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Individuals at the Center of Biology: Rudolf Leuckart's *Polymorphismus der Individuen* and the Ongoing Narrative of Parts and Wholes. With an Annotated Translation

LYNN K. NYHART
Department of the History of Science
University of Wisconsin-Madison
1225 Linden Drive
Madison, WI 53706
USA
E-mail: lknyhart@wisc.edu

SCOTT LIDGARD
Department of Geology
Field Museum
1400 S. Lake Shore Drive
Chicago, IL 60605
USA
E-mail: slidgard@fieldmuseum.org

Abstract. Rudolf Leuckart's 1851 pamphlet *Ueber den Polymorphismus der Individuen* (On the polymorphism of individuals) stood at the heart of naturalists' discussions on biological individuals, parts and wholes in mid-nineteenth-century Britain and Europe. Our analysis, which accompanies the first translation of this pamphlet into English, situates Leuckart's contribution to these discussions in two ways. First, we present it as part of a complex conceptual knot involving not only individuality and the understanding of compound organisms, but also the alternation of generations, the division of labor in nature, and the possibility of finding general laws of the organic world. Leuckart's pamphlet is important as a novel attempt to give order to the strands of this knot. It also solved a set of key biological problems in a way that avoided some of the drawbacks of an earlier teleological tradition. Second, we situate the pamphlet within a longer trajectory of inquiry into part-whole relations in biology from the mid-eighteenth century to the present. We argue that biological individuality, along with the problem-complexes with which it engaged, was as central a problem to naturalists before 1859 as evolution, and that Leuckart's contributions to it left a long legacy that persisted well into the twentieth century. As biologists' interests in part-whole relations are once again on the upswing, the *longue durée* of this problem merits renewed consideration.

Keywords: individual, Leuckart, polymorphism, division of labor, part-whole relations, alternation of generations, colonial organisms

Darwin's *Origin of Species* is widely considered one of the best pieces of scientific rhetoric ever written. Among its manifold impacts has been a mute, largely unquestioned acceptance of the idea that the origin of species was not only "that mystery of mysteries," as Darwin wrote in the book's second sentence, but that it was *the* mystery of mysteries for the cohort of scientists working before 1859.[1] Generations of historians have probed the history of the species question before 1859, uncovering a rich tradition of pre-Darwinian ideas about transmutation and species concepts. But what if Darwin's claim was largely a rhetorical flourish, identifying his own question as *the* question – as it would later become?

We contend that the long shadow cast backward in time by the *Origin* has hidden another, larger question that occupied the European biological community in the two decades before 1859: the nature of organic individuality. If we review the major new discoveries and theories of the period 1838–1858, we find discussions of individuality enmeshed in the development of the cell theory, the debate over alternation of generations, the lively discussions about compound organisms (especially colonial invertebrates and plants), and the debate over the existence and nature of single-celled organisms. If we consider the major philosophical issues in mid-nineteenth-century biology, we find the problem of the individual a major component of the debate between reductionist physiologists and more teleologically inclined morphologists over the relations between parts and wholes in the organic world. We can see it in discussions concerning the relationship between the animal and plant kingdoms. And we find it, too, in the ongoing debate over the nature and definition of species. In short, the problem of the individual was intertwined with nearly every major topic in British and European natural history in the 20 years preceding Darwin's *Origin of Species*. Certain strands of this thick knot of topics trace back into the mid-eighteenth century, while others extended forward influentially. The perceived importance of this problem ebbed and expanded repeatedly over the next 150 years, and is once again at the forefront of biology.

Why hasn't organic individuality been recognized by historians for the central problem that it was? Why don't we have an "individuality

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[1] Sir John Herschel used the phrase "mystery of mysteries" to refer to "the replacement of extinct species by others" in an 1836 letter to Charles Lyell that was then excerpted in Charles Babbage's widely circulated *Ninth Bridgewater Treatise* (1837) (quotation on p. 203).

industry" in the history of biology? As the citations in this paper will show, in a way, we do. Numerous historians have recognized the importance of conceptions of biological individuality to the scientific questions mentioned above, treated as separate topics. But few have viewed these problems as related – related, indeed, via the common thread of individuality (for important examples, see Schmitt, 2004; Elwick, 2007). This is partly because scientists at the time seldom presented individuality as an autonomous problem. Rather, it was more often treated as prerequisite to other theoretical or empirical problems that constituted the naturalist's main focus. Yet, we suggest, defining biological individuality and putting that definition to work in solving biological problems was one of the central underlying philosophical issues for working biologists in the mid-nineteenth century. Solving any of the theoretical and empirical problems mentioned above required addressing questions of part-whole relations, such as the relative autonomy, dependence, and continuity of parts over time, that were intrinsic to definitions of individuality. So biologists found themselves defining individuality, whether implicitly or explicitly, as a matter of necessity. And as they worked across different problems, they toted their definitions along with them.

Rudolf Leuckart's 1851 pamphlet *Ueber den Polymorphismus der Individuen, oder die Erscheinungen der Arbeitstheilung in der Natur. Ein Beitrag zur Lehre vom Generationswechsel* (On the polymorphism of individuals, or the phenomena of the division of labor in nature: A contribution to the theory of the alternation of generations) exemplifies this process. We translate this essay for the first time in the accompanying article. Its significance is not that Leuckart invented the problem of individuality, nor that he solved it, nor even that he was the most important player in the field (although see Winsor, 1972, for a high assessment of its significance). Rather, Leuckart's *Polymorphismus* was one of those relatively rare cases where individuality itself was drawn out as *the* problem. Here we can see a novel effort to create a concept of individuality that united different biological problem areas, and sought to do so, moreover, in a way that was grounded in the material world while also retaining holistic commitments. It thus represents a key contribution to a number of overlapping discussions of the period, and to our understanding of the problems of part-whole relations faced by mid-nineteenth-century biologists.

Already in his lengthy title, Leuckart touched on some of the topics he and his contemporaries viewed as connected: individuality, polymorphism (two or more forms deriving from a common origin),[2] the division of labor in nature, and alternation of generations – the last a subject of particularly contentious debate in the period. Leuckart's own mode of connecting these topics was novel in holding the alternation of generations to be merely an instance of a more fundamental principle, the division of labor, which manifested itself in polymorphism. To make this claim work, however, he had to persuade his readers to consider the different parts of colonial organisms to be "individuals." This is the burden of his argument.

In the present paper, we seek to contextualize the accompanying translation of Leuckart's essay, but our purpose goes further. We also advocate for an intellectual history of mid-nineteenth-century biology that recognizes the centrality of individuality as a deep-rooted underlying problematic that occupied an international community of biologists. They engaged with individuality through work on a range of organisms and topics, at times as a necessary logical predicate to a specific argument being made, and at other times as an overarching solution in which a given concept of individuality was offered as a key to explanation or understanding. As such, this problematic belongs as much to a historians' category of analysis as it does to one of historical actors alone.

To address both the translation and the broader topic of individuality, we first offer some biographical background on Leuckart, a major shaper of biology in the nineteenth century. We then draw out three central themes from the paper's argument – the nature of individuality, polymorphism and the division of labor, and the alternation of generations – and situate them historically. Finally, we briefly trace some of the repercussions of Leuckart's pamphlet and the problematic of individuality as it moved forward in time. Even today, we suggest, debates over levels of selection and aspects of biological modularity are

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[2] "Polymorphism" has gained new and divergent meanings since Leuckart's time (Fusco and Minelli, 2010). Today, most students of animal colonies continue to use "polymorphs" to refer to distinct morphological phenotypes within a colony (zooids, polyps, castes, etc.). Excepting work on a few insect groups, knowledge of the genetic and developmental mechanisms producing these alternate phenotypes is usually lacking. However, for many biologists, polymorphism refers only to alternate phenotypes under strict genetic control. For geneticists, polymorphism is shorthand for genetic polymorphism, irrespective of phenotypic effects. A newer term, polyphenism, describes cases wherein a single genotypic individual develops alternate phenotypes in response to different environmental cues, either outside or inside the body. Within genotypic individuals, alternate phenotypes as polyphenisms may eventually be shown to be as common or more common than polymorphisms in the modern sense (Gilbert and Epel, 2009).

conditioned by early responses to this problematic in the mid-nineteenth century.

Rudolf Leuckart: The Zoologist as Synthesizer

Rudolf Leuckart (1822–1898) was a leading figure among the many important European zoological morphologists in the mid- to late-nineteenth century, especially those whose work embraced invertebrates (Winsor, 1976; Wunderlich, 1978; Nyhart, 1995). Starting in 1842, he studied under and then lectured alongside the anatomist and physiologist Rudolf Wagner at Göttingen, moving in 1852 to Giessen and in 1869 to Leipzig, where he spearheaded the creation of a new institute and museum and spent the remainder of his career as professor of zoology. He has been called "the father of parasitology" (Farley, 1992, p. 38), having made fundamental contributions to the understanding of *Trichina* and *Trichinella* and combating the scourge of trichinosis in the human food chain. His pioneering work on the life histories of parasites ranged across many organisms, including nematodes, liver flukes, and tapeworms, and his two volumes on the parasites of man (1863–1876) helped to cement parasitology as a discipline.

The early years of his career had equally profound consequences for understanding the systematic relationships of animals and the morphological organization and reproduction of invertebrates. His first major works (Frey and Leuckart, 1847; Leuckart, 1848) convincingly split apart Cuvier's subkingdom Radiata, creating the group Coelenterata and resurrecting Echinodermata as a second group (see Winsor, 1976). Leuckart is commonly credited with resolving the early classificatory framework for the metazoans, which he divided into six major groups: Coelenterata, Echinodermata, Annelida, Arthropoda, Mollusca, and Vertebrata. His textbook *Anatomisch-physiologische Uebersicht des Thierreichs: Vergleichende Anatomie und Physiologie* (Anatomical-physiological overview of the animal kingdom: comparative anatomy and physiology, 1852), written with the physiologist Carl Bergmann, introduced a more physiological perspective into the teaching of comparative anatomy and morphology; it became widely influential.

During the 1850s, Leuckart focused intensely on biological concepts of the division of labor, alternation of generations, parthenogenesis, and the nature of organic individuality. Leuckart's approach to biology was holistic and multifaceted. He devised a synthetic framework that embraced anatomical, physiological, functional, and developmental perspectives. Conceptualizing the organism across its entire life cycle, he thought of “parts” as both temporal and structural entities. He observed and analyzed a wide range of invertebrates, including medusae, polyps, and animal colonies in general. He described physiologically connected colonies such as hydroids, corals, siphonophores and tunicates (Leuckart, 1851a, d, 1853; Bergmann and Leuckart, 1852), as well as the anatomy and generation of social insects such as honey bees (e.g., Leuckart, 1855, 1857). Concurrently, Leuckart was developing ambitious, inclusive means of understanding many challenging problems arising from the study of “lower animals.” These broader theoretical problems concerned metamorphosis, parthenogenesis, and complex life histories involving sexual and asexual reproduction (Leuckart, 1851a, b, 1853). His synthetic framework was fundamentally comparative, as he sought to understand how similar functions are carried out under different structural plans across different groups of organisms. We place *Ueber den Polymorphismus der Individuen* within this synthetic genre of his work.

Leuckart exerted a profound yet greatly underappreciated influence on zoology as it diversified into new sub-disciplines. Researchers from around the world came to work in his lab. Together with his collaborators and more than 115 doctoral students he mentored in his long career (*Festschrift*, 1892; Wunderlich, 1978, pp. 41–58), they assured that his research approach and ideas continued to flourish well into the next century. All in all, Leuckart’s topics, interests, and functionalist approach to nature may be seen sprinkled through the works of his many students and co-workers. His signature issues were already evident in 1851, in *Polymorphismus*.

***Polymorphismus* in its Intellectual Context**

Leuckart’s pamphlet fed into and united a number of lively discussions among naturalists in the 1840s and early 1850s. Two fundamental changes in biological investigation in the 1830s and 1840s facilitated these discussions. First, the number of investigators committed to understanding development increased rapidly, especially in German-speaking Europe. Second, attention to invertebrates, especially marine invertebrates, increased in parallel. These two changes together wrought a new appreciation of life cycles and their diversity (Nyhart, 1995, esp. pp. 95–96; Jahn, 2000, pp. 336–342). Furthermore, since the turn of the nineteenth century the prevailing intellectual climate had encouraged scientists to connect individual phenomena into a larger picture, preferably as expressions of laws of living nature. All of these together meant that many unusual life cycles viewed earlier as isolated cases came to be recognized by the late 1840s as having broader value for biological generalization and problem-solving (Elwick, 2007). Leuckart's *Polymorphismus* exemplified these newer efforts at synthesis. We concentrate on the ways his work united three strands of the ongoing conversation: individuality, functionalism, and alternation of generations. Biological individuality, in particular, had a longer history as a philosophical and practical problem of part-whole relations that provides a necessary backdrop for Leuckart's paper. In setting up Leuckart's contribution, we therefore begin with a more extended history of the problem of individuality, tracing its tendrils back to the ancients but concentrating on developments around 1800.

The Problem of Individuality

What defines an individual, biologically speaking? From a casual perspective, one might expect individuality to be tied up with variation or uniqueness, but by longstanding tradition in Leuckart's pre-Darwinian world, individual variations were considered "accidental" and biologically insignificant. The notion of the individual as an imperfect embodiment of an idealized 'kind' or 'type' had held sway from Plato's *eidos* through Aristotle's essentialism and hylomorphism, the Scholastics' separation of substantial and accidental forms, Linnaeus' *Systema naturae*, and more formalized nineteenth-century classifications (Atran, 1990; Stevens, 1994). Biological individuality had to do with something else: the making of a singular living being that could be considered a distinct "whole" based on its morphology, its physiology, and the continuity and integration of its parts (Geddes and Mitchell, 1911).

When we use ourselves and other higher vertebrates as models, wholeness presents few apparent difficulties: we understand the human body to be a single structural–functional unit that persists from conception to death. But what is the whole "individual" when one is dealing with a compound organism such as a hydroid, an aquatic invertebrate in which certain parts can live independently for part of their life cycle, but at other times form colonies? When is a unit a "part," and when should it be considered an autonomous "individual," as with the separate clumps of a creeping strawberry or the separate mouths of a colonial sea anemone? This problem has long faced students of compound organisms such as plants, jellyfish and corals; organisms with more obvious metamorphic stages, such as butterflies; and "colonial" (eusocial) insects such as ants, termites, and bees that are morphologically autonomous but require individuals of different forms for the whole colony to survive (Perrier, 1881; Geddes and Thomson, 1890, chs. 13–15; Winsor, 1976; Elwick, 2007). The problem also extended to parasites such as tapeworms, which have complex life cycles that can include both autonomous stages and stages in which the organism's survival depends on its host. In the 1840s and 1850s all of these part-whole relations were understood as having to do with the same problem: individuality.

The problem of part-whole relations in defining the biological individual was hardly new in this period, having excited interest among naturalists and philosophers since at least the late seventeenth century. For instance, Gottfried Wilhelm Leibniz developed a theory of nested individuality of organic bodies, a hierarchy of individuals, contradicting the Aristotelian notion of "one body, one soul" (Nachtomy et al., 2002; Nachtomy, 2007). Further, early microscopists such as Marcello Malpighi and Jan Swammerdam discovered aspects of development and metamorphosis in animals that challenged the singularity of an individual body. Charles Bonnet's 1740 declaration that aphids can reproduce without mating (parthenogenesis) further eroded the older notions of parts and wholes, prompting disbelief and attracting others like Abraham Trembley to repeat his experiments (Dawson, 1987). Then in 1744, Trembley announced that the freshwater polyp *Hydra* could be cut into pieces that could all survive and grow into new wholes (Trembley, 1986). Initially this astonishing attribute (along with the hydra's green coloring) cast doubt on its animal nature: although plants were known to be able to grow by cuttings, animals were thought not to have this property. However, Trembley persuaded himself and the rest of the world that hydras were indeed animals, a finding seemingly confirmed when other animals such as earthworms and seastars were also found to share the same regenerative properties (Morgan, 1901).

The part-whole relations of plant individuals, too, constituted a topic of longstanding discussion, which sometimes approached and intertwined with animal individuality but had its own historical trajectory. Theophrastus, writing around 300 B.C., spoke of the likeness of leaves to the sepals and petals of flowers (e.g., Theophrastus, 1916, p. 91). He noted the complexity of defining "essential" parts of plants, because the body differentiates into many kinds of repeating parts or members during its growth: "for the plant has the power of growth in all its parts, inasmuch as it has life in all its parts" (Theophrastus, 1916, p. 7). The equivalence of leaves and leaf-like components of flowers is also apparent in the works of early modern naturalists Marcello Malpighi, Sébastien Vaillant and Nehemiah Grew. Thus by the time of Carl Linnaeus, many botanists viewed plants as consisting of at least some repeating parts – usually the leaf was the key referent. Linnaeus furthered a morphological approach to plant development by innovatively describing it as "metamorphosis," comparing the sequence of flowering to insect metamorphosis. Just as the true insect could not be known until it reached its adult stage, which it achieved through a remarkable series of transformations, so too did various pre-existing plant parts transform into the parts of the flower, only then completely revealing its true nature (Schmitt, 2004, p. 103).

