Haeckel developed his theory of relative individuality in the first volume of his *Generelle Morphologie* of 1866. He started his expositions with a review of what had earlier been written about biological individuality in plants: 'to consider a plant as a composite *Cormus* or *Stock*, i.e., as an aggregate or a colony of individuals, is an ancient conception…and has most recently been substantiated in detail by Alexander Braun' (Haeckel 1866a: 246). The shoot in phanerogams and higher cryptogams he compared to an animal 'person', but noted that in lower plants—lower cryptogams, lichens, mushrooms, and algae—the individual independence of shoots cannot be unequivocally established neither from the morphological, nor from the physiological point of view (Haeckel 1866a: 246; mushrooms and lichenized fungi are no longer considered plants today). He reviewed Schleiden's categorization of plants as individuals of first order (the cell), second order (bud), and third order (whole plant), but in conclusion he himself distinguished six categories of individuals in plants. Ascending from the lower to the higher categories of individuality, Haeckel distinguished: 1) the cell; 2) the organ (leaf organ or axial organ); 3) the symmetrically corresponding axial part or antimere; (4) the successive axial part or metamere; 5) the shoot (*Gemma*); and 6) the *Stock* (*Cormus*) (Haeckel 1866a: 251).

Analyzing these nested levels of individuality in plants in some greater detail, he noted: 'Every one of these individualities represents, if considered in its own right, a self-sufficient entity both in form [i.e., morphologically], and well as in function [i.e., physiologically]; each one, however, is at the same time a multiplicity of the next lower category *and as such no longer an individual*. From this follows that we must give up the search for *absolute individuality*, and be content to recognize the *relative individuality* of superimposed parts of the plant. This conclusion has long been recognized by eminent botanists, and has given rise to the doctrine of the relative individuality of the plant' (Haeckel 1866a: 250).

Drawing a parallel between the plant and animal kingdoms, Haeckel further concluded: 'the theory of relative individuality also quite generally applies to…animals as much as to plants, and we can also discern several superimposed categories of individuals in animals, of which the higher one always represents a self-contained entity, but also at the same time a multiplicity of subordinate individuals of the next lower category' (Haeckel 1866a: 264). What this says is that individuality obtains only relative to a certain hierarchical level of the complex whole that is a plant or an animal; relative to the next subordinated hierarchical level, the individuality of the superordinated level dissolves into an 'multiplicity' of lower-level individuals (Haeckel 1866a: 264). Such relativity of individuality Haeckel gleaned from Schleiden's (1842: 43) botany textbook. In the opening pages of the second volume of his textbook, Schleiden drew attention to the seemingly never-ending debate surrounding the concepts of individual and individuality. These in their essence senseless debates have their origin, he claimed, in the failure to clarify the species concept (*Artbegriff*) relative to which individuality obtains. Schleiden (1843: 5) specified: 'relative to the species concept "solar system," ours is an individual; relative to the species concept 'celestial bodies', ours is an aggregate of multiple individuals'.

The Aristotelian species concept here deployed by Schleiden is hierarchically structured. The species concept is logically subsumed under its generic concept and hence is of lesser generality than the latter, but also of greater content. Celestial bodies can form galaxies, the milky way, the solar system. The solar system is a species in the genus milky way, and the milky way is a species in the genus galaxy. Similarly, the tiger, *Panthera tigris*, is a species in the genus *Panthera*, whereas *Panthera* is a species in the genus *Felidae* (in *bio*logical classification, *Panthera* is a genus in the family Felidae). In Schleiden's example and language, the celestial bodies correspond to cells, the solar system corresponds to an individualized part of the plant, for example, the shoot. Relative to the hierarchical structure of the universe, the solar system, considered by itself, is an individual; relative to the next lower level, it is an aggregate of celestial bodies. Relative to the hierarchical structure of the plant, the shoot, considered by itself, is an individual; relative to the next lower level, the shoot is an aggregate of cells. Notably, where Schleiden (1843: 5) spoke of an 'aggregate', Haeckel spoke of a 'colony' (1862: 123), a 'sum' (1866a: 261), or a 'multiplicity' (1866a: 264), with consequences to be discussed below.