Approaches to part-whole relations of organisms entered a new phase with the surge of Romantic perspectives in the 1790s. Romantic biologists sought the general laws governing life. By weaving together broad-based comparative anatomy, consideration of the cycle of life, and transcendental principles, they sought to understand part-whole relations, development and generation, and how the scientist was to sort out their mutual relations. This tradition of organic teleology and the way it subsequently developed in both plant and animal morphology, beginning in continental Europe and somewhat later in Britain, was in good part what Leuckart was responding to, even in 1851, in *Polymorphismus*.

Here we choose Johann Wolfgang von Goethe's work in botany and vertebrate comparative anatomy as a proxy for broader late eighteenth- and early nineteenth-century scientific discussions. We do not maintain that Goethe himself was the fountainhead of either plant or animal morphology in the nineteenth century. Other botanists, including Augustin-Pyramus de Candolle and Pierre-Jean-François Turpin independently developed similar, influential approaches to plant morphology (Guédès, 1969, 1972; Stevens, 1994; Schmitt, 2004). And there was no lack of claimants among animal morphologists and physiologists to establishing general laws of life, as historians have amply demonstrated (Russell, 1982; Lenoir, 1989; Jardine, 1991; Richards, 2002; Gliboff, 2008). But Goethe worked as much on plants as on animals, explicitly comparing them, and he addressed head-on the problem of part-whole relations in connection with individuality. Moreover, his towering stature in his lifetime and since then makes him a central figure for this period. Since at least Whewell (1837), many historians, biologists, and even non-specialists have associated Goethe's 1790 *Metamorphosis of Plants* and 1820 compendium *On Morphology* (Goethe, 2009, 1988, respectively) with the emergence of modern ideas about plant individuality and biological individuality more generally.

Goethe's views on part-whole relations and individuality cannot be separated from three concepts: the primordial plant (Urpflanze), the archetype, and metamorphosis. Goethe's concept of the Urpflanze was an emergent Proteus, a generalized system of which all plants are built (Pfau, 2010). By contrast, the plant archetype was an original, ideal form, an abstract entity that was collectively "represented" in the material world by the whole range of iterated parts – leaf, stalk, sepals, petals, and so on (Pratt and Brook, 1996; Richards, 2002; Bersier, 2005; von Mücke, 2006; Pfau, 2010).[3] A plant is composed of these parts, which for Goethe shared a morphological equivalence and were repeated stages of development. Goethe's archetype was a "transcendental" model in that it could not be known in its entirety from any *single* observed organ or stage of development, yet it did not imply final causes, nor a theological appeal to providential design, nor descent from common ancestry (Richards, 2002; Huneman, 2006b; von Mücke, 2006; Pfau, 2010).

Goethe's metamorphosis followed a broader transformation of eighteenth century Romantic thought about the meanings of organic form and difference that revitalized models of nature-as-process. It was the process of "becoming" itself – epigenetic transformation or "metamorphosis" – that rendered the ideal real (Pfau, 2010, p. 9). Thus the leaf, adopted by Goethe only as a material referent, made the abstract archetype real through the varied stages of morphologically equivalent (but visually different) parts during a plant's growth. The transformation of the archetype, made material through the cycles of the leaf, allowed one to deduce the system of all plants (Huneman, 2006b). Goethe's metamorphosis was thus an overarching means of conceptualizing transformation and differentiation, uniting abstractions "seen" in the mind's eye with patterns observed in the material world.

In addition to presenting a picture of the plant as a dynamic whole composed of variants on a single archetype, Goethe explicitly suggested that the plant was a composite of individuals. His derivation of various plant organs from a single ideal structure later became a fundamental theory of the repetition of parts, one that has gained renewed currency in modern botany and certain aspects of biological modularity (Vergara-Silva, 2003; Barthelemy and Caraglio, 2007; Pfau, 2010). Extending his claims beyond plants to animals as well, he asserted in *On Morphology*, "No living thing is unitary in nature; every such thing is a

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[3] Goethe's archetype concept owed much to previous scholars, particularly Kant (Pratt and Brook, 1996; Huneman, 2006b; Pfau, 2010).

plurality. Even the organism which appears to us as individual exists as a collection of independent living entities'' (Goethe, 1988, p. 64).[4]

Asserting the composite nature of organisms was only the beginning. After 1790, Goethe began applying his ideas of the archetype and increasing differentiation to the comparative anatomy of vertebrates.[5] Influenced by the zoologist Carl Friedrich Kielmeyer, he embraced the importance of physiology and function, to stress the integration of organismal parts and wholes (Bersier, 2005). He sought to characterize this integration, both internally and with respect to the external world:

> We thus think of the closed animal as a small world, existing for its own sake, by its own means. Thus each creature is also an end unto itself, and because all its parts stand in the most direct interaction, have a relationship to one another, and thereby continually renew the circle of life, so should every animal be viewed as physiologically perfect. Viewed from within, no part of it is useless, or as people sometimes imagine, brought forth arbitrarily though the formative force [Bildungstrieb] (Goethe, 1954, p. 125).

Several ideas connect here. All parts of an organism are closely related and interact among themselves, serving the physiological perfection of the whole as a dynamic changing entity. A ''formative force'' guides that dynamic process toward perfection, where perfection is understood as the expression of manifold possibilities through internal differentiation (von Mücke, 2006). Goethe thus perceived the unity of nature through its continuum of internal differentiation. The organism exhibits a balance between internal harmony and adaptation to its external conditions, and this balance produces the variations in form we observe around us: ''If we ask what causes the appearance of this ability to assume manifold shapes, we will for the time being answer that the animal is formed by circumstances for circumstances; hence its inner perfection and its external adaptedness'' (Goethe, 1954, p. 126). Nonetheless, for both plants and animals Goethe continued to emphasize the importance of the transformation of form, privileging the derivation of parts through metamorphosis over their functional interpretation (Pictet, 1839; Stevens, 1994; Richards, 2002).

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[4] Despite this similarity, according to Goethe the type of metamorphosis undergone by plants differed from that of animals (see Richards, 2002, pp. 452–453).

[5] Nicolaas Rupke (1994) points out significant differences between Goethe's concept of archetype and the concept as later developed by Richard Owen. In particular, Goethe's concept was inclusive of all parts and their basic variations, whereas Owen's concept was one of reduction to a shared commonality, at its most extreme limit this was represented by a series of vertebrae. For further discussion, see Camardi (2001).

Goethe was not particularly innovative in these commitments, which are usually traced to Kant, Blumenbach, and a welter of other philosopher-naturalists of the period (see especially Schiller, 1978; Löw, 1980; Lenoir, 1989; Pratt and Brook, 1996; Huneman, 2006a, b). The problematic nature of part-whole relations, and the importance of development in resolving them, were familiar elements of early nineteenth-century idealistic biology, and biologists were still wrestling with them at mid-century. However, *On Morphology* also reveals an aspect of Goethe's view of the organism that has received somewhat less attention, and that is particularly relevant to our understanding of Leuckart. Here he writes of limits on nature, principles that constrain the modifiability of parts:

> In the above observation we encounter this law: nothing can be added to one part without subtracting from another, and vice versa.... The formative impulse is given hegemony over a limited but well-supplied kingdom. Governing principles have been laid down for the realm where this impulse will distribute its riches, but to a certain extent it is free to give to each what it will. If it wants to let one have more, it may do so, but not without taking from another. Thus nature can never fall into debt, much less go bankrupt. (Goethe, 1988, pp. 126–127).

Here Goethe followed his compatriot Kielmeyer in contending that growth obeys a law of nature, balancing or compensating the increased development of one part at the expense of another – a view that would later, much more famously, be associated with the French naturalist Étienne Geoffroy Saint-Hilaire (Appel, 1987, p. 159). In 1793 Kielmeyer had argued that three different fundamental life-forces – reproduction, motility, and sensibility – produced this balance by playing off against one another (Kielmeyer, 1993; Richards, 2002; Bersier, 2005). Goethe reverted to a single force, emphasizing the variety of directions it might take. The formative force directed the resulting structures toward perfection, but within limits imposed by the inclusive body plan of each large group of similar organisms.[6] As we will see, this same view would be developed in new directions both by Geoffroy's much younger

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[6] Robert J. Richards (2002, p. 445) describes Goethe in a 1794 essay speaking of organismal structures being derived from two forces, "an intrinsic one, which determined the general pattern … for all animals; and an extrinsic force, which shaped an organisms to its particular circumstances." There is some ambiguity in Goethe's archetype embracing a lawlike pattern (with a possible implication of constraint), and simultaneously freedom of the material expression of parts, correlated with (extrinsic) circumstances.

colleague Henri Milne-Edwards and – using a strikingly similar "accounting" rationale – by Leuckart.

The problem of individuality in both plants and animals gained added piquancy in the late 1830s, through the language of the new cell theory. Matthias Schleiden (1838, p. 1) declared that the concept of the individual as understood in the animal world was completely inapplicable in the plant world, and especially among the lowest plants, in which a single cell must be reckoned as the individual. "But every plant developed in any higher degree is an aggregate of fully individualized, independent, closed entities – the cells themselves." Schleiden and the important Swiss botanist Alphonse de Candolle (son of Augustin Pyrame de Candolle) would extend this conception of *relative* individuality in plants, regarding the cell, the shoot, and the plant body as successive, hierarchical levels (Geddes and Mitchell, 1911). In 1839 Theodor Schwann extended Schleiden's initial claim to animals, arguing that animal cells, like plant cells, were individuals that exhibited all the basic vital phenomena: generation, growth, internal transformation, secretion and absorption. Nevertheless, in most animal cases, these cellular individuals "are not ranged side by side as a mere aggregate, but so operate together, in a manner unknown to us, as to produce an harmonious whole" (Schwann, 1847, p. 2). In his *Mikroskopische Untersuchungen* (Microscopical researches), Schwann set out a research program of investigating how in higher organisms, differentiated tissues developed out of a common origin in undifferentiated cells. This, too, would find a parallel in Leuckart's developmental approach to polymorphism, as we will see.[7]

Polymorphism and the Division of Labor

By 1851, then, there was already a long history of naturalists engaging with the question of individuality, and *Polymorphismus* participated directly in that ongoing conversation. Leuckart opened his pamphlet, however, not by defining individuals directly, but by defining species. In sharp contrast to the debates over species underway in Britain in the 1840s (Stevens, 1994; McOuat, 1996), he argued that the definition of species was fairly straightforward. All definitions (he presented four) shared the idea that

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[7] Robert J. Richards (2002, pp. 260–261) has noted that the physician and physiologist Johann Christian Reil introduced a political metaphor for the animal body as a "large republic" in his 1795 tract "Von der Lebenskraft." It is possible that Schleiden and/or Schwann had this in mind when thinking about the relatively autonomous relations between cells and whole organisms, but evidence is currently lacking for a direct connection.

the species "represents a closed and self-maintaining form of animal life." But what individual beings perfectly represent this species ideal? He found that few animals completely fulfilled the criteria of "closed and self-maintaining." In some instances, not all the developmental stages were completed by a single being. For most animals, moreover, the sexes are divided, cooperation of beings is necessary for the "entire unfolding and reproduction" of the species, and the diverse capabilities or functions of life are divided among beings. In any of these instances, more than one individual being is needed to depict the entirety of the species as a closed unit that maintains itself in all manner of its needs.

Right from the beginning, then, Leuckart undermined the idea that a single individual by itself could perform all the functions of life needed to "fully represent" and maintain the species. This may have been a jab at an overly simplistic concept of the ideal type specimen in classification, though certainly systematists had long been accustomed to the notion that a full species description was rarely fulfilled by any single real specimen (Farber, 1976); and even Goethe had maintained (with respect to the Type) that no individual could possibly represent the whole (Goethe, 1954, p. 121). More importantly, Leuckart used this point to set up the central argument of the paper, which connected the need for a multiplicity of individuals to the emergence of polymorphism via the division of labor.

Leuckart showed how the division of labor was manifested among animals by leading his reader through a stepwise series. He categorized groups of organisms not simply along taxonomic lines, but by the degree to which their life histories, their parts (or members) and related behaviors partitioned the tasks of life. He began with isolated organisms that had separate sexes: the primary division of labor was a sexual one in which males differed from females only in their sexual organs and products (sperm and eggs). In the simplest case, those organisms had external fertilization, while organisms in the next step required a union for internal fertilization. This step then led to sexual pairs that divided labor in brood care, then polygamous unions in which brood care and other functions were separate. The next most complex form was the "animal state," represented by insect societies in which different individuals had strictly circumscribed tasks and both asexual and sexual individuals were common (especially among ants, bees, and termites – the eusocial insects). In his description, the economy of the state was served by the organization of individual beings in the society, and the state was held together through communal interests and needs. In contrast, the last step comprised physiologically contiguous animal colonies ("animal stocks" [Thierstöcke][8]), in which the colony developed by asexual multiplication of its members. Here the "individuals" were integrated parts or members of the physically unified colony, which in turn grew by iterated budding (asexual multiplication) of these individuals. Thus Leuckart drew a sequence from one group of organisms to the next that simultaneously moved from familiar to unfamiliar and from simple to complex. He presented a functional division of labor that gradually increased as individuals took on specialized tasks; in consequence, the forms of individuals also changed to suit their purposes, while serving as parts of integrated wholes. The different forms produced by this functional differentiation were what Leuckart called "polymorphic individuals."

In fleshing out his argument, Leuckart concentrated on animal stocks. He focused primarily on two groups of colonial marine invertebrates, siphonophores and hydroids (both now placed in the Phylum Cnidaria). Siphonophores are entirely planktonic, floating and swimming colonies that produce sub-colony propagules, spawned gametes or isolated larvae (Figure 1). Hydroid colonies of polyps and stolons are attached to the sea bottom, but typically produce free-swimming medusae that carry out the sexual life history stage (Figure 2). The medusae of hydroids are usually distinguished clearly in the biological literature. However, for siphonophores, the interpretation of medusae and their related polymorphs present difficult problems (Dunn et al., 2005; Bardi and Marques, 2007); in the nineteenth century, these were further confounded with problems of coelenterate (now cnidarian plus ctenophore) classification (Winsor, 1972, 1976).[9]

Leuckart asserted that polymorphic individuals in colonies of hydroids, siphonophores, and other groups had often been "misunderstood" as "mere organs" (Leuckart, 1851a, p. 12). In the context of these colonies, he made a strong claim that essential life needs were met by different functions; that structure, form, and connections of individuals followed from these functions; and that polymorphism "depend[ed] on" the "principle of the division of labor." This was a definite pattern across different animal stocks. Within the different body plans of these stocks, the need to fulfill these essential physiological functions shaped the structural polymorphism of individual polyps,

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[8] Here Leuckart is analogizing from horticulture, in which a plant stock – the basic structure from which offshoots develop – is used for propagation.

[9] In our translation, we have used "disc-shaped medusa" (Scheibenquallen) and "medusa" (Medusen) in the broad descriptive sense of form, irrespective of taxonomic affinity. Thus we have not attempted to interpret any taxonomic commitment Leuckart may have had to the former term.

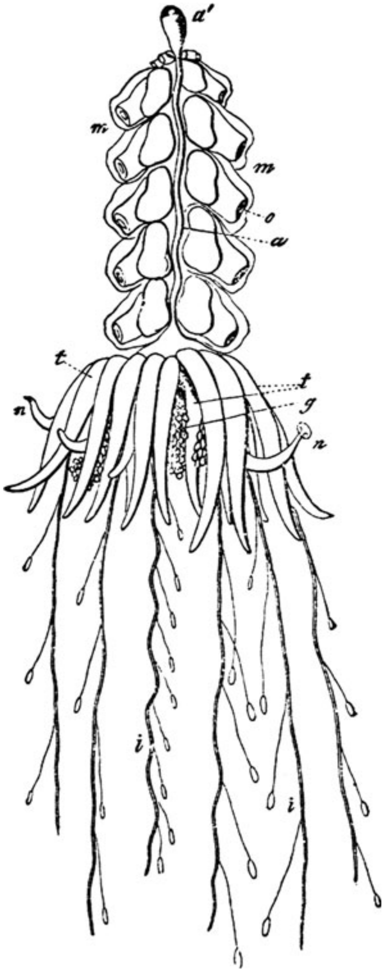

Figure 1. Siphonophore (*Physophora*). "*a*: air-bladder or swimming-bladder at its top end; *m*: swimming-person or swimming bell; *o*: opening of the bell; *t*: sensory-persons or tactile polyps; *g*: egg-forming or female persons; *n*: nutritive-persons or eating-polyps." Note Haeckel's use of the term "person" for polymorphic individuals. From Ernst Haeckel (1878, p. 120).

medusae and the like. Thus although there existed differences in the particular resulting forms, the process was a general one. He then marshaled diverse evidence – from physiological function, comparative anatomy, and similar developmental beginnings – to support his claim. He combined these lines of reasoning and evidence to validate separate categories, not of organs, but of individuals: nutritive, chylomotor (circulatory), locomotive, stem, rootlet, proliferating, and sexual

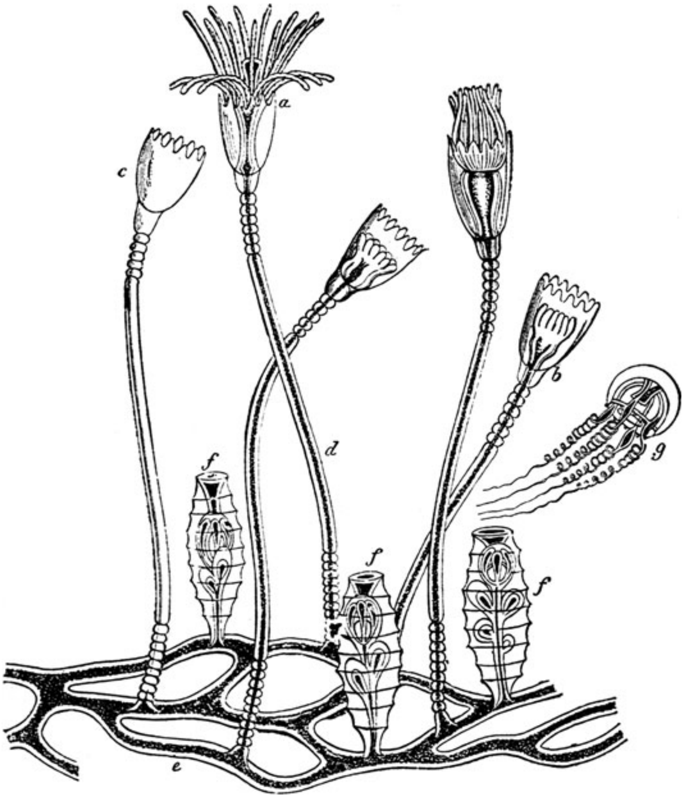

Figure 2. "A creeping polyp-stock (*Campanularia johnstoni*). On the stolonal network (*e*) sit entirely differently developed hydroid-polyps: long-stalked 'feeding polyps' (*a–d*) and short-stalked 'reproductive polyps' (*f*). The latter form buds that transform themselves into medusae and swim away (*g*). The former can retract (*b*) their extended body (*a*) into a horny casing (*c*). Their stalk (*d*) is ringed at the top and bottom." From Ernst Haeckel (1878, p. 118).

individuals, among others. Together these individuals performed all the functions needed by the whole colony.

Leuckart thus brought a new meaning to the terms "polymorphic individual" and "polymorphism" within biology. Previously, "polymorphic" or "polymorphous" had referred in a general way to life-forms that showed great variability within a genus or species, rather than to the diversity of forms within a colony.[10] But the functional division of labor that produced his polymorphic individuals was already a well-known biological concept in 1851, having been introduced by the

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[10] Oxford English Dictionary s.v. "polymorph" and variations on this term; see also Darwin-Hooker correspondence, letters 803, 804, 945, Darwin Correspondence Project at www.darwinproject.ac.uk, accessed 14 June 2010.

French naturalist Henri Milne-Edwards in 1827. The latter had developed the concept first in encyclopedia articles on "organization" and "nerves" (Milne-Edwards, 1827a, b) and then enhanced it in subsequent writings, first in his research articles (e.g., 1833) and multivolume monograph on crustaceans (1834–1840); it gained greater visibility via the various versions of his zoology textbooks (1834–1837; 1841–1842; 1851; and many later editions) and their translation in American (1841), German (1844–1847), and British (1856) editions.

Leuckart was familiar with Milne-Edwards' researches of the 1840s, as evidenced by his citing the French scholar in *Polymorphismus* and earlier works (Frey and Leuckart, 1847; Leuckart, 1848). He clearly shared Milne-Edwards' functionalism, which viewed the form of a part or organ as adapted to serve a particular function. This was a strong feature of the Cuvierian approach adopted by both Milne-Edwards and Leuckart's teacher Rudolph Wagner, who had studied in Paris under Cuvier's patronage in 1827. (Leuckart acknowledged his debt to Wagner by dedicating *Polymorphismus* to him.) Leuckart further developed his functionalist approach in his work with the physiologist Carl Bergmann, with whom he had become acquainted when both were students at Göttingen. In examining the relations between anatomy and physiology, the two men attended closely to the ways that functional efficiencies could be effected through structural-anatomical means, and to the effects that such factors as size and shape had on the ways that physiological functions needed to be carried out. Although their co-authored *Anatomisch-physiologische Uebersicht des Thierreichs* (Anatomical-physiological overview of the animal kingdom) would not appear until 1852, it was completed by the end of 1850, and it is clear that by that time Leuckart was already pursuing questions of organismal efficiency. In his view the division of labor afforded by polymorphism worked to the advantage of the larger entity by "sav[ing] time and effort" (Bergmann and Leuckart, 1852, p. iv; Leuckart, 1851a, p. 33).

What exactly was the nature of the advantage afforded by polymorphism? We have seen already in Goethe and Geoffroy the view that resources necessary to the lives of organisms may be limited, producing shifts in the balance of organs. But Leuckart went a step further, arguing that as each part contributes to the well-being of the whole, efficiencies in certain functional tasks free resources for other critical tasks, among them generation, which also contributes to the perpetuation of the species (Bergmann and Leuckart, 1852, p. 27).

Leuckart further shared with Milne-Edwards a developmentalist approach toward understanding the division of labor: for both men, the division of labor manifested itself over time, via development (on Milne-Edwards in this regard, see Perru, 1997, pp. 155–157). Leuckart took pains to show that the individuals with different functions – feeding, locomotive, proliferating, and so on – all originated developmentally from an initial protuberance that would take on its individual nature only as it assumed its functional role in the colony. Similarly, Milne-Edwards (1844) argued that tissues and organs should be viewed as developing from an initial "bundle" (faisceau) that branched into successive secondary, tertiary, and quaternary bundles of differentiated forms during the course of development. These may be viewed as two versions, among many, of the concept of development as differentiation from a common amorphous origin – a concept that emerged in the late eighteenth century as a prevailing theme in European (especially German) science. Not only did Goethe's differentiated plant emerge as successive expressions of an archetype and all plants from a primordial form (Urpflanze), but Johann Friedrich Blumenbach's races of mankind derived from a single originary form, and Karl Ernst von Baer's chick expressed ever-more particular taxonomic features in its development. Only slightly later, in 1839, Schwann traced the development of diverse, functionally differentiated animal tissues back to a common cellular origin. Leuckart could have drawn on any of these as models; they were available all around him. But his connection of differentiation to the division of labor points us toward Milne-Edwards.

However, two key features of Leuckart's approach to the division of labor in development distinguished it from that of Milne-Edwards. First, whereas Milne-Edwards (1827a) was interested in the organization of parts (tissues and organs) within a single organism – arguing, for example, that different kinds of tissues could best be understood as mechanical or chemical modifications of a common cell structure – Leuckart explicitly applied the division of labor to a higher level of organization: the animal stock or colonial organism. As he put it (1851a, pp. 10–11):

> In this regard the separate individuals of an animal stock behave just like the individual parts [Glieder] of an organism, which share in the benefits and risks of a common nutrition in the same way. And just as this arrangement enables the freest and [most] exclusive application of the individual organs to this or that goal of life, so too the commonality [Gemeinschaft] of the nutritive processes

Figure 3. Sars' observations of *Medusa* and *Cyanea* development. Numbers 1–24: ▶ Development of *Cyanea capillata*, 12–24 October 1839. Numbers 25–42: Depiction of the polyp-like developmental stage of either *Medusa aurita* or *Cyanea capillata*, 9 September 1836. Numbers 43–46: Transition from polyp stage to acaleph-stage, August 1830. From Sars (1841), plate I, explanation of plate, pp. 30–33.

> provides the animal stock the physiological condition of a freer division of labor.

Second, and perhaps more significantly, although both Milne-Edwards and Leuckart incorporated a temporal, developmental dimension into their conceptions of individuality, they did so toward different ends. For Milne-Edwards, both development and the division of labor bore on the level of "perfection" of an organism: although he rejected a single chain of being, he did view organisms as higher or lower on a scale of perfection, depending on how differentiated and integrated their parts were – something that would appear in the organism's development (Milne-Edwards, 1844; Limoges, 1994; D'Hombres, 2010). Leuckart, by contrast, did not prioritize "higher" and "lower" forms, and does not seem to have been committed to a scale of being in any idealist sense; his highest value appears to have been functional efficiency. This may clearly be seen in the stance he took with regard to a major controversy in the study of organic development in the 1840s and 1850s: alternation of generations.

Alternation of Generations

"Alternation of generations" refers to a cycle of reproduction and development differing from both the simple vertebrate sequence from birth through development and sexual reproduction to death and the metamorphic sequence familiar in butterflies and moths. The term was introduced in 1819 by the French-born German voyager Adelbert von Chamisso to describe an odd cycle that connected two morphologically distinct forms of the salp, a free-living pelagic tunicate (Chamisso, 1819; see also Geus, 1972). A solitary form would bud asexually, producing a hermaphroditic chain-form, which in its turn would sexually produce the solitary form again. Thus the term "alternation of generations" implied both that the different stages comprised different individuals (of different "generations") and that the mode of generation (sexual or asexual) alternated as well. The Norwegian Michael Sars later described a similar phenomenon in the jellyfish *Cyanea* and *Aurelia* (Figures 3 and 4), in which the colonial polyp stage of the life cycle releases a

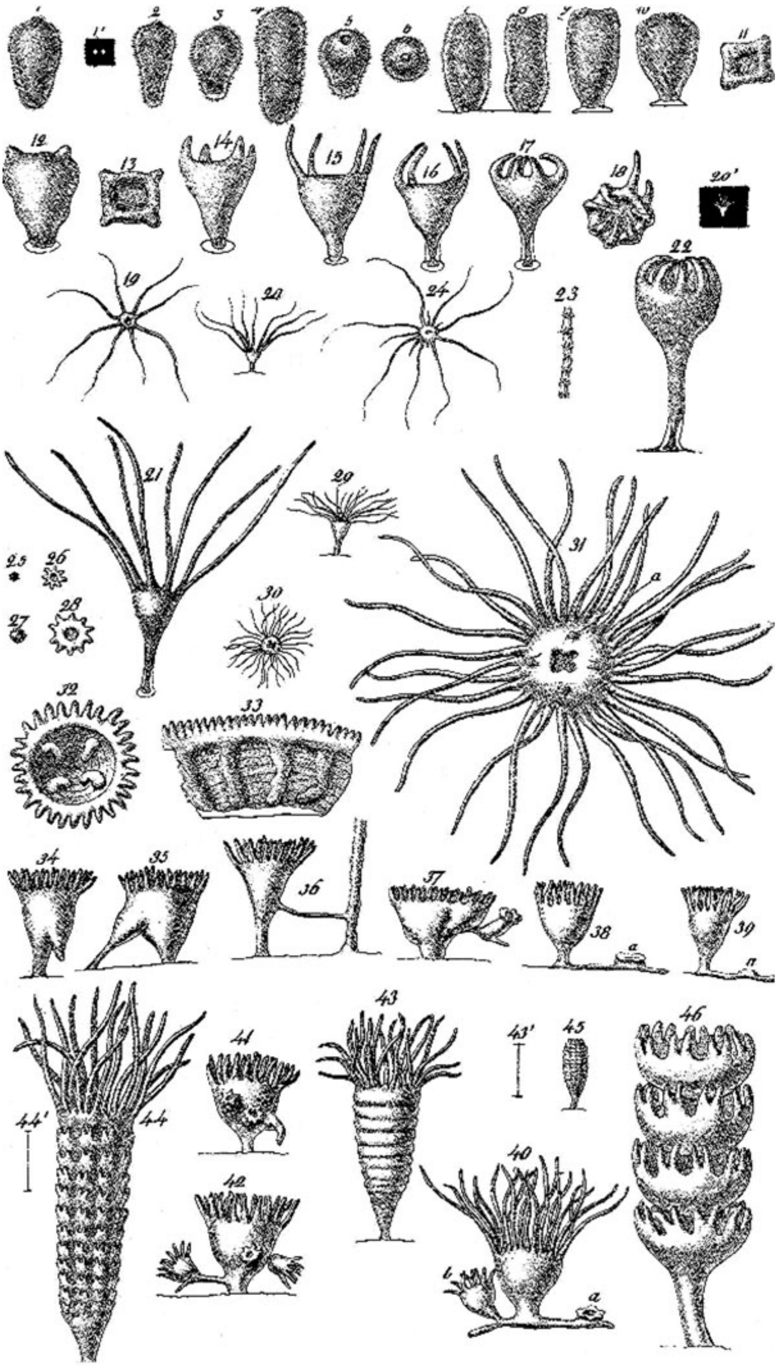
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Figure 4. "The fully developed *Medusa aurita* [*Aurelia aurita L.*], seen from the side, with its four descending, fully divided oral arms and its numerous extended peripheral tentacles." From Sars (1841), plate IV, Fig. 61, explanation of plate, p. 34.

medusa that sexually produces eggs, which are fertilized by sperm from another adult medusa; from these eggs emerges a different larval form that begins the life cycle anew (Sars, 1841; Cornelius, 1977). The polyp does not itself develop into an adult form, but asexually produces a bud that grows into the medusa form. In 1842 the Danish biologist Johannes Japetus Steenstrup collected these cases together with observations he had made in other species, to argue that this cycle was widespread in the animal kingdom, appearing in all groups except the vertebrates, and could even be extended to plants (Steenstrup, 1845; Geddes and Thomson, 1890, ch. 15; Miall, 1897; Churchill, 1979; Farley, 1982). In a move that would create considerable controversy, he named the asexual form (which could actually continue to produce its own kind for numerous iterations before producing a new sexual form) the "nursing" generation, expressing the teleological view that it existed for the purpose of nurturing the next sexual generation.

The interpretation of this strange cycle and its relation to ideas about metamorphosis, parthenogenesis (production of offspring by the female without a contribution by the male), asexual generation in general, and individuality was the subject of widespread debate in international biological community of the 1840s and 1850s. The well-known rivalry between Richard Owen and T. H. Huxley began with their opposing contributions to it (Winsor, 1976; Desmond, 1984). Owen's 1849 *On Parthenogenesis* and his later lecture "On Metamorphosis and

Metagenesis" (Owen, 1851) as well as Huxley's answering 1852 "Upon Animal Individuality" (Huxley, 1898) engaged both the problem of alternation of generations and that of individuality. Necessarily, deciding what constituted a "generation" also meant deciding what constituted an "individual." Owen and Huxley were just the most famous British protagonists in this discussion, which also engaged (among others) William B. Carpenter, Edwin Lankester, Edward Forbes, George Busk (who translated Steenstrup's text into English), the philosopher and social theorist Herbert Spencer, and even Charles Darwin in the *Origin*; the Belgian zoologist Pierre J. van Beneden; in France the zoologist Jean Louis Armand de Quatrefages; in America the zoologist and geologist James Dwight Dana; and in Germany the physiologists Johannes Müller and Carl Theodor Ernst von Siebold, and the zoologists Theodor Schwann, Friedrich Stein, Julius Victor Carus, Carl Vogt, Carl Gegenbaur, and, eventually, Ernst Haeckel.

The discussion was not confined to zoologists. Between 1849 and 1851, Wilhelm Hofmeister interpreted the reproductive cycle of cryptogamic plants as an alternation of generations (Hofmeister, 1851). Once articulated this way, the phenomenon was subsequently determined to be widespread among fungi, algae, and higher plants (Radlkofer, 1857; Klebs, 1898). Hofmeister's articulation, and his accompanying rejection of Schleiden's view of the cell as the "elementary individual" of the compound plant, reopened the question of plant individuality (Farley, 1982, pp. 86–100) – and quite a number of botanists, including (among others) Alexander Braun and Carl Wilhelm von Nägeli in Germany, and George Thwaites in Britain, took up the challenge. The union of the problem of alternation of generations with that of individuality in botany also invited naturalists to hope that a more expansive conception of generation and individuality might be forthcoming that would encompass both plants and animals (Carpenter, 1848; Carpenter and Dana, 1850–1851; Geddes and Thomson, 1890).

Leuckart's chief original contribution to this discussion, "Ueber Metamorphose, ungeschlechtliche Vermehrung, Generationswechsel" (On metamorphosis, asexual multiplication, alternation of generations) appeared in June 1851, just before the *Polymorphismus* pamphlet (Leuckart, 1851b). Here again, he revealed his preoccupation with functionalism and efficiency. He argued that metamorphosis was simply a form of development that took place outside the egg, adopted by nature because it was less costly to the mother than nurturing it in her own body: by prematurely sending the offspring into the world to fend for itself, the mother could produce more offspring for the same expenditure of matter. Again, adopting a "budgetary approach in analyzing the various modes of reproduction," Leuckart further argued that asexual propagation was another means of making more offspring without excessive investment by the parent (Churchill, 1979, p. 160). Alternation of generations, in turn, was nothing more than a combination of free metamorphosis with asexual reproduction, a form of asexual multiplication that took shape during a larval stage of life. Steenstrup made alternation of generations the more inclusive phenomenon within which asexual multiplication occurred, but in Leuckart's view, this was exactly backward: asexual reproduction was the more inclusive category, and alternation of generations was just a particular form of it (Leuckart, 1851b).

Both Steenstrup and Leuckart's positions took shape within a context in which knowledge about both sexual and asexual reproduction was increasing rapidly, and the respective status of the two was shifting. Looking back from the mid-nineteenth century, Ehrenberg (1851, pp. 762–765) asserted that the notion of a cycle of life going from egg to egg (i.e., a view structured around sexual reproduction) went back to Aristotle and Harvey, and that the only taxonomic groups Linnaeus considered worthy of serious taxonomic study were those with adults that had a closed, sexual cycle. But as Churchill (1979) has argued, new attention to alternation of generations, parthenogenesis, and hermaphroditic reproduction in the decades around mid-century called into question the hegemony of sexual reproduction. Whereas Steenstrup himself believed that the "nursing" and other intermediate generations existed only to prepare the way for the production of more perfect, sexual individuals, Leuckart did not privilege sexual reproduction, but treated both modes of reproduction as simple functional needs, alongside locomotion, nutrition, and others.