Morphological versus physiological individuals in the Great Chain of Being

Focusing on individuality in animals. Haeckel found the concept of individuality unproblematic in higher forms, where there prevails 'an inclusion of all organs in a spatially sharply delineated body'; the individuality of such a person is intuitively obvious. The further one descends in the scale of animal organization, however, the independence and delimitation of individuals become increasingly blurred (Haeckel 1866a: 255). The situation, he found, could be clarified if a distinction was drawn between morphological and physiological individuality: 'This very important distinction…was drawn only when kinds of lower animals became better known where one can be in doubt whether they represent singular individuals or a society thereof'—as had been the case in the radiolarians (Haeckel 1866a: 256). He went on to cite Leuckart's 'superb treatise' of 1851 (Nyhart and Lidgard 2011), which motivated not only a hierarchical approach to animal individuality, but also the distinction of the morphological and physiological point of view (Haeckel 1866a: 257). Continuing his literature review, Haeckel again emphasized with respect to animal life that morphological versus physiological individuality has to be sharply distinguished, as also the different hierarchical levels of individuality. The morphological or 'form' individual he defined as a simple, unified spatial entity which, at the time of its consideration as an individual, must represent an immutable appearance (*Gestalt*) (Haeckel 1866a: 265). The physiological or 'performance' individual he defined as a living entity which for a longer or shorter duration is capable of a completely independent existence, hence is capable of self-preservation (Haeckel 1866a: 266). He then went on to introduce the six levels, orders, or categories of individuality he wanted to distinguish in animals, specifying that each of these categories corresponds to a mature physiological individual at some level in the scale of animal beings. The cell, or elementary organisms, represent the first order of individuality—called plastids by Haeckel (1866a: 266). The second-order individuals are the organs, which represent cell colonies (*Zellstöcke*) or cell fusions. The third-order individuals are the antimeres, or homotypical parts, i.e., parts corresponding to each other across a plane of symmetry. The metameres or homodynamic parts represent the fourth-order individuals, i.e., successive parts in a sequence (e.g., of segments). The fifth-order individuals are the 'persons', i.e., the individuals commonly identified among higher animals. The sixth-order individuals, finally, are colonies, or *Cormen*, *Stöcke*, of organisms (of persons). 'Each of these six orders of morphological individuals can occur as independent entity of life, thus representing the physiological individual' (Haeckel 1866a: 266). To the morphological category of the plastid corresponds the physiological individual of protists, single celled organisms. The morphological category of the organ corresponds to the physiological individual represented by algae or coelenterates. The antimeres correspond to physiological individuals instantiated by many protists, and some lower plants, and animals; the physiological individual corresponding to the metameres is instantiated in many mollusks and lower worms, as also in algae. The morphological category of the person corresponds to the physiological individual represented by most of the higher animals. The morphological order of the *Cormus* finally corresponds to the physiological individual represented by most plants and coelenterates.

Haeckel (1866a: 267) went on to illustrate the case of humans, who start out as a plastid, a morphological individual of first order (fertilized egg-cell). Cell cleavage results in a multicellular stage that has the morphological value of an organ. With the development of the primitive streak, the antimeres make their appearance, or so Haeckel claimed. The metameres become apparent as the paraxial mesoderm segments to form the somites. The developmental differentiation of the somites finally results in the formation of the person, the fifth order of morphological individuality, which from thereon persists as a mature physiological individual (Haeckel 1866a: 267).

To the two categories of individuality, morphological and physiological, Haeckel added a third one in the second volume of his *Generelle Morphologie*, the genealogical individual. Genealogical individuality is again relative and hierarchically structured. The first category, or order of genealogical individuality, is the '*Cyclus Generationis*', the organism from conception to reproduction, as originally defined by Huxley (1852) and Haeckel (1866b: 28, 30). The second order of genealogical individuals is the species, i.e., the sum of the reproductive cycles of conspecific organisms. The third order of genealogical individuals is the phylum, the sum of species of common phylogenetic origin. At the time of writing his *Generelle Morphologie*, published in 1866, Haeckel still followed Georges Cuvier and Karl Ernst von Baer as he divided the animal kingdom into four separate phyla, each with an independent evolutionary origin (this would change when Haeckel developed his Gastraea Theory, on the basis of which he stipulated the monophyly of metazoans: Haeckel 1874a; Rieppel 2011). There is an important asymmetry, however, among the three orders of genealogical individuals: The reproductive cycle of the individual organism and the species are open and variable entities, as they both give rise to descendants—new reproductive cycles in the first, new species in the second case. Only the genealogical individual of third order, the phylum, is a closed entity. In fact, Haeckel's continued wavering and eventual rejection of the reality of species in nature effectively undermined his hierarchy of genealogical individuals (see discussion in Rieppel 2011, 2016). But Haeckel held fast to his distinction of three orders of genealogical individuals, as it fit well into the grander scheme of things as discussed below.