In *Polymorphismus*, Leuckart condensed this argument and combined it with the division of labor to yield a slightly different claim: "The alternation of generations is a polymorphism that is determined by a division of labor in the realm of developmental life" (p. 34). In Leuckart's presentation, both sexual and asexual generation were tasks best handled within the colony by special individuals, just as feeding and locomotion were. He renamed Steenstrup's "nursing" generation "proliferating individuals" that bore or budded "sexual animals," the reproductive structures that typically develop into medusae (the sexual stage of the life cycle). Generation was just another functional task required for the maintenance and perpetuation of life, neither mysterious nor special, as Steenstrup seemed to want to make it.

Despite Leuckart's disagreement with Steenstrup over the special character of sex and the priority of alternation of generations over metamorphosis, he shared one of the latter's broader goals: to establish a broad law of morphogenesis that could be extended beyond invertebrates to other realms of the organic world as well. Like Steenstrup (and many earlier writers), Leuckart thought that the patterns of colonial invertebrate generation and part-whole relations were like those of plants, and he devoted the end of *Polymorphismus* to articulating the similarities he saw. Here he drew on the work of the botanist Alexander Braun, who in 1850–1851 was Leuckart's colleague at Giessen. Most important, Leuckart represented plants as "polymorphous plant stocks, just as the hydroids and siphonophores are polymorphous animal stocks" comprising "nutritive, attaching, vegetative, proliferating, and sexually developed individuals" (Leuckart, 1851a, p. 36).

Thus the picture that Leuckart presented of polymorphic individuality drew together the functional division of labor, developmental considerations, and alternation of generations into an expansive view. Most explicitly, it brought the life cycles of colonial marine invertebrates into line with other organisms, by analogizing the cooperation of multiple individuals in colonial invertebrates first with plant "stocks" and then with the unified part-whole relations of the solitary, non-colonial individual, as expressed through the division of labor into tissues and organs. At the same time, Leuckart's presentation also incorporated the temporal dimension, by arguing that the division of labor also took place via development – both the division of labor and the higher unity that conversely derived from reuniting the parts into the whole needed to be seen as operating over time. Parts cooperated to form a whole not just at a static moment in time, but in the dynamic developmental cycle as a whole. The criterion of functional efficiency was critical here in motivating an explanation that worked at both organismal and colonial levels of organization and also over time.

Less explicitly, Leuckart's strongly functional orientation also worked to mediate between the discourse of organic individuality operating in a transcendental framework and one more grounded in the concrete, material world. To understand this, we must return to definitions.

In a paper on the differences between animals and plants published in February 1851, Leuckart wrote, "The organism is a closed whole, whose individual parts and functions are all embraced by the same bond of internal necessity" (Leuckart, 1851c, p. 152). The resemblance to his species definition at the opening of *Polymorphismus* is striking: there, he wrote that the species "represents a closed and self-maintaining form of animal life." It would appear that Leuckart viewed the species as an individual, or at least analogous to one. But "represents" is also an important part of this picture, for here Leuckart seems to be answering Steenstrup as well. The latter had argued that, peculiarly to the small cluster of organisms that exhibit alternation of generations, the species

> is not wholly represented in the solitary, full-grown, fertile individuals of both sexes, nor in their development, but that to complete this representation, supplementary individuals, as it were, of one or of several precedent generations are requisite. Thus, the distinction between this course of development, and that which is generally recognized in nature, in which the species is represented by the individual (of both sexes) and its development, is the want on the part of the individuals of a complete individuality as representatives of the species, or of a specific individuality, if I may so express it. (Steenstrup, 1845, p. 106).

Thus when Leuckart wrote at the beginning of *Polymorphismus* that in almost no case could an individual serve as the representative of the species, he was countering Steenstrup's claim that this was a peculiar feature of organisms exhibiting alternation of generations. The division of labor accounted more broadly for the need for many individuals to be involved in "representing" the species.

The background to Leuckart's idea of the relationship between organism and species is still more complicated, however, and relevant for understanding why he might have wanted to answer Steenstrup in this way. In analyzing the shifting discourses around the term "organism," Tobias Cheung (2006, p. 335) has argued that this term came to be associated with "individual" only around 1830. Whereas in the seventeenth century, "organism" referred to a principle of organization, the German *Naturphilosophen* redefined "organism" into an entity. As Lorenz Oken wrote in his 1810 *Lehrbuch der Naturphilosophie*, "an individual, total, closed, internally driven [selbst erregter] and self-moving body is called an organism"; in a later section he wrote more baldly, "an organism is an individual" (quoted in Cheung, 2006, p. 333). In the system of *Naturphilosophie*, a key characteristic of this sort of organism or individual was that it existed at both macrocosmic and microcosmic levels. The microcosmic organism repeated the macrocosmic organism in its own organization, and this repetition at multiple levels was a unifying feature of the world as a whole (on Oken in this regard see also Gould, 1977, pp. 39–45; Schmitt, 2004, esp. pp. 51–64). In the 1830s, however, according to Cheung, the term "organism" came to be stabilized internationally around the lower-level individual. Cheung's article doesn't address quite how this happened, or what was at stake in narrowing the "organism" to the "individual" organism.

As Cheung makes clear, part-whole parallels and multiple levels of individuality were associated in Germany with Goethe, Oken, and idealist speculation (the botanist Alexander Braun, who did much to further the idea of multiple levels of plant individuality, also "remained true… to idealistic views" [Sachs, 1890, pp. 170–181]). Although *Naturphilosophie* had already been on the decline since the 1820s, it was not entirely dead (indeed, Oken himself was active until his death in 1851), and in the late 1840s, an up-and-coming generation of physicalist physiologists once again denigrated this approach – and morphology more broadly – as unscientific (Lenoir, 1989, pp. 195–245; Otis, 2007, esp. chs. 3 and 4). Leuckart had already been burned on this score in 1849, when Carl Ludwig scathingly reviewed his *System der thierischen Morphologie* (System of animal morphology; see Nyhart, 1995, pp. 97–98). How, then, to redeem morphology and the possibility of an analysis that retained part-whole parallels but did so without recourse to a reliance on seemingly mystical "correspondences" between levels?

In *Polymorphismus*, Leuckart offered two related keys to a new approach. First, he recognized those polymorphic individuals involved with sexual reproduction as playing a role in the maintenance of the colony (here, the organism), but also a role in perpetuating a higher-level entity, the species. But Leuckart's species was neither the same as the metaphysical "stem-types" of Kant nor the "Urpflanze" type of Goethe (see Jardine, 1991, esp. pp. 38–43). Leuckart's species was not an archetype, and he invoked no "formative force" in the development of polymorphic individuals. His species, we suggest, was a higher-level union of individuals, and itself an individual. However, the individual at the level of species and higher is idealized, and can only be instantiated through multiple real or material individuals. The polymorph is also an ideal, but one that is expressed in the material world.

The division of labor on functional grounds provided his second key. Efficiency and an increase in productivity (that is, an increase in offspring per amount of "expenditure"), through saving parental labor and materials, supplied a materialist substitute for "representation" that was very much in line with the physicalist physiologists' emphasis on efficiency (Churchill, 1979; Lenoir, 1989). Meaningfully, it operated equally well at multiple levels of organization. Leuckart took the division of labor to explain the part-whole relationship among polymorphic individuals and the organism, and brought it to yet a higher organizational level in his interpretation of the species concept. Although Leuckart drew criticism for his teleological reasoning in other writings of 1851 (see Leuckart, 1851b; Carus, 1851), with respect to part-whole relations he seems to have found a new way out of the idealist world.

Perhaps the most striking difference in comparison with earlier ideas of Kant, Goethe, Candolle, Milne-Edwards, and Steenstrup is that Leuckart did not care about the noble ‘perfection’ of organisms to any great degree. Both Kant and Goethe had ideas of purposiveness in nature that were strictly teleological, frequently expressed in attainment of perfection (Pratt and Brook, 1996; Schmitt, 2004). Thus in the introduction to his work on comparative anatomy, Goethe wrote of the human being’s “exalted perfection as an organism” in contrast with “the imperfect animals” (Goethe, 1988, p. 118). Candolle also thought that the species reflected a “type” that in its turn derived from a “superior cause of order,” although unlike Goethe he saw individual plants as purely material (Schmitt, 2004, pp. 186–187). The idea of perfection was present even in the earliest of Milne-Edwards’ works on the division of labor (e.g., Milne-Edwards, 1827a; see also D’Hombres, 2010), and did not diminish over time. Steenstrup – to whom Leuckart was most directly responding in this pamphlet – constructed a graduated series of groups from incompleteness to completeness to autonomy, a series showing increasing perfection (Churchill, 1979, pp. 143–145). In describing the transition following an asexual “nursing” generation of one life cycle, for example, Steenstrup (1845, p. 2) wrote of the “later, succeeding generation of animals destined to attain a higher degree of perfection.” These allusions did not find their way into *Polymorphismus*. For Leuckart, teleological reasoning was justified as an approach to understanding how the whole governed the parts, and to an orientation toward the future (see also Bergmann and Leuckart, 1852, pp. 20–24), but not to perfection. *Polymorphismus* thus also encapsulates the ways in which scientists of the mid-nineteenth century – other than Darwin – were starting to substitute other values aside from an ascent to perfection in their thinking.

The Discussion After 1851

Both the questions addressed in *Polymorphismus* and the solutions Leuckart offered had a rich legacy after 1851. We have already alluded to the famous dispute between Owen and Huxley over alternation of generations and the nature of biological individuality, after which Huxley’s developmentally inspired view eventually became the prevailing one, that an individual exists from ovum to ovum (Huxley, 1851a, b, 1856, 1859, 1898). But this was hardly a foregone conclusion, and in the 1850s numerous zoologists and botanists continued to debate these topics. The stakes were high, and involved not only empirical questions of what processes of generation different organisms used, but also questions concerning the ontological reality of biological individuality, the relations between teleology and mechanism, the generalizability of biological processes across plants and animals, and the politics surrounding whose views would prevail. However individuality at different levels was viewed, the recognition of alternation of generations and polymorphism spread quickly and widely, among both botanists and zoologists. Discussions in terms of separate plant individuals or polymorphs and levels of individuality continued to appear in the botanical literature (Radlkofer, 1857; Lubbock, 1882; Sachs, 1890; Green, 1909; Haig, 2008), joined in the 1860's by discussion of the compound individuality of lichens (Klebs, 1898; Honegger, 2000). Rudolf Virchow wrote philosophically in 1859 of the individual and the organism alike, "A decision has not yet been reached. To one investigator the whole plant is the individual, to another the branch or sprout, to a third the leaf or the bud, to a fourth the cell, and each of these points of view has a weighty basis" (Virchow, 1958, pp. 130, 134).

Into the early twentieth century, the problem of individuality continued to permeate biologists' discussions of part-whole relations and alternation of generations. These concepts were taught and *Polymorphismus* (or its perspectives) cited in major zoological and embryological textbooks and reviews (Agassiz, 1859; Haeckel, 1866; Perrier, 1881; Claus, 1876, 1885; Geddes and Thomson, 1890; Korschelt and Heider, 1895; Geddes and Mitchell, 1911; Radl, 1930). The physiological division of labor also become an influential idea in biology, seen, for example, in the multiple editions and translations of Milne-Edwards' zoology textbook (1856) and Darwin's theory of divergence as a division of ecological labor (Ospovat, 1981; Kohn, 2008). Having been inspired by sociological concepts, this idea together with concepts of the part-whole organization of biological entities remained in frequent contact with social theory, notably in the works of Herbert Spencer and Émile Durkheim (Limoges, 1994; Guillo, 2002).

After 1859, all of these discussions were recast by their engagement with Darwinian evolution. Three brief German examples will suffice to show how biologists interested in individuality in the 1840s and 1850s incorporated these interests into their responses to Darwin. In the course of his investigations into tissue structure and development across the animal kingdom, Albert Kölliker was led in the early 1860s to study a group of colonial marine invertebrates, the sea pens (pennatulids), in which he had discovered polymorphism among the polyp-individuals across many of its taxonomic subdivisions, a result that had "not even been imagined" before (1872, p. 1), and that appeared with law-like regularity. At the same time, he wrote, a closer study of this highly varied division of the animal kingdom would allow him to test Darwin's theory. Opposing both unconscious purposiveness in nature and Darwin's mechanism of natural selection, he proposed an alternative, single "law of development" with domain over "all levels of the organic world" (Nyhart, 1995, p. 124). One striking aspect of his theory was its mechanism for saltational species formation via changes in development of the fertilized egg or during parthenogenesis – a model he explicitly derived from his understanding of the alternation of generations.

For Ernst Haeckel, Germany's leading Darwinian, individuality played an even more central role. Haeckel, who had been taught at different times by Braun, Müller, Virchow, and Kölliker, shared the widespread idea (at least in Germany) that evolution was a form of development (Richards, 1992, 2008). In his *Generelle Morphologie* (1866), Haeckel recognized individuality beginning with three perspectives: morphological, physiological, and genealogical. The morphological and physiological perspectives shared six abstract levels of individuality, ranging from the lowest, the "plastid," to the highest, the "corm"; each level was instantiated by different material forms, depending on one's perspective (for example, from a morphological perspective the "plastid" was represented by the cell, from a physiological perspective by the protist). Genealogical (temporal) individuality, by contrast, contained only three levels: organism, species, and phylum. For all of these, individuals of a higher order included and were composed of individuals at lower ones. Thus for Haeckel, individuality occurred at manifold levels, and in both material and abstract forms (Rinard, 1981; Nyhart, 1995; Reynolds, 2008; Richards, 2008). This multiplicity of levels is what ultimately justified his famous biogenetic law, "ontogeny recapitulates phylogeny."

Finally, let us return to Leuckart. In 1877, speaking as Rektor (vice-chancellor) of the University of Leipzig, Leuckart gave a public address on important developments in biology over the previous several decades. From his perspective, Darwin's theory was significant at least partly because it justified the notion that the animal kingdom was comparable to an individual. Researchers before 1859, he wrote, had come to view the *physiological* dependency of organisms on each other as analogous to the dependency of the internal parts of an individual to the whole. But Darwin reinforced their belief in the analogy by demonstrating that

> the animal world is not simply physiologically but also genetically an interdependent whole; its parts did not originate independently and from the beginning in full possession of their characteristics, but emerged through the transformation of [earlier] ones. Like the different states of the same organism, so do the different animal species form a connected developmental series, only one that stretches the time of development over many hundred thousands of years (Leuckart in Wunderlich, 1978, p. 99).

Leuckart had earlier viewed the species as an idealized individual instantiated by lower-level material individuals. Here for a broad audience he took the analogy a step further; in presenting the animal species as "a connected developmental series," he compared the animal kingdom as a whole to an individual, as a way of showing his support for Darwinian evolution.

Looking beyond the interfaces of individuality with evolution, we can see it ramifying into numerous other problem areas in the latter part of the century, even as biology itself was evolving and splintering into subdisciplines. Consider parasitology. Leuckart's own later career was dominated by work on parasites, some with extreme morphological transformations and complex life-history transitions involving both sexual and asexual reproduction. It seems possible that Leuckart's interest in parasites grew out of his interest in organismal parts and wholes – specifically, the question of incomplete individuals. In Steenstrup's presentation of alternation of generations, for example, the author had not realized the importance of intermediate hosts and full parasitic life cycles of almost unrecognizably different morphological stages (Farley, 1992). The establishment of continuities among these different morphological stages, host–vector relationships, and alternation of generations, would be taken up by Leuckart's American students Charles Stiles and Henry Baldwin Ward, as well as the Scottish "father of tropical medicine" Patrick Manson, with significant results for understanding and combating human and animal parasitic diseases (Cassedy, 1971; Li, 2002, 2004).

Three other avenues along which the discussion of individuality traveled passed through Leuckart's own lab, where colleagues studied after finishing their degrees. Otto Bütschli, adopting Leuckart's functionalist outlook and perspective on the division of labor, became the principal architect of protozoology (Jacobs, 1989), published the first comprehensive treatise on the subject, accurately described the process of conjugation, and was among the first to recognize chromosomes within cell nuclei. Elie Mecznikoff not only discovered phagocytosis, a mechanism for defending the "self" from "non-self" invaders, but also established the study of cellular immunology, for which he was awarded the Nobel Prize in 1908. His work on the immune self became another basis for the establishment of organismal identity (Tauber, 2009). August Weismann, perhaps the most famous biologist to pass through Leuckart's lab, became renowned for his seminal contributions to Neo-Darwinism and his 1892 germ plasm theory. The nested hierarchy of developmental units that was central to the latter theory, as well as Weismann's view of the differentiation of cell lineages through division, betrays remarkable affinities with Leuckart's career-long interest in organismal part-whole relations (Churchill, 1968; Griesemer and Wimsatt, 1989). Weismann's opposition to the neo-Lamarckians, and particularly his separation of the germ plasm from the material of the body (soma), provided one of the bases of the early twentieth-century neo-Darwinian shift of focus away from the organism as a whole and toward certain of its parts, specifically, the hereditary material. The Modern Synthesis furthered and reinforced this shift toward gene-centric views that dominated the 1940s, 1950s, and 1960s.

This leads us to one last but crucial direction in late nineteenth-century part-whole relations of the biological individual: cell theory and its transcendence by a "cell state," a socially-derived metaphor prominent from Virchow to Haeckel and beyond (see e.g., Richards, 2002, p. 260; Weindling, 1981; Mazzolini, 1988; Jacobs, 1989; Reynolds, 2007, 2008). Broadly, this was a conception of the multicellular organism as a state (aggregate, assemblage, colony, or commonwealth were also referents) in which single-celled individuals were mutually dependent and (for Haeckel) co-operated in a hierarchy of sorts where physiological division of labor served the whole. Reinforced by Ernst Brűcke's (1862) explicit identification of the cell as the "elementary organism," and the subsequent development of protozoology, in 1897, Max Verworn, one of the founders of cell physiology, formalized the growing view in Germany of the cell as the elementary complex organism, both in unicellular protists and multicellular organisms. Drawing on Haeckel, he distinguished five stages of individuality – cells, tissues, organs, persons, communities – but explained that "constituents of an individual of the higher order are not always real individuals, i.e., they are capable of self-preservation when living in union with, but not when separated from, their fellows; in other words, they are only virtual individuals" (Verworn, 1899, p. 62). Haeckel's student Oscar Hertwig also viewed the cell as an ‘‘elementary organism,’’ applying the division of labor to the progression of development. Lower to higher organic individualities formed as parts (beginning with cells) lost their independence and became more integrated into higher-level entities (Hertwig, 1898). At the turn of the century, focus on the cell and its constituents as the elementary individual seemed assured, but the role of these entities as the *sole* factors in differentiation of parts and in relation to development of the whole was to become increasingly questioned. These different directions and their historical antecedents together form a large part of the ‘‘knot’’ that is nineteenth-century biological individuality.

The debates among biologists in the 1890s and the early twentieth century over the nature and levels of individuality involved metaphors that crossed between biology and the social sciences, and led to the organicist movement in biology that peaked in the 1920’s to 1940’s (Phillips, 1970; Mitman, 1995). New theories of part-whole developmental biology emerged, for example, ‘‘We may regard the body of a highly complex organism as a sort of symbiotic community, each part being dependent on the others, and prevented from abnormal development by the very fact of this dependence’’ (Holmes, 1904, p. 278).

Among Leuckart’s students, Charles Otis Whitman, studying embryology, heredity, and evolution, and helping to establish the discipline of animal behavior, observed, ‘‘On the same grounds that affirm that a society is an organism, the biologist declares that an organism is a society’’ (Whitman in Mitman, 1995, p. 255). He saw in *Volvox* colonies a path to the evolution of metazoans and, reminiscent of *Polymorphismus*, a functional division of two cell types for locomotion and reproduction that could lead to composite individuals. Another Leuckart student, Charles Manning Child, also championed the organicist movement (Child, 1915). His major works concerned regeneration and the nature of animal individuality, in which coordination and control played an important role in morphogenesis. His gradient theory foreshadowed the modern understanding of metabolic signaling in organismal development. In *The Unity of the Organism* (1919), the eminent marine biologist William Emerson Ritter drew on both Whitman’s and Child’s ideas of the organism as societal entity, but took an extreme position in asserting the domination of the organism as a whole in development, as opposed to primacy (or simple interactions) of the atomistic cell individual. While these fervent discussions of individuality were soon overshadowed by the reductionism of physicochemical approaches and the Modern Synthesis (Benson, 1989), key conceptual steps like those of Ludwig von Bertalanffy (1933), Joseph Needham (1933), Alex B. Novikoff (1945) and others laid foundations for the realization of interactive hierarchies of development, genes, and evolutionary entities, and for systems biology decades later (Zylstra, 1992; Gilbert and Sarkar, 2000; Classen-Bockhoff, 2001; Drack, 2009).

Still more distant but nonetheless compelling are the echoes of *Polymorphismus* and the nature of individuality in the interest in levels of organization and selection, modular organisms, and developmental modularity that resurfaced in the 1970's and have since grown exponentially within today's biology. Richard Lewontin's "The Units of Selection" (1970) was a bellwether of change, partly reinstating levels of biological organization following an era in which the Modern Synthesis had sharpened biology's focus more and more on the gene as the elemental unit of evolution, but his was hardly the only objection heard. David Hull (1988), among many others, argued influentially that species should be considered individuals. Interest in what are now called modular organisms (Vuorisalo and Tuomi, 1986), precisely the same kinds of plants and colonial animals with which we began our story, became resurgent because they did not neatly 'fit' many of the models of population biology and genetics that had been developed around solitary or unitary organisms (Harper, 1977; White, 1979; Jackson et al., 1986; Buss, 1987; Tuomi and Vuorisalo, 1989). The broad conception of biological modularity embraces these organisms – as well as evo-devo, molecular genetics, proteomics and others – within its scope (Winther, 2001; Schlosser and Wagner, 2004; Callebaut and Rasskin-Gutman, 2005). Moreover, the biological "module" bears more than a slight resemblance to the "individual" in nineteenth-century biology. Intense discussions of the nature of individuality and part-whole relations have returned to center stage (Wilson, 2005; Okasha, 2006; Wake, 2008; Gilbert and Epel, 2009; Godfrey-Smith, 2009; Sapp, 2009).

Thus in the century and a half since the intense discussions in which polymorphism (along with Leuckart's *Polymorphismus*) played a central part, the problems of organic individuality and part-whole relations have ebbed and flowed in scientific interest. As we have seen, individuality remained central to European biological discourse throughout the nineteenth century, even as it diffused into new problem areas. It intensified with the organicist movement of the 1920s and 1930s, but the concerns of its proponents were overshadowed by the successes of the Modern Synthesis in subsequent decades. The current wave of interest in biological individuality and part-whole relations invites both historians and biologists to reflect further on the intermittently compelling nature of this problem, and the ways in which different biological problem-complexes have coalesced around individuality over time.

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Rudolf Leuckart, ***On the polymorphism of individuals, or the phenomena of the division of labor in nature. A contribution to the theory of the alternation of generations.***[1]

(Giessen: J. Ricker'sche Buchhandlung: 1851)

Translated and annotated by Lynn K. Nyhart and Scott Lidgard

Dedicated to my dear teacher and friend, Rudolf Wagner, in celebration of the twenty-fifth anniversary of his doctorate, on 15 June 1851.

[1] There has never been a lack of efforts to define and establish the concept of the [natural] *kind* or *species*, which constitutes the foundation of all zoological research. Numerous definitions[2] have emerged from these efforts, which at first glance seem quite diverse, but which nevertheless pretty much all, on closer inspection, [2] can be traced back to a certain common basic idea. *The species*, they teach, *represents a particular closed and self-maintaining form of organic life*.

If we apply this criterion to the observation of living nature, we will find only a few individual beings that we may regard as perfect

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[1] A note on the translation: We have stayed as faithful as possible to Leuckart's words while rendering his syntax into readable English. Bracketed numbers in the text reflect the original pagination. We have expanded Leuckart's notes [RL] to give the complete bibliographic references to the original source. Editors' notes [Eds] serve to clarify ambiguous phrases and to help readers translate Leuckart's terms into modern taxonomic and biological terminology. [Eds]

[2] "One is obliged to admit certain forms, which have persisted since the origin of things, without exceeding these limits; and all beings appertaining to one of these forms constitute what we call a species." Georges Cuvier, *Le règne animal*, 4 vols. (Paris: Belin/Deterville, 1817), 1:19.
"The word species should only be used to include individuals that so resemble one another, that all the discernable differences among them may be explained through known and well established effect of natural causes, and for which nothing stands in the way of us regarding them as descendants of *one* stock, or several completely similar races, which is the same thing." James Cowles Prichard, *Naturgeschichte des Menschengeschlechts*, Trans. and ed. Rudolph Wagner, 4 vols. (Leipzig: Voss, 1840–1848), 1:242 [backtranslated by LKN].
"The criterion of species is a voluntary and lasting fertile possible interbreeding through all generations." R.Wagner, Ibid., 452.
"To one species belong all individuals that derive from the same parents, and that either themselves or through their descendents resemble their progenitors." C. Vogt, *Lehrbuch der Geologie und Petrefactenkunde*, 2 vols. (Braunschweig: F. Vieweg, 1846–1847), 2:296. [RL]

representatives of a specific[3] form of life, that is, which fully exhaust the idea [Bild] of a particular species.

As complete representatives of the species we may naturally only consider those individual beings that fulfill all the tasks of a specific[4] life-form as a closed unit, thus those that not only exist independently, but that also develop in a simple uninterrupted sequence and that maintain their life-form beyond the narrow bounds of their own existence through the production of descendants. There are, however, only a few animals that meet these requirements, only those few hermaphroditic species with self-fertilization and without so-called alternation of generations. In this case, every individual is a complete representation of its species, which fully corresponds to the other representatives in form and development, abilities and functions.

By contrast, where the developmental stages of a specific life-form are not completed by one single creature, or where, through unequal division of the capabilities and functions within one species, the cooperation of several individuals is necessary for the entire unfolding and reproduction of a specific life-form – here the individuals have ceased being the "representatives" of the species. In this case, only through a summary consideration of the many individual members, through their ideal [3] summation into a closed specific unit, can we depict the entire picture of the species.

To this latter group of creatures belong the great majority of animals. First there belong here *all animals with separate sexes.*

The dual nature of sex, the division of male and female organs between two individuals, is so widespread in the animal kingdom that we can almost treat the cases of a hermaphroditic union of these parts in one creature as exceptions. The striking difference that exists in this regard between animals and plants[5] which, as is well known (with few exceptions), are hermaphrodites, is explicable as soon as we take into account the varying conditions of life of these organisms, namely the ability of animals to move in comparison with the fixed nature of the plant body. That which must be mediated by the plant through a suitable connection, through proximity and arrangement of the sexual organs, that is, the contact of the male and female reproductive material (without which no sexual reproduction is thinkable) – that selfsame contact is possible in freely moving animals even after a spatial division of those organs, after their distribution into various individuals. Among

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[3] That is, pertaining to species. [Eds]

[4] Again, pertaining to species. [Eds]

[5] Here Leuckart probably refers to Phanerogams, or seed-bearing plants. [Eds]

animals that are attached like plants, the sexes are once again combined, as in plants, unless their association in large quantities or in some other complex of especially favorable conditions (which can also sometimes allow a sexual difference of individuals in plants) makes this combination unnecessary. [4] To be sure, there is no lack of hermaphroditic species among freely moving animal forms, but these are always distinguished by some peculiarities in their appearance and mode of life, peculiarities that [if the sexes were separated] would either completely prevent contact of the sexual material or hinder it (as, e.g., spatial isolation of individuals, slowness of movement, smallness, or rarity).[6,7]

With the sexual organs of animals, naturally those functions and tasks that are dependent on them or determined by them are correspondingly distributed between male and female individuals. Indeed, we must characterize this division of labor as exactly that which should be achieved through this duality of the sexes.

One single individual would not always fulfill all the sexual necessities with equal completeness [compared with separate sexes], if its other connections to surrounding nature were to remain the same.[8] Only through a sexual division of labor was it possible that animal life could develop a certain universality, gradually to prepare and to mediate that completion and realization of potential to which it [animal life] has elevated itself in human life, with its historical development and spiritual meaning.

[5] Now, the degree of this *sexual division of labor* is extraordinarily varied.

Where the phenomena of sexual life appear to us in their simplest form, there we barely see any difference in the expressions of life of male and female animals. In the same way, both pursue the same nutritive needs; at the time of sexual maturity, both empty the contents of their

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[6] For more on this subject, see the forthcoming *Anatomisch-physiologische Uebersicht des Thierreichs: Vergleichende Anatomie und Physiologie* by C. Bergmann and R. Leuckart (Stuttgart: J. B. Müller, 1852), [section on] "Organe und Functionen des geschlechtlichen Lebens" [Organs and functions of sexual life]. [RL]

[7] Leuckart is asserting that self-fertilization is diminished or prevented among animals that are at once hermaphroditic, unitary and motile. According to him, this hindrance is visible morphologically or ecologically, much as it would be in animals with separate sexes. [Eds]

[8] It is known now that self-fertilization does occur in some animals that are simultaneous hermaphrodites, such as certain unitary, motile gastropods or in a sessile colony of certain bryozoans. [Eds]

generative apparatuses. The contact between spermatozoa and eggs takes place outside the body, made a little easier, at best, when the different sexes are near each other, [and] the development of the young [takes place] far from the parents.

Under such circumstances, it is, of course, completely unnecessary to equip the male and female animals differently. If the reproductive organs are enabled through their construction and condition to produce, in the one case, spermatozoa, in the other, eggs – and this requires only certain very delicate, hardly perceptible special features –, in this case fully enough has occurred to meet the conditions of such a division of labor.[9]

With most animals, and especially the land-inhabiting species (whose existence [Leben] in general rests on much more complicated conditions[10] and also presupposes a greater complex of abilities), the expressions of sexuality are, by contrast, much more compound and diverse, so that they themselves are set off as a particular group of unique activities from the usual phenomena of life. Here it is not merely a question of forming the sexual substances internally and emptying them externally, unconcerned with whether some accident would lead to contact of the two.[11] Here the two sexes must [6] seek out this contact, even to the innermost physical touch; here mating is required, and later, care for the new brood, for eggs and young, in the most diverse ways. Protection and feeding, care and raising of the offspring form here a very meaningful stage in the life-history of the animal.

And the more these activities increase in number and diversity, the more they demand an expenditure of effort and time, so much the more distinctly are they split between the two sexes. Each sex will be entrusted with those tasks that go along most naturally with its other functions. Thus the male animal usually undertakes to seek out the female, to stimulate her to mate, and to grasp onto her in this act, whereas the female is tasked with the care of the fertilized eggs and offspring, according to their needs.

It is easy to see how these different tasks of the two sexes also demand different equipment and organization to carry them out.

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[9] Internal microanatomy is not Leuckart's focus here. Processes of sperm exchange between two simultaneous hermaphrodite individuals have since been shown for many species across the animal kingdom. Such individuals are frequently indistinguishable using morphological criteria alone. [Eds]

[10] Presumably environmental conditions. [Eds]

[11] This is the case in most sedentary marine invertebrates and land plants. [Eds]

This explains the differences between males and females in the development of the sexual organs, the locomotive apparatus, body size, form, etc.[12] – differences that have already attracted the attention of naturalists so often and in so many ways, and which occasionally go so far that practically any similarity between the corresponding male and female parts and animals disappears, such that their morphological connection can be entirely misunderstood.[13]

[7] The most striking example of such sexual dimorphism is offered to us by the parasitic lernaeids[14] and certain cephalopods.[15] Here the male individuals are hardly more than free-living, individually organized organs of generation, whose entire purpose lies in the production of the male sexual substance, in the mediation of a fertilization. Incapable of an independent life, these creatures can only live as parasites on the female body. It is only a step from these forms to hermaphroditism. This step is taken when these apparatuses, with loss of their individual organization, become integrated into the organization of the female body, a body to whose existence their own maintenance is now assigned.

The sexual connections of individuals lead in many animals to a temporary *union of the different sexes*. Single pairs or larger groups isolate themselves from the others and live united, as long as their common interest in sexual reproduction – as in other cases their common interests in individual maintenance – persists.

In some species these unions extend beyond the breeding period. This is the case when the numerical ratio of the two kinds of individuals in a society is very uneven – for example, where it appears most commonly, only one male or perhaps a few are found with a larger quantity of females. Under such circumstances the males not only have the task of mating; they also are the protectors of the society, which they shelter from pending danger or defend against attacks. The attributes of such a leading [8] role are then given mainly by size and weapons (horns, spurs, etc.), power and strength, courage and endurance.

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[12] For the more detailed justification of this connection I must once again refer the reader to the previously mentioned *Comparative Anatomy and Physiology* [Bergmann and Leuckart, op. cit. n. 6]. [RL]

[13] Leuckart is implying here that dimorphic males and females may be taken to belong to different species of animals. [Eds]

[14] A group of parasitic copepods (Phylum Arthropoda), now within the family Lernaeidae Cobbold 1879. [Eds]

[15] Probably a reference to a member of one of the octopus families now in the Superfamily Argonautoidea Naef 1912, in which the females are much larger than the males; the latter have an unusual detachable "arm" that passes the sperm from male to female and that might itself be mistaken for an entire male. [Eds]

In these lines of social life, we encounter the first beginnings of those wonderful *animal states*,[16] which, through a more rigid separation and more consequential division of labor among the various individual forces, give the appearance of a well-ordered organism, whose individual parts complement each other in purposeful ways and cooperate in the maintenance of the whole.

The most elaborate of these states, as is well known, are those of bees, ants, and termites. In the formation of these unions not only do male and female individuals take part, entrusted in the usual way with safeguarding the sexual interests, but also so-called asexual individuals (that is, undeveloped and atrophied females), to whom the care of the material well-being of the state is assigned. They acquire the food and collect supplies, defend the colony from enemy attacks, and take care of the developing offspring.