Haeckel returned to the issue of morphological and physiological individuality in his 1872 monograph on calcareous sponges, where he embarked on a revision of his *Individualitätslehre* (Haeckel 1872: 89–124). He conceded that his earlier distinction of six orders of morphological individuality was a bit contrived and not easily applied across the animal kingdom. He therefore dropped two categories, the antimeres (originally third-order individuals) and the metameres (originally fourth-order individuals). Yet he maintained that he 'still considered the foundation of this theory of individuality as correct' (Haeckel 1872: 91), since it entailed an important corollary. Each of the successive orders of morphological individuality was represented, somewhere along the scale of animal life, as a mature physiological individual. This is the core concept that underlies Haeckel's famous biogenetic law: Ontogeny recapitulates phylogeny, at least in part and in an abbreviated manner (Nyhart and Lidgard 2011: 402; see also Hoßfeld and Olsson 2003; Olsson et al. 2017). Similarly, the distinction of three orders of genealogical individuals entailed an equally important corollary: the threefold parallelism.

> This extremely interesting and important relation, which we consider one of the most striking and informative phenomenon of living nature, is the three-fold parallelism of the three orders of genealogical individuality. This concerns the extraordinary correspondence of the consecutive conditions of form which becomes apparent in the three categories of genealogical individuality. This three-fold parallelism in the individual, systematic, and paleontological developmental history…delivers the most irrefutable proof for the truth of the theory of descent, because only the latter offers a causal-mechanistic explanation for that parallelism (Haeckel 1866b: 31).

In other words, the successive conditions of form revealed in the course of the ontogeny of the individual organism are reflected in animal classification as well as in the sequential analysis of the fossil record. The more general condition of form represented in early ontogenetic stages corresponds to the mature condition of form in lower organisms that also appear early in the fossil record. The less general condition of form apparent in later ontogenetic stages corresponds to the mature condition of form that characterizes higher organisms which appear later in the fossil record. This threefold parallelism (Hoßfeld and Olsson 2003; Olsson et al. 2017) had previously been forcefully argued by Louis Agassiz in his *Essay on Classification* of 1857 (1859), but there it was cast in a Creationist perspective. In his *Natürliche Schöpfungsgeschichte* of 1868, Haeckel summarized: 'The paleontological developmental history of organisms, which can be called phylogeny, stands in the most curious and important relation to the other branch of developmental history, that of the individuals or ontogeny. The latter runs more or less parallel to the first. Or, expressed briefly in one sentence: the individual development or ontogeny is a rapid and brief recapitulation of the paleontological developmental history of phylogeny, conditioned by the laws of inheritance and adaptation' (Haeckel 1868: 9).

The social dimension of Haeckel's *Individualitätslehre*

Developing his theory of relative individuality in plants, the botanist Alexander Braun (1853: 105) had drawn parallels between the hierarchically structured *Pflanzenstock* and human social structures. Haeckel, as well as other biologists, would do the same, with important consequences for the infusion of identity in the German *Volk* (Rieppel 2016, 2017). The discussion of social ramifications of the doctrine of relative individuality revolved around polymorphism and division of labor in the sixth (later fourth) order of morphological individuals, the colonial invertebrates treated by Leuckart in his 1851 monograph (Nyhart and Lidgard 2011).

In his *Anthropogenie* of 1874, Haeckel again returned to the issue of *Cormogenie*, the developmental history of colonial invertebrates, or *Stöcke*. These he found to constitute social individuals, composed of 'persons', or individual organisms, which may differ in form and function. Such a *Cormus*, or social individual, subject to polymorphism and division of labor, he compared to a train: 'At the head of such a jointed organism is the locomotive. Behind it follow carriages loaded with coal, cars carrying the mail, passenger cars, cattle cars, etc. Each railway carriage is a morphological individual, and yet the whole train corresponds to a single physiological individual' (Haeckel 1874b: 245). Whether segments in an annelid worm or an otherwise segmented organism, or zooids in a hydrozoan colony such as a siphonophore, they are the railway carriages forming a physiologically integrated whole. Just as the human body, or 'person' in Haeckel's terms, is composed of specialized cells that come together to form organs which again are functionally integrated to form a physiological individual, so is the siphonophore composed of specialized zooids that are precisely organized and functionally integrated at the level of the colony. In siphonophores, the colony is not formed by the coming together of originally independent zooids (polyps), but those instead originate from one another through budding, the first one developing from a fertilized egg. Haeckel (1874b: 18) went on to distinguish two types of developmental history of such social organisms, or *Cormus*, *Stöcke*: The first is the individual development of the colony, its ontogenesis or *Cormogenie*; the second is the phylogenetic history of the social organisms, or *Cormophylogenie*. But the concepts of *Cormogenie* and *Cormophylogenie* apply not only to plants and colonial animals, but also to human social structures: the family, the community, the state (Haeckel 1874b: 18).

To illustrate such parallelism, Haeckel raised the question: 'How would the originally unicellular organism have behaved in founding the first cell-state, thus becoming the primogenitor of all multicellular higher organisms? The answer is very simple. It will have behaved in the same way as a human individual, which according to a rational purpose and plan founds a state or a colony' (Haeckel 1874b: 118). He went on to imagine a couple of South Sea islanders who in the wake of shipwreck found themselves stranded on a remote, initially uninhabited island. The couple would beget numerous children and thus lay the foundation for an island population. Only concerned with their daily survival, these indigenous people (*Diese Wilden*) would initially live simple lives, as do lower plants and animals. But after a long period of time, some families would come together to form a community, within which the first steps toward a division of labor would become manifest (Haeckel 1874b: 19). The formation of a state would be accompanied by continued social and commercial differentiation of the society, the whole state still functioning as an integrated and unified whole. In that way, the cell state that is a multicellular organism is directly comparable to the organized human society that represents a state (Haeckel 1874b: 120; see also the discussion in Reynolds 2008).

Haeckel returned to his concept of *Cormophylogenie*—now called *Cormophylie*—in 1875, on the closing page of his overview of the theory of descent: 'In its narrow sense, the concept of *Cormophylie* would apply only to the phylogeny of colonial plants and animals; but in a broader sense it can also be applied to the phylogeny of associations, families, communities, states etc. composed of free persons. This is a large part of the history of peoples, indeed of the so-called "world history"' (Haeckel 1875: 96). That way, the theory of descent provides an empirical, monistic, and causal-mechanistic perspective not just on organic nature, but also on human culture.

Discussion

Did Haeckel succumb to a 'mania for puzzle solving' (Richards 2008: 134)? It is certainly legitimate to raise the question why Haeckel would, again and again, return to the issue of biological individuality? In his first public exposition of Darwin's theory of descent at a meeting of the Society of German Naturalists and Physicians at Stettin in 1863, Haeckel (1864: 28; emphasis added) noted already that a truly natural system had to encompass both fossil (extinct) and living organisms: 'Only if this is the case will the whole natural system appear as a single, large, organically structured *body*, as a widely ramified tree, of which all the clusters of branches, divisions and subdivisions are connected through radially extending connecting lines'. A *body* is of course what Haeckel would later call a 'person', a morphological individual of fifth order, nested as it were in a hierarchy of intimately connected complex wholes. The affinities expressed in such a tee-like natural system are not just meant to reflect degrees of similarity and dissimilarity, but rather are taken to express blood relationships (Haeckel 1864: 29). Any doubt in that respect will be dispelled by the 'three-fold parallelism of the ontogenetic, systematic, and paleontological development of organisms, which I take to be the strongest proof of the truth of the theory of descent' (Haeckel 1864: 29).

Similarity and dissimilarity are abstract relations, and blood relationships are undeniably real. A classification based on logical subordination is conceptual; a body in the form of a tree is real. A species that is nothing but a collection of organisms that share one or several diagnostic features is conceptual: 'The species is as much an arbitrary *abstraction*, depending on the subjective views of the author, as much a category with a *relative* meaning only as are the varieties, the genus, the family, etc' (Haeckel 1872: 477). But a species that gives rise to descendant species is real. For Haeckel (1864), Darwin's theory of descent offered a unified explanation of how organismic diversity and complexity came about in the course of geologic time: a process of descent with modification, governed by the laws of inheritance and natural selection. In contrast to earlier theories of species transmutation, Darwin's explanation was a purely causal/mechanistic one, a process of descent with modification in which cause is linked to effect. Concepts cannot partake in causal relations. Only real things can partake in a process that links cause with effect. Haeckel was obviously deeply concerned with the metaphysics of evolving entities. Conceptual constructs are abstract; they are not spatiotemporally located. Individuals—at least biological ones—are concrete, spatiotemporally located entities. Only the latter can enter into causal relations and can be concatenated in a process that links cause and effect.