It goes without saying that here too, overall, the organization accords with each particular task, and with the relation of the relevant single individual to the economy of the whole. The activities [Leistungen] of a creature are of course inseparably bound to the structure of its body – its size, form, and equipment [Ausrüstung]. Whereas in other cases only males and females, where they have different obligations, differ from one another, the same is true here [9] – and to an even greater degree – in the ones that are termed asexual.[17,18]

The societies touched on up to now encompass a lesser or greater number of isolated individual beings, which are held together through

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[16] In modern biology, communities of eusocial insects (ants, bees, wasps or termites) and physiologically contiguous, modular animals such as corals are often referred to as colonies. Among the variety of insect societies, those at the highest levels of caste organization and reproductive specialization are termed eusocial. Here, Leuckart distinguishes between eusocial insect colonies and physiologically contiguous colonies, calling the first "Thierstaaten," (animal states) and the second "Thierstöcke" (animal stocks; see below). The units of the latter are now typically termed zooids or polyps. [Eds]

[17] Among termites, soldiers and workers can be distinguished as particular groups of individuals. As the investigations of *Munck of Rosenschild* have shown, however, only the first of these are truly asexual; the workers by contrast are the larvae of individuals that will later develop sexually. [E. Munck af Rosenschöld, "Entomologiska underrättelser från Paraguay," *Őfversigt af Kongl. Vetenskaps-akademiens Förhandlingar*, 1849, 6(2):59–62.] [RL]

[18] Leuckart's description of termite reproduction (note 17) presumably reflects what was known at the time. It is now known that termite eggs can develop into a variety of castes – "groups of individuals" in Leuckart's words – including asexual workers and soldiers, sexual "reproductives," and the winged founders of new colonies (aletes). Multiple pairs of reproductives are sometimes found in a colony. In some species, potential reproductives may function as workers, but can also develop into performing reproductives or aletes. [Eds]

the community of their interests and needs, not through an external necessity. But the latter sort of societies also exist in the animal world.

These are the so-called *animal stocks*, the members of which emerge gradually from a single, initially simple individual through continued asexual multiplication,[19,20] but which don't then split off from one another, but stay permanently united in a common ‘‘family body,’’[21,22] which in a certain sense depicts a ‘‘living family tree’’ [Stammbaum].

[10] The kind and degree of this connection between the single individuals of an animal stock are quite varied. In only a few cases does [this connection] appear to be confined to the external integuments and envelopes, a simple union through fixed accretion. In the majority of cases the internal nutritive organs (circulation apparatuses) are also connected with one another. This is the case, for example, in the acaleph[23] colonies

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[19] Only the Salp-chains form an exception here, insofar as they constitute the product of a shared production by budding [Knospenzeugung] on the so-called germ-tube [Keimröhre]. The individuals of such a chain are, with respect to their relationship to one another, siblings, not descendents of different generations [Grades]. Therefore they are also all the same size. [RL]

[20] Note 19 refers to the salps (Class Thaliacea van der Haeven 1850, Subphylum Urochordata [= Tunicata]), a group of considerable interest among zoologists in this period (see Elwick, 2007). These swimming, planktonic animals have sequential hermaphrodite life histories involving sexual and asexual stages with translucent, gelatinous, barrel-shaped body forms. During the asexual stage, an aggregate chain of attached, functional body forms (blastozooids) develops by iterative budding from a solitary progenitor. Leuckart describes members of this aggregate as ‘‘siblings’’ in contrast to an sequential alternation of forms, in which a descendent from is morphologically different from its immediate progenitor. [Eds]

[21] It was a long time before animal stocks were recognized as truly compound animals. Even the polyp colonies were taken to be simple individuals by Schweigger. In general, people still also consider the siphonophores [Röhrenquallen] as unified animals. (On the structure of these animals, see my essay in the *Zeitschrift* of Kölliker and Siebold, vol. III. [Rudolf Leuckart, ‘‘Ueber den Bau der Physalien und der Röhrenquallen im Allgemeinen,’’ *Zeitschrift für wissenschaftliche Zoologie* 3 {2}:189–212.]) [RL]

[22] In note 21, Leuckart sets up a contrast between his views of compound individuality in contiguous animal colonies (‘‘Thierstöcke’’) against views that a colony as a whole is a ‘‘simple individual,’’ as exemplified by Schweigger (1819). However, the *general* idea of numerous individuals constituting a higher-level individual or organic body in an aggregate or compound manner was not a new one. See accompanying text and note 99 below. [Eds]

[23] A former classificatory grouping of medusoid forms including what is now the Phylum Ctenophora and the jellyfish and medusae of the Phylum Cnidaria. These groups appeared under the early version of Coelenterata, established by Leuckart (1848) and Frey and Leuckart (1847) in their division of Cuvier's embranchment Radiata. See also Winsor (1976) and note 29, below. [Eds]

of the hydroids and siphonophores,[24] in which the body cavities that conduct the blood (or chyle[25]) of the individual animals communicate directly [ohne Weiteres] with one another. The case is similar in polyp stocks, also in colonies of Bryozoa,[26] at least in some species. In others this connection is limited to small gap-like [spaltförmige] openings in the outer body integument (the so-called cells), through which nevertheless the blood-plasm can be seen to flow from one individual into another. Even in those cases in which no direct connection is supposed to exist, such communication does not cease, as long as there is an endosmotic traffic between the fluids of two individuals that are next to one another.

A necessary consequence of this arrangement is the community of the nutritional processes for all members of the same stock. What is acquired by one individual becomes the property of the community [Gesellschaft] and is available to every member. In the same way the loss for the individual is borne by all. As in a communist state there are here no poor next to the rich, no hungry next to the sated – but also no lazy next to the industrious. Each contributes its own to the sustenance and health of the whole, each according to its powers.

In this regard the separate individuals of an [11] animal stock behave just like the individual parts [Glieder] of an organism, which share in the benefits and risks of a common nutrition in the same way. And just as this arrangement enables the freest and [most] exclusive application of the individual organs to this or that goal of life, so too the commonality [Gemeinschaft] of the nutritive processes provides the animal stock the physiological condition of a freer division of labor.

So long as the individuals lived separately from one another, almost the only division of labor could come in the tasks of sexual life. The

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[24] Both hydroids and siphonophores are now placed the Class Hydrozoa Owen 1843 (Phylum Cnidaria). A wide variety of medusoid forms occurs in this class. Hydroids in Order Limnomedusae Kramp 1938 have a benthic, usually colonial polyp stage in which stolons, polyps, and medusae are budded asexually. The detaching medusae typically begin the transition to a sexual stage. Siphonophores are placed in Order Siphonophorae Eschscholtz 1829. Siphonophores are almost entirely pelagic swimming or floating colonies composed of a variety of polyp-like and medusa-like zooids; certain types of individual medusae are specialized for reproduction. [Eds]

[25] In the mid-1800s, chyle was understood to be a body fluid with several varieties, all products of digestion and absorption of food. In humans and some higher mammals, its content was known to be nutritive, partly fatty material that was circulated in chyliferous or lacteal vessels (now considered part of the lymphatic system) to the tissues of the body. [Eds]

[26] The Phylum Bryozoa (= Polyzoa), comprised exclusively of bottom-dwelling colonial forms, was separated from Anthozoa (now in Phylum Cnidaria) in Cuvier's Class Polypes by Ehrenberg (1831). [Eds]

individual animals were left to themselves to provide for their own maintenance, if they were not to sacrifice their independence of life (as with the above-mentioned parasitic males of some lernaeids and cephalopods). At most, the burden could be lessened through particular distribution of the protective activities and the nutritional supply.

In the animal stocks, as I have said, the need for these limitations falls away. Through the arrangement of these colonies, the activities of vegetative and animal life may be distributed across the separate individuals in the same way that the tasks of sexual life are. Nutritional uptake and digestion, movement and defense, reproduction and asexual multiplication can be transferred as exclusively to particular individuals as special organs are in a simple individual. And just as these latter then have to be appropriately equipped for their various functions through their structure, form, and connection with the other organs, so too there emerges the same need for the individuals of the animal stock, which are organized according to the same principle of the division of labor.

[12] When we thus perceive how strikingly the separate individuals of an animal stock are distinct from one another in form, structure and arrangement, we can see how their morphological autonomy and significance can be completely misunderstood. Even today many such polymorphic individuals are viewed as mere organs – and must be understood as such, as long as one seeks in an individual a certain sum of different, interconnected organs and functions, as long as one only views such forms [i.e., mere organs] as members of the same specific organizational series,[27] which must completely agree in their basic structure.

Now, the principle of the division of labor and the polymorphism that depends upon it is expressed in a very varied and extremely changeable manner in the different animal stocks. Some animal stocks consist in a simple aggregation of completely equivalent individuals; that is, their members participate in all life functions in the same manner (compound tunicates). Others show some differences in only a few members (some bryozoan stocks). And finally there are others, whose members have divided the separate tasks of life in the most colorful ways that mutually support one another, and only through their internal cooperation present the picture of a complete, closed and self-maintaining life.

The outer unity has thus become the bearer of an internal organic connection; the family-body [has become] the body of a structured, well-ordered state. The coordinated [13] performance of life that we

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[27] Presumably a developmental series. [Eds]

otherwise see fulfilled in a simple individual, is transferred here to an entire larger or smaller series of unified generations.

The most widespread application of this division of labor is to be found in the nurse-colonies[28] of the disc-shaped medusae, which are known under the names of the *hydroids* and *siphonophores*.[29] In variable form and sequence we see here some individuals that have the task of feeding; others, that take on the tasks of attachment or movement; and those that are entrusted with the enlargement of the colony, with the production of a sexual brood, and so forth.

Let us then consider especially these forms, weaving in parallels from the life and structure of the other polymorphic animal stocks only now and then, as circumstances warrant.

In the already-named nurse-colonies, as everywhere where we meet with a division of labor, the majority of the individual animals consists of *feeding individuals*,[30] which are outfitted with mouth and digestive apparatus and possess in these organs the unmistakable attributes of an individual life-form.

The digestive apparatus is extraordinarily simple, just a digestive cavity without special walls, which at most is lined with an epithelium of yellow liver cells.[31] Distally this continues directly into the common

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[28] Here Leuckart is referring to an idea introduced by Steenstrup (1842, English translation 1845), in which asexual stages of the life-cycle of some animals are interpreted as "nurses." See accompanying text. [Eds]

[29] Leuckart uses the term "Scheibenqualle" here, which could refer either to the disc-shaped form of some medusae or to a taxonomic group "Discomedusae," which was undergoing considerable adjustment in the mid-nineteenth century. By 1887 Discomedusae were established as a subclass of the Class Scyphozoa Goette 1887 (Phylum Cnidaria). The scyphozoan medusae are floating or swimming, mostly pelagic forms often referred to as "true jellyfish" with a translucent, gelatinous appearance. They differ from hydrozoan medusae (including those of hydroids) in the cnidarian Class Hydrozoa Owen 1843, in the manner by which the asexually reproducing polyp stage produces immature medusae by budding (polydisc strobilation). Recent reclassifications of these and other related groups, notably Daly et al. (2007) and Cartwright et al. (2008), have altered rankings and begun clarifying the non-monophyletic components of some prior taxonomic arrangements. [Eds]

[30] Now called gastrozooids in siphonophores, or the terminal portion of polyps (hydranths) in the typical asexual stage of hydroids. These are the only colony members that ingest food. [Eds]

[31] Here Leuckart is probably referring to the basal region, or "basigaster," of gastrozooids, which have gland cells that contribute to extracellular digestion of food. [Eds]

body cavity of the whole stock, which is filled with blood (or chyle) and water – and which in the siphonophores is usually designated the reproductive canal.[32] The mouth opening lies at the opposite, front end, and in the hydroids (at least in most of their forms), it is surrounded by branching tentacles, which serve as trapping structures. Among the siphonophores [14] (the feeding animals of which, under the term "siphons"[33] [Saugröhren] are still today usually considered to be organs) these filaments are much longer, less numerous and located at variable distances behind the mouth-opening.

Because of the varying placement of these filaments, one might have some doubts about their morphological identity with the tentacles of the hydroids. But even among the latter, this varying placement is anticipated – namely among the tubularia,[34] the grasping-structures of which similarly stand a bit away from the mouth opening, in that their sphincter-like boundary has elevated itself to the form of a special conical or cylindrical cap.

To be sure, among the siphonophores this mouth-shaft is considerably longer, but this is necessary because it supports the tentacles in their role as trapping organs. As mobile animals, the siphonophores have in any case a more substantial metabolism than the hydroids – and this also doubtless explains the difference in their [nutritional] apparatuses, upon the activities of which, in the first instance, the amount of nutritional uptake depends. The length of the tentacles clearly has the same relation, in that the activity [Wirkung] of this structure can spread out in a broader and more extensive circle. But since the presence of a larger number of such long tentacles (despite their strong contractility) would have somewhat hindered movement from place to place, their number must be reduced.

Thus the variations in the arrangement of these structures are explained on physiological and mechanical grounds.

[15] The functional value of these tentacles depends largely on their mobility. This mobility rests partly on the contractility of its tissue, but also partly on another sort of contrivance [Einrichtung], through which a kind of erection is enabled. The tentacles are actually hollow, and connected with the body cavities of the individual animals. From these, they can be filled with fluid, so that they extend and lengthen until a

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[32] Siphonophores have a more or less confluent gastrovascular system. This body cavity takes the form of a stem or stolon from which the colony members are budded asexually. In hydroids, a similarly confluent gastrovascular system exists, whose lumen permeates asexually budded stolons, stalks and hydranths. [Eds]

[33] Today these "siphons" are called gastrozooids. [Eds]

[34] *Tubularia* is a hydroid genus now placed in the Order Anthoathecatae Cornelius 1992. [Eds]

later contraction pulls their contents back into the body cavities. This filling occurs through the contraction of the individual animals when the mouth-opening is closed.

However, there are a few siphonophore stocks (*Physalia, Physophora, Apolemia*) whose tentacles are not connected with the actual nutritional animals, but with special cyst-like appendages (the so-called tentacle-cysts, or fluid-containers). The only significant way these differ from the tentacle-bearing nutritional animals of other colonies is in the absence of a mouth opening (and the lack of the liver-epithelium). Of course, they also have a different functional significance. They do not serve for nutritional uptake and digestion, but for filling the tentacles.[35]

In these appendages we likewise see individuals like the nutritional animals – these creatures are entrusted with a task that in other cases is only temporarily fulfilled by the nutritional animals, but in this case certain individuals are occupied with it for their whole life; their entire structure is therefore expressed in a suitable way.

To be sure, one might think that we should take the simple cyst-form appendage to be the individual. But the most striking aspect [16] of this interpretation disappears as soon as we consider the simple structure of the other individual animals in the relevant colonies, as soon as we see further, that (among siphonophores and hydroids) the feeding individuals also initially possess this same form. When they first bud out, they appear as squat bumps or short, closed-ended tubes, that sit on the common body and enclose a diverticulum of the common internal bodily space. The mouth-opening and tentacles originate only later, in order to make the individuals into feeding animals. If the mouth opening remains absent, the relevant individuals appear as so-called tentacle-cysts.[36]

The fluid with which the tentacle is filled for the purpose of the erection comes from the common body cavity and is a part of the

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[35] The connection Leuckart observes between the tentacles and the "cyst-like appendages" is described today in terms of clusters of zooids known as cormidia. Among these polymorphic zooids, those we call ampullae bear tentacles but lack a mouth. Nonfeeding palpons may have a tentacle as well. It is unlikely that the "tentacle cysts" (what we today would call ampullae or palpons) alone serve to fill the tentacles, as Leuckart suggests, because their fluid volume is insufficient. [Eds]

[36] Recent work (Dunn, 2005) has shown that rather than a single bud giving rise to a single zooid as in most hydrozoans, a siphonophore bud subdivides to produce a sequence of zooids. In one of the two major budding zones of the colony, each iterated sequence (cormidium) along the stolon includes various zooid polymorphs. This new information would still seem to support Leuckart's general inference of developmental similarity among polymorphs, if not his precise explanation. [Eds]

general nutritional fluid that is acquired during the digestion process, and that is kept in constant flow by a lining of cilia in the body cavity. Considering the nature of this fluid, we might want to designate these so-called tentacle-cysts as *chylomotor individuals*,[37] although their actual functional task is not completely expressed by this term. This designation might be further recommended if it were confirmed that there existed among *Stephanomia*[38] and *Agalmopsis*[39,40] similar fluid containers without tentacles,[41] the contractions of which serve [17] to support and strengthen the flow of the nutritional fluid inside the common body cavity.

It hardly needs special emphasis that the activities of these chylomotor individuals and of the feeding animals complement each other to form a whole. The provision of the food and the further working of it have the same end-goal of material maintenance and are so intimately joined that it cannot strike us as strange if we observe that a division of these tasks among two different individuals even in animal stocks is relatively rare.