And yet, Haeckel's theory of relative individuality, gleaned as it was from Schleiden's (1843) text, may appear to suffer from some ontological tension. Classically, and as in Schleiden's (1843: 5) text, the philosophical contrast is between classes and individuals. Classes are universal, infinite in their possible instantiations; individuals are spatiotemporally located, finite in their possible instantiations. Individuals can be members in a class, but are themselves subject to the part–whole relation. Individual objects that occur in nature and are governed by the same causal laws are members in a class known as natural kind. Every single nugget of gold is an individual which, in virtue of its atomic number (in virtue of its microstructure) shares the causal propensities of all other nuggets of gold and hence instantiates the natural kind gold. In Schleiden's (1843: 5) example and language, the term 'solar system' is a proper name, denoting an individual. In contrast, the term 'celestial bodies' is a natural kind term (general name), denoting the kind of very large bodies that all obey the law of gravity and as a consequence can come together in the formation of a solar system, a milky way, a galaxy. By analogy, each and any one of the undifferentiated (embryonic) mesenchyme cells represents an individual, but collectively they instantiate a natural kind, one of omnipotent cells. Some of these may differentiate into erythrocytes or osteoblasts: Each erythrocyte or osteoblast represents an individual, but collectively, erythrocytes or osteoblasts instantiate a natural kind: Erythrocytes bind oxygen, osteoblasts form bone. To keep the discussion at the same level of generality as Haeckel's argument, assume there existed something like 'liver cells': Each liver cell represents an individual, but collectively they represent a natural kind: cells with the propensity to form a liver. If the liver is the relevant reference point, the liver represents an organ, a morphological individual of second order. But if its cellular structure is the relevant reference point, the liver is composed of lower level individuals.

Classically, natural kinds are treated as classes, subject to the membership relation. Individuals, by contrast, are subject to the part–whole relation. The interpretation of Haeckel's theory of relative individuality thus would seem to imply an ontological dualism that is hard to reconcile with his steadfast support for, and defense of monism. A crucial difference lies in the fact, however, that where Schleiden (1843: 5) spoke of an 'aggregate', Haeckel spoke of a 'colony' (1862: 123), a 'sum' (1866a: 261), or a 'multiplicity' (1866a: 264). It is conceivable that Haeckel recognized the danger of committing a category mistake and hence used terms like 'colony', 'sum', and 'multiplicity' for aggregate entities which he wanted to be understood to be subject not to the membership relation, but to the part–whole relation. The reason is that unlike nuggets that instantiate the natural kind gold, cells originate from other cells through division, polyps originate from other polyps through budding, and species originate from other species through speciation. Haeckel's concept of biological individuality is a relational one (for further discussion of this tension, see Wilson 1996; Rieppel 2010).

This is particularly apparent in Haeckel's discussion of genealogical individuals. Of genealogical individuals, Haeckel (1866b) distinguished three levels: the individual reproductive cycle, the species, and the monophyletic supraspecific taxon (the phylum was the only monophyletic taxon accepted by Haeckel 1866b; Rieppel 2011). If the individual reproductive cycle is the focal point of interest, it represents a genealogical individual of first order; relative to the next lower level of inclusiveness, the individual reproductive cycle represents the 'sum' of the life-cycle stages that are manifest throughout the individual reproductive cycle (Haeckel 1866a: 261). If the species is the focal point of interest, it represents a genealogical individual of second order. Relative to the next lower level of genealogical individuality, the species instead represents the sum of individual reproductive circles that it comprises (Haeckel 1866b: 30). The monophyletic taxon considered by itself is a genealogical individual of third order. Relative to the next lower level of individuality, the monophyletic taxon represents the sum of the species which it comprises. The sum of species that constitutes a phylum must be considered to be subject to the part–whole relation, given that they are united through blood relationships (Fig. 1).

Fig. 1 Ernst Haeckel. Smithsonian Institution Archives. Image # 85-4454

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