I know only one single group of animals that presents something like this. These are the Bryozoa. What is described in these animal stocks as "bird's head-like or pincer-form organs" (in *Cellaria avicularis*, *Bicellaria ciliata*, *Flustra avicularis*, *Retepora cellulosa*[42]), are clearly equally particular,[43,44] uniquely developed individuals (lacking gut and sexual organs), whose functions are probably equally connected to the seizure

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[37] Cilia do occur in the body cavity, but their relative importance in circulation of the gastrovascular fluid is unclear when compared to movement and contraction of zooids, including those in other regions of the colony. [Eds]

[38] Henri Milne-Edwards, "Observations sur la structure et les fonctions de quelques zoophytes, mollusques et crustacés des côtes de la France," *Annales des sciences naturelles: Zoologie* 2nd ser., 1841, 16:193–232, on 228. [RL]

[39] Sars, *Fauna littoralis Norvegiae* (Christiania: Dahl, 1846), p. 35. [RL]

[40] *Stephanomia* is a siphonophore genus in the order Siphonophorae Eschscholtz 1829. *Agalmopsis* is now synonymized into the genus *Agalma*, also in Siphonophorae. [Eds]

[41] It would also be possible, of course, that these cyst-like appendages would simply be undeveloped feeding animals. [RL]

[42] These bryozoan species are now apparently synonomized, although their determination is provisional without author-date attribution: *Cellaria avicularis* (*C. avicularia* Linnaeus 1758) into *Bugula avicularia*; *Bicellaria ciliata* into *Bicellariella ciliata*; *Flustra avicularis* into *Bugula flabellata*; *Retepora cellulosa* (with considerable uncertainty) into *Reteporella cellulosa*. [Eds]

[43] If I am not mistaken, *van Beneden* has already called attention somewhere to the individual nature of these remarkable structures. [RL]

[44] Note 43 probably concerns Van Beneden (1845). [Eds]

of food. To be sure, these structures are always found next to the tentacles, which no feeding animal lacks, but this does not undermine our interpretation. Incidentally, these may also sometimes or here and there even continually serve as protective apparatus for defense – the active weapons and grasping apparatus are certainly such, and [18] are often used as more passive defensive organs – at least, where they (as in other cases) appear as simple, sunken-in[45] spines, in a form that might not seem very suitable for catching and holding the prey.[46]

Above, in order to establish the difference in the development and arrangement of the grasping-apparatuses among the hydroids and siphonophores as physiologically necessary, we already had to point to the different relations of the relevant animals to the surrounding environment [der umgebenden Natur].

The hydroid-colonies are robbed of locomotion and are permanently fixed to foreign objects, like the true polyps; the siphonophores, by contrast, are mobile, like the medusae that bring them forth.

For the adherence of these colonies, just as for their locomotion, there serve certain appropriately developed structures, which upon closer examination we can likewise recognize as particular individual animals.

Of these, let us consider first the so-called locomotion-organs of the siphonophores, which, as is well known, appear formed as bell-shaped appendages with a fixed outer integument and a contractile internal membrane. The attachment of this integument to the common body of the colony is in the center of its dome, so that the opposite opening of the internal cavity is completely free. When the contractile membrane is contracted [19], the enclosed water is pushed out of this opening. The recoil of the water serves to move the whole forward.

That these structures are individual animals (that is, *locomotive individuals*) follows already from their being completely the same as the other individual animals with respect to their origin and relation to the common body. They too are, in the beginning, simple hanging vesicles, like the feeding animals and the chylomotor individuals, so that one could identify them with the so-called fluid-containers. Only gradually do they acquire their later form and significance. The general body

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[45] To be distinguished from the sometimes spiny outgrowths of the bryozoan body! [RL]

[46] Leuckart makes an analogy here between functional interdependence of feeding zooids and nonfeeding polymorphs in an entirely different group of animals. He refers to avicularia, a category of zooid polymorphs that occur in cheilostome bryozoans. Avicularia lack a digestive system and have a modified mandible that can close firmly against a fixed palate. Their full scope of functions remains uncertain, but the strongest evidence supports a defensive role. [Eds]

cavity also remains connected to them; however, not through a simple diverticulum, but through a thin, vessel-like and branching canal, which extends through the bell-shaped mantle. In an obvious way we see expressed here the accommodation to the given anatomical conditions, which itself is once again determined by the tasks and intended functions of the entire apparatus.

A comparison of the swimming bells[47] with the disc-shaped medusae will place their nature as individuals even further beyond doubt. We need only to strip away the apparatus for food intake and digestion – and a possible union of these with other feeding individuals into a common colony would justify such an incomplete apparatus – in order to obtain an exclusively locomotor, individually developed apparatus, which bears the greatest resemblance to those swimming bells. And this similarity is not merely a formal one. We would not mistake [20] it in the structure itself, ever since we learned from Forbes[48] and Agassiz[49] that the contractility of the disc-shaped medusae doesn't extend through the entire parenchyma of the body, but only [through the] membranous muscle layers [Muskellagen] which run through the characteristic gelatinous body tissue[50] [durch welche das eigenthümliche gelatinöse Körpergewebe bekleidet ist]. Moreover, the mode of attachment of the swimming-bell and its connection to the rest of the colony is the same as that of the disc-shaped medusae, when these bud out according to the law of so-called alternation of generations.[51] The middle of the dome is thus also the connection-point [Anheftungspunkt] in the disc-shaped medusae.[52]

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[47] Today called nectophores; these are zooids that resemble medusae and are attached near the apical end of a siphonophore colony. Their muscular contractions propel the colony through the water. Leuckart compares the nectophores to the general structure of hydrozoan Discomedusae in which, hypothetically, tentacles and digestive organs are removed. [Eds]

[48] See Kölliker in the *Zeitschrift für wissensch. Zool.*, 1851, p.110. [Here Leuckart almost certainly means p. 105, as this is where K. refers to Forbes' and Agassiz's work on contractility of medusae. A. von Kölliker, "Skizze einer wissenschaftlichen Reise nach Holland und England in Briefen an C. Th. von Siebold," *Zeitschrift für wissenschaftliche Zoologie* 3(1):81–106.] [RL]

[49] Louis Agassiz, "Contributions to the natural history of the Acalephae of North America," *Memoirs of the American Academy of Arts and Sciences*, 1850, 221–374, p. 235. [RL]

[50] Mesoglea, the gelatinous material between the inner and outer layers of the body wall in cnidarians. [Eds]

[51] Here Leuckart refers to Steenstrup 1842 (English translation 1845). See below and also note 94. [Eds]

[52] See note 29. [Eds]

If we unite the swimming bells with the siphons in our minds, that is, if we construct a siphonophore-stock in which there is no division of labor with respect to feeding and movement, we arrive at a colony formally resembling the disc-shaped medusae. That such a division of labor in this animal stock has taken place, however, is clearly a result of mechanical causes. The individual forces of motion are able to achieve in this way a sufficient concentration to allow a much stronger effect than the[ir] otherwise inevitable fragmentation.

To be sure, there are other swimming animal stocks without such division of labor (*Pyrosoma*, Salpa compositae[53]), but these generally possess a much more thickset body form than the siphonophores. Their movement is also easier, because their surface area resistance [21] to the surrounding medium has become relatively smaller. Under these circumstances a different, less favorable arrangement of the locomotive powers will suffice, since these latter depend not only on the form of motion but also on the amount of difficulty standing in the way of movement.

With hydroid stocks, which branch in many directions in the manner of plants (as is well known), it would be hard to overcome these difficulties without changing the external form of the colony. Hydroid stocks are therefore immobile[54] and fastened to a base.

The connection-point of the hydroids corresponds morphologically to the same place where we encounter the locomotive individuals in the Siphonophores. Instead of those, here we see more or less numerous simple or ramified runners, which creep out like roots or stolons over the ground or other foreign bodies; snuggle into their uneven places; push into cracks and crevices; and in such ways[55] serve as organs of attachment.[56]

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[53] *Pyrosoma* is a genus of colonial pelagic tunicates (Class Thaliacea van der Haeven 1850, Subphylum Urochordata [= Tunicata]). Pyrosome colonies, unlike those of salps, are composed of many individual zooids joined within a gelatinous tunic, which is typically translucent and conical or cylindrical in overall form. We interpret "Salpa compositae" here as "compound salps," rather than a species binomial. [Eds]

[54] On the question of the connection of animal form and organization with mobility, see my essay "Ueber die physiognomischen Unterschiede zwischen Thieren und Pflanzen" [On the physiognomic differences between animals and plants], *Archiv für Naturgeschichte* 1851 [17: 146–158]. [RL]

[55] According to Cavolini, *Abhandlungen über die Pflanzen-thiere des Mittelmeers* (tr. Wilhelm Sprengel, ed. Kurt Sprengel, [Nűrnberg: Schrag, 1813], p. 70), a particular sticky substance is also secreted to this purpose. [RL]

[56] Here Leuckart draws an analogy between the confluent rootlet buds, stolons and stalks of a benthic hydroid colony, and the confluent stem or stolon of a planktonic siphonophore colony. [Eds]

The growth of these creeping root-fibers corresponds so closely to the upright [aufgerichteten] and branching stem [22] that one can hardly draw a firm boundary between the two. They originate as small bud-like swellings that gradually lengthen and form new buds. The internal canal-form lumen is directly connected to the common body cavity.

If we call the buds of the stem "individuals," then we cannot deny the rootlets the same designation. To be sure, these *runners* never gain a mouth-opening and tentacles, but because of their connection to the other individuals they do not require these for their own maintenance. For their simple functions a simple structure, a fiber-like or tendril-like form, is fully sufficient.

The interpretation of these rootlets as individuals is confirmed, finally, by Cavolini's experiments.[57] In stocks that have been removed and suspended freely in water, their blind ends [Blindende] after several weeks grow mouth and tentacles, like the feeding animals. By the same token it was possible, through appropriate manipulations, to transform the branches into roots, or more properly, to coax out runners from them instead of feeding animals, in that the young buds certainly lengthen into fiber-like runners, but form neither mouth nor tentacles.

In natural growth, too, individual buds of the runners frequently separate themselves from their base, stretch up and become feeding animals, which [23] then develop through continued further production of buds into new colonies with stems and branches. For the maintenance of hydroids this phenomenon is important because storms and the breaking of waves often destroy all colonies down to the runners, as seems to be the constant situation for some forms during the fall and winter. This ability allows these animal forms to survive the lasting effects of such destruction – it makes it possible for them to revive with new generations from time to time, from year to year.

On several occasions it has already been pointed out how animal stocks emerge through the continued building of shoots from an individual that initially is completely simple. The multiply variable physiognomy of individual colonies results from the differences in the number, position and orientation of these shoots. Only in this way does that endless abundance of forms originate that appears to imitate so deceptively the regular yet so endlessly rich forms of vegetable creation.

It cannot be my purpose here to analyze the architectural design [Architektonik] of the animal stock as a whole or in particular according to the characteristic features of each form, nor to show how each different form fits itself closely and appropriately to particular external

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[57] Cavolini, op. cit. (n. 55), p. 71. [RL]

conditions. I only want to call attention to the fact that in the sphere of vegetative life, too, a division of labor makes itself known, in that the individual animals of a stock participate in various ways in the development of shoots.[58]

In the investigation of this situation it is substantially a question [24] of the nature and origin of the parts that participate in making the animal stock – of the axis, of the stem [des Stammes], of the branches etc.

It is already clear from a superficial comparison that here, as in the plant stock, a manifold variety obtains.

We see the simplest form of axis development [Achsenbildung] in the animal stocks of the Bryozoa and some hydroids (e.g., *Sertularia cupressina*[59]), in which the stem and branches originate through a linear ordering of the particular individuals, such that the new shoots always appear at the end of the previous ones. The terminal animals here are the youngest. That in any given cross-section the individuals stand next to one another in changing numbers, multiple or singular, are variations of subordinate importance; [these are] of interest, however, when we consider that in this way through the leaf-like stalk a gradual transition is mediated to the disc-like, cup-like, and other forms.

We find a further, more autonomous development of the axes in most of the *Sertularia*, followed in this respect by even more numerous other forms, hydroids and Anthozoa.[60] What we call here stem and branch is, like the so-called sympodium[61,62] of the botanist (for example, the trunk of the linden, the asparagus, or the vine) formed from a concatenation [Verkettung] of the basal parts of the given individuals,

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[58] In the above paragraphs, Leuckart reiterates his conception of a division of labor among individuals (colony members), emphasizing that even the rootlets of a hydroid colony should be recognized as individuals. These rootlets often form a dense mat-like network (hydrorhiza), and each rootlet resembles nothing more than a filamentous undifferentiated stolon. [Eds]

[59] *Sertularia cupressina* is a species of hydroid now placed in the Order Leptothecatae Cornelius 1992. This species and *Sertularia* in general have erect branching colony forms. Asexual buds are almost all developed in a distal or distolateral direction, relative to the preceding colony members, much as Leuckart describes. [Eds]

[60] Class Anthozoa Ehrenberg 1834 in Phylum Cnidaria contains the anemones and corals. [Eds]

[61] See A. Braun, *Betrachtungen über die Erscheinungen der Verjüngung in der Natur* (Freiburg im Breisgau: Poppen, 1849–1850), p. 47. [RL]

[62] In plants and fungi, sympodium refers to a combined series or fusion of multiple buds (or branches) occurring along stems or hyphae, respectively. One botanical example is the formation of a stem axis that is made up of the bases of lateral branches; another is a grapevine made up of many tendrils. [Eds]

which grow out of one another in a winding series. Here, too, the terminal animals are of course the youngest.

[25] The siphonophore-stocks, however, behave completely differently. The stem (reproductive canal) here is a single shoot – like the trunk of the poplar – which increases in length through continuous growth and ends in the terminal feeding animal. This main shoot is simultaneously the oldest of the whole stock. All later buds have a subordinate architectonic significance and originate laterally from the main shoot.[63] A similar situation seems to hold among some hydroids, only here the side shoots, too, take over the role of further (secondary) main shoots (that is, branches), through repetition of the same subordinated shoot-development. At least, this is the case as seen in the observations of Cavolini[64] on Pennaria.[65]

In these animal stocks there are thus special *individual animals*, which exclusively appear as building the stem or axis, before the others carry out the phenomena of vegetative life. To be sure, these individuals here are not marked out in any special way, but are simply feeding animals with the further task of bud development. It appears, though, that there are also other animal stocks that – like pine trees[66] – contain such purely *vegetative individuals*, from which the other individuals bud forth, while they themselves grow into stem and buds, without ever participating in any other sorts of tasks. Here I have in mind the remarkable group of halopterids or sea feathers.[67,68]

[26] Like the functional tasks considered up until now, so too, in just the same way, the activities of sexual life in animal stocks are not seldom the object of a division of labor, which then involves various numbers of individuals, some more exclusively, some less so, each according to its particularity.

The simplest case of this phenomenon appears where, like free-living individuals, only the feeding animals of a stock are outfitted with male and female organs. And this is usually the case. In other stocks, however, there are also special sexual animals that differ from the others,

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[63] See Sars op. cit. (n. 39), p. 34. [RL]

[64] Op cit. (n. 55), p. 69. [RL]

[65] *Pennaria* is a hydroid genus in the Order Anthoathecatae Cornelius 1992. Colonies have a pinnate form: branches with hydranths arise from both sides of a common axis or stem. [Eds]

[66] Braun, op. cit. (n. 61), p. 35. [RL]

[67] Their developmental history will no doubt illuminate the miracle of this structure [Bildung]. [RL]

[68] Refers to hydroids now in the family Halopterididae, Order Leptothecatae Cornelius 1992. Many colonies have long, thicker axial stems with delicate alternating side branches with hydranths. The stems often appear segmented, or as basal parts of the lateral extensions. [Eds]

which then either emerge on those feeding animals, or on special proliferating individuals according to the law of bud-development.

The final, very complex form of division of labor, which is characterized by the presence of special *proliferating individuals*,[69] can be found among the sertularians in Hydractinia,[70] Physalia and some others with a siphonate opening [Siphonostomen].[71,72] These individual animals are sufficiently marked out from all the other individuals by their size, lack of mouth-opening and tentacles (which at most, in the Hydractinia, may be recognized in rudiment as little pellet-shaped protruberances), and even moreso by their ability to produce the actual sexual animal. Among the sertularians, moreover, they have a very characteristic position in the corner of the branch, to which feature theyowe their name "axillary cells," [27] under which name they were already recognized by the earliest observers "as external sex organs."[73,74]

A special proof for the individual nature of these forms appears hardly necessary, partly because this would merely repeat the reasons already given multiple times, and partly because the relevant parts are currently already generally recognized as individuals.

Where such proliferating individuals are absent, then the *sexual animals*[75] develop on the feeding animals (if – as in the hydroids and siphonophores – they appear as individual participants in development at all), and indeed generally rather close by the mouth opening and the

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[69] Now called gonozooids, reproductive zooids, or polyps; these are present in siphonophores and hydroid colonies. Gonozooids generally lack tentacles or have only a few. Gonozooids may bear more than one gonophore, an asexual reproductive structure that typically develops into medusa buds. Also extending from the gonozooid may be an arcocyst, a gelatinous brood chamber where embryos develop. Across different taxa, gonozooids and gonophores exhibit a great variety of morphological forms. While they are involved with the sexual stage of the life cycle and typically produce a medusa, this process is also characterized by variation across taxa. [Eds]

[70] Sertulariidae is today a hydroid family in the Order Leptothecatae Cornelius 1992; in the nineteenth century, sertularians were considered to be an order of hydrozoa. Leuckart is probably referring to the family rather than to the included genus *Sertularia*. *Hydractinia* is a genus of hydroids in the Order Anthoathecatae Cornelius 1992. [Eds]

[71] See my above-mentioned essay on the anatomy of these animals. [Op. cit. n. 54.] [RL]

[72] *Physalia* is a genus in the Order Siphonophorae Eschscholtz 1829. It is the Portuguese man-of-war, with a large apical gas-filled float (pneumatophore). The pneumatophore is only present in two of the three orders of siphonophores. [Eds]

[73] See my essay "Zur Naturgeschichte der Hydroiden" in Heinrich Frey and Rudolf Leuckart, *Beiträge zur Kenntniss wirbelloser Thiere* (Braunschweig: Vieweg u. Sohn, 1847), p. 21. [RL]

[74] Gonozooids or gonophores. See note 69. [Eds]

[75] Presumably gonophores. See note 69. [Eds]

tentacles. Only rarely do they originate on the stem or on the branches of the colony, as in *Perigonimus*[76,77] and *Agalmopsis*.[78,79] At first these sexual animals do not differ from the other shoots except, at most, by their position. They originate according to the same law of budding, as squat little protruberances that gradually take on a more vesicle-like appearance.

If these individuals are fated to remain with the others in the same alliance [Verband], then they persist at this level of morphological development. Their only transformation consists in [28] this, that they fill internally with sperm or eggs,[80] so that one could take them for vesicle-shaped genitalia – and this has actually occurred.[81,82]

But this is not always the case. Very often the sexual animals are destined for a later free and independent life. Then these vesicle-like appendages develop into new, variously formed beings, with their own organs for movement and feeding; into creatures that detach themselves from the animal stock upon which they grew and after a shorter or longer period of free life enter into the stage of sexual maturity.[83,84] If one unites in one's mind the main organs of a locomotive and feeding siphonophore-individual into a common body, then one has the basics of the structure of such a sexual animal. A bell-shaped mantle from which there hangs a central mouth-stalk offers it sufficient means for feeding and movement.

In older zoological systems these developed sexual animals were placed far away from the hydroids and siphonophores. They were

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[76] See Sars, op. cit. (n. 39), p. 9. [RL]

[77] *Perigonimus* has now been synonymized under the hydroid genus *Bougainvillia* in the Order Anthoathecatae Cornelius 1992. [Eds]

[78] Sars, op. cit. (n. 39), pp. 38 and 43. [RL]

[79] Now genus *Agalma*. See note 40. [Eds]

[80] In most cases (*Tubularia*, *Eudendrium*, *Pennaria*, *Coryne*) the sexual animals of the same colony are of the same sex. Only hydra is an exception, insofar as here the individual animals almost always carry male and female sexual animals next to one another. [RL]

[81] I myself previously held this view on the nature of such sexual animals (see *Beiträge* of Frey and Leuckart [op. cit. n. 73], p. 29). [RL]

[82] While some feeding polyps do undergo a change that involves a transformation to sexual competency, this is not a uniform phenomenon across hydroid taxa. For the siphonophores, see notes 30–33, 36, and 69 on gastrozooids and gonozooids. Leuckart's reasoning is again understandable given his premises, and what was known at the time. [Eds]

[83] Are these freely living sexual animals of the same sex, when they come from the same animal stock? [RL]

[84] Typically, but not always, a free-living medusoid form. [Eds]

reckoned to the disc-shaped medusae – and perfectly justifiably so, according to their form and structure – [29] whereas the siphonophores were considered a special group of the acalephs, and the hydroids were even ascribed to the polyps.[85,86]

That these disc-shaped medusae really do correspond to the previously mentioned so-called genital vesicles follows not only from the fact that both originate in the same way in the same place, but also – even more persuasively, perhaps – from the fact that the same proliferating individual[87] is able to produce sometimes one form of these sexual animals, and sometimes the other form. What determines this, we frankly don't know, but it seems very likely that it has to do with some difference in external conditions of existence (amount and kind of food, time of year, etc.). In principle, the difference between these two forms of sexual animals is in any case neither more nor less mysterious than the polymorphism of individuals belonging to the same species, or even, if you like, the variety in form and structure of the various species.

The question of Why these differences? has a more immediate solution. We recognize ever more, that [30] every special form is created for a specific, equally special purpose – and this same correspondence of structure and function we believe we have shown also between the two forms of the sexual animals and the other individuals in our animal stocks entrusted with particular tasks.

If we now survey the life history of the polymorphic animal stocks once more in general, we recognize in them *a connected union of individuals or entire generations, which originate from the same morphogenetic laws, but which do not agree in form and function, but which adapt themselves [sich anpassen] to the physiological requirements of the entire union in many [manchfach] variable ways*. Not one of these generations by itself represents through its individuals the species (that is, the whole course of development) of this animal stock. Only the entirety of them can present the picture of a complete cyclical life-development with its varied and reciprocally complementary processes. *The single individuals appear as*

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[85] I believe that I was the first to have demonstrated that the polyps (that is, the Anthozoa) and acalephs are built on a common plan. See *Beiträge* of Frey und Leuckart [op. cit. n. 73], p. 37, and Rudolf Leuckart, *Ueber die Morphologie und die Verwandtschaftsverhältnisse der wirbellosen Thiere* (Braunschweig: Vieweg, 1848), p. 13. Recently J. Müller has also spoken out for the necessity of a systematic union of the two classes. I have named the resulting division the Coelenterates. [RL]

[86] See, for example, Cuvier (1817), Johnston (1838), Owen (1843), and discussions in Winsor (1976). [Eds]

[87] In our hydra the second individual form of the sexual animal has not yet been observed. It is probable that it is lacking. [RL]

only more or less rich fragments of the life-history of these creatures, as individual links from an entire series of connected representations.

Among the varied features of the division of labor, which constitutes the physiological character of polymorphism, we also encounter among the hydroids and the siphonophores the phenomena of the so-called alternation of generations. The disc-shaped medusae, which we have come to know as the sexually developed members of a polymorphous animal colony, and which [31] distinguish themselves from its other members only through a greater autonomy in their later life, originate asexually from a deviantly [abweichende] structured brood (a so-called "nursing brood") – and in this way, as is well known,[88] characterize the remarkable phenomenon of alternation of generations.

Now, the relationship between these sexually developed animals to the proliferating individuals is the same[89] as that of the other polymorphic individuals among themselves. With respect to their genesis [in genetischer Hinsicht] they are all alike, and with regard to physiology they all integrate themselves into a connected picture of life. From this it follows consequentially *that all these polymorphic individuals originate as the product of one alternation of generations, if any of them at all does so.*

It would follow that a polymorphic animal stock should be seen as a union of multiple nurse-generations, which would be as different in number and succession as in form and function. Each of these generations would then prepare for the production of a later, sexually developed brood in its own way – the stalk of the halopterids, which (like the so-called "head" – the scolex-like nurse among the cestodes[90])[91] [32] already

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[88] See Steenstrup, *Über den Generationswechsel*, tr. C. H. Lorenzen (Copenhagen: Reitzel, 1842), p. iii. [RL]

[89] That the sexual animals that develop into disc-shaped medusae later detach themselves is based on a gradual difference in the genetic process and cannot be viewed as a specific difference of these from the other individuals in a colony. [RL]

[90] See C. Th. v. Siebold, "Ueber den Generationswechsel der Cestoden nebst einer Revision der Gattung Tetrarhynchus," *Zeitschrift für wissenschaftliche Zoologie*, 1850, 2(2–3): 198–253, on p. 198, and van Beneden, "Recherches sur la faune littorale de Belgique: Les vers cestoïdes," *Mémoires de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, 1850, *25*:1–199, on p. 65. [RL]

[91] Cestodes, or tapeworms, are members of Class Cestoda Rudolphi 1808 (Phylum Platyhelminthes). Various species are parasitic in humans and other animals. Cestodes were frequent subjects of medical, anatomical and developmental studies in the mid-1800's. Behind the head (scolex), the numerous body segments each contain organs, including reproductive organs, and are thus nearly sufficient for independent existence. The severed segments have remarkable regenerative powers capable of producing additional bodies after fission. Steenstrup used cestodes as one of his main examples in presenting his theory of alternation of generations. [Eds]

bears the sexually mature individual in the first generation, as well as the vegetative individual (the so-called vesicle)[92] of the *Physalia*, which produce such sexual animals only in the third generation,[93] the swimming bells of the siphonophores as well as the rootlets of the hydroids.

These are to be distinguished from the nurses in Steenstrup's sense partly (like the just-mentioned swimming bells and rootlets) in that, in the forming of the sexual animals, they don't act as producing individuals – in fact, they participate only very indirectly in this process, in that they fulfill certain tasks necessary for the living and flourishing of the entire stock (thus also of the actual nurses, the above-mentioned proliferating individuals).

The (normal and necessary) appearance of such sterile nursing generations in the developmental life of certain animal forms is, according to the well-known definition of Steenstrup,[94] absolutely extraneous to the alternation of generations. If we nevertheless try to incorporate this phenomenon into the processes of alternation of generations, we cannot take as its characteristic feature the production of a sexually developed brood from asexual individuals different from them in form, as Steenstrup has done, but rather [33] only see it as a polymorphism of a particular animal form.[95]

Given this situation, we can only view Steenstrup's alternation of generations as a particular – if very significant – part [Glied] of this division of labor;[96] a phenomenon that, with its multiply changing

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[92] Presumably the protozooid, the primordial zooid developed (through various stages) from a fertilized egg, that through subsequent budding produces the other zooids of a new Physalia colony. [Eds]

[93] See the above-mentioned essay on the structure of the siphonophores [Leuckart, op. cit., n. 21]. [RL]

[94] "Alternation of generations is when an animal bears a brood that does not and will not resemble the mother, but, unlike the mother, *itself produces a brood* that returns to the form and import [Bedeutung] of the mother animal." Steenstrup, op. cit. (n. 88), p. iii. [RL]

[95] Into this [concept of] polymorphism also fits what Steenstrup (op. cit. [n. 88], p. 118) terms the essential aspect of alternation of generations: "the lack of species-individuality among the individual members of the representatives of the species." [See the accompanying article.] [RL]

[96] Steenstrup himself says of his theory of alternation of generations: "I believe I am giving only the first rough coastal contours of certain stretches of a large *Terra incognita*, which lies here unexplored, and whose investigation promises us a yield of which we barely have an inkling." (op. cit. [n. 88], p. xiv). [RL]

[manchfach wechselnde] expressions – now clearly expressed, now more hidden – runs through all animal life, and makes itself felt in the developmental course of nature with a certain necessity, which we see primarily in the savings in time and effort that is thereby achieved.

[34] *The alternation of generations is a polymorphism that is determined by a division of labor in the realm of developmental life.*[97]

The intimate connection of alternation of generations to the other types of polymorphism already comes out clearly from the fact that Steenstrup could view the brood-care in bee colonies, which we have already met as a particular form of the division of labor, as a peculiar form of the alternation of generations. He interpreted the female workers as nurses[98] that distinguish themselves from other nurses only through their particular form of nursing [Aufammung].

If one admits the warrant of this expression, then one barely has to go a step further along the same path to come to the view that the female individuals are also simple nurses. As little as we would sanction this assertion, however, just as little can we view the brood-care of the bees etc. as an alternation of generations. Rather we should view all these phenomena – alternation of generations, brood-care, sexual dualism, etc. – as particular more or less complicated forms of a division of labor.

[35] It is not my intention here to give a full account of polymorphism in all its rich diversity, according to its distribution, external appearance and connection to individual life. I only wanted to emphasize here, in broad strokes, the existence and significance of this interesting phenomenon, only so far as it was necessary to an appropriate evaluation of many facts that were otherwise so mysterious. But I cannot suppress the remark that the arrangement of a division of labor expressed in these ways is in no way limited to the animal kingdom, but also rules the individual forms of the plant world – indeed, in an even more general and freer way.

For a long time already, plants have been considered "things that grow" ["Gewächse"], not as separate isolated individuals. "Totidem

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[97] I have shown in another place ("Ueber Metamorphose, ungeschlechtliche Vermehrung, Generationswechsel," *Zeitschrift für wissenschaftliche Zoologie*, 1851, 3[2]: 170–188) that the alternation of generations is also not an isolated phenomenon with respect to morphology. In this perspective, alternation of generations is reduced to an asexual multiplication [Vermehrung] during larval life. [RL]

[98] Steenstrup, op. cit. (n. 88), p. 122. [RL]

gemmae, totidem plantae" is an old expression, coming from Linnaeus.[99] But only in recent and very recent times (and here I cannot suppress the name of A. Braun[100]), since the plant individual has been recognized with certainty in the separate shoots of the plant, has a complete insight been won into their morphological and physiological connection.[101]

[36] Among the plants, too, there are certainly many species that complete their entire developmental cycle as a single individual, but as a rule the complete realization [of this cycle] is entrusted to a larger or smaller society of individuals. And here such a division of labor is carried out that much more unrestrictedly, since the colony formation, as already mentioned, has developed into a very common character of plants and could easily occur on account of plants' immobility.

What we call a plant [Gewächs] is thus not only the living stem-tree [Stammbaum] of a family increasing and rejuvenating itself asexually, but also a coherent whole, whose individual parts differ through unlike propensities and only offer a total picture of plant life through complementing one another.[102] *Plants are polymorphous plant-stocks*, just as the hydroids and siphonophores are polymorphous animal stocks. That the number and character of the individual developmental series within the overall cycle can differ, according to the type of division of labor, hardly requires explicit mention. In general, though, we can distinguish particular feeding, attaching, vegetative, proliferating, and sexually developed individuals.

The feeding individuals are distinguished by their possession of the true leaves (that is, of the herbaceous part [des Krautes]), the attaching

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[99] The ideas behind the aphorism "Just as many buds as plants" appear in Linnaeus' *Philosophia Botanica* (1751), aphorism 132 (Linnaeus, 2003, p. 99) – what Linnaeus actually said was "Gemmae totidem herbae" ("the shoots are equal in number to the buds"). Whereas Linnaeus used the phrase to indicate the fecundity of nature, later botanists, following Johann Wolfgang von Goethe, took it to express the notion that buds as individuals are analogous in some ways to plants as individuals. [Eds]

[100] I cannot mention the name of this man and his well-known work on the phenomena of rejuvenescence (already mentioned several times previously above), without acknowledging with a thankful heart what friendly love, what stimulating teaching I received from him during our time – unfortunately so short – working together at this university. It was also he who, through text and word, exercised the greatest influence on the development of the perspective expressed more fully in the present little work. [RL]

[101] Alexander Braun was clearly important in the revival of the idea that the plant was a compound individual (Braun, 1855–1856), but Leuckart's attribution of this idea to him is exaggerated. See our accompanying article. [Eds]

[102] See A. Braun, op. cit. (n. 61), 54. [RL]

ones appear as rootlets, the vegetative ones as axis-builders. We consider the flowers to be the proliferating individuals and [37] the so-called ovules (or seed-buds) to be the sexually developed individuals (though the latter are actually only female[103]).[104]

In most cases, however, the division of labor is not so complete. When it is more restricted, then usually the first individual structures to be lost are the vegetative and proliferating shoots [Sprossen]. Stem and flower then become integrated parts of the feeding individuals, which then in the same connection also gain in "species individuality" and physiognomic significance for the character of the plant.

In this way, all of the phenomena of individual life can gradually come to be realized in the same ongoing developmental series, in a self-contained single being. Stem, root, leaves, flowers are then connected parts of a simple individual. But at least the phanerogamic plants can never achieve a perfect oneness.[105] Sexual reproduction always demands here its own bearers, the (very falsely) so-called ovules, which, like the other individuals of a common stock, originate according to the law of bud-formation, but which through small size and hidden location lack any influence on the habitus and the expression of the plant.

With the [38] help of a special organ (the so-called embryo sac),[106] this sexual individual internally produces the female procreative contents (the so-called germinal vesicle[107] [Keimbläschen] – the analogue of the animal egg). In the phanerogams these sexual individuals, like the so-called genital sacs [Genitalkapseln] of the hydroids, always remain in the same unit, and limit their functions only to the goals of sexual reproduction.

But in the plant kingdom, too, it is not unheard-of for the sexual individual to detach itself from this unit and achieve an independent development, like the disc-shaped medusae that originate through the alternation of generations. The so-called proembryo [Vorkeime] of the

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[103] The male sexual substance (the pollen grains) are prepared in special organs (the pollen-pouches) of the flower. Only the plants with separate sexes have their own male individuals, and even then these correspond only to the proliferating individuals, never to the ovules. [RL]

[104] The ovule is part of the flower structure near its base. It is an internal part of the ovary that surrounds the female ovum. [Eds]

[105] Here Leuckart refers back to the beginning of his paper, where he discusses the ability or inability of a single individual to "represent" a species, that is, a closed and self-maintaining system. [Eds]

[106] In flowering plants, the embryo sac is a structure inside the ovule in which pollination (fertilization) of the ovum takes place and the embryo develops. [Eds]

[107] The female ovum, or the contents of the ovule. [Eds]

leaf-cryptogams are probably nothing other than such sexual individuals,[108] which already detach themselves[109] at an earlier time – as simple cells, so-called spores, and through a suitable organization are enabled to maintain an independent vegetative and sexual life.[110]

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[108] The pro-embryo here refers to the protonema, which in mosses or liverworts consists of the first cellular filaments that grow from a spore into a leafy plant body. The term "cryptogam," now used only informally, referred in the early 1800s to plant taxa whose mode of sexual reproduction was uncertain, and in many (but not all) classifications it included both leafy taxa (such as ferns) and non-leafy ones (such as fungi). Protonema are part of the haploid gametophyte phase of the life cycle (still referred to as alternation of generations), and will produce male and/or female organs containing egg or sperm cells. [Eds]

[109] I cannot agree with the view of [J.] Leszczyc-Suminsky (*Zur Entwicklungsgeschichte der Farrnkräuter*, Berlin: Decker, 1848), when he opines that these proembryos correspond to the flowers of the phanerogams, the spore being a "flower-bud that detaches itself from the mother-plant." [RL]

[110] The work of Hofmeister (1851) was probably the first to clarify the alternation of generations – sporophyte and gametophyte – in cryptogams. [Eds]

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