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# The Origins and Evolution of Animal Identity

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## Abstract

The Darwinian synthesis focuses on speciation as the leading edge of evolution. But species are poor candidates for bearers of well-defined biological identity because they are always susceptible to giving rise to something new. Physicalist evolutionary developmental biology presents an alternative scenario in which broad differences between organismal types were ontologically and temporally prior to subtypes and species-level variants. The cell masses that first developed into the metazoans, or animals, for example, arose from unicellular antecedents by a set of molecular innovations that constituted the embryos of these organisms as an unprecedented form of matter – liquid and liquid crystalline tissues – and thus a natural kind. This novel material embodied a set of morphogenetic processes and motifs that laid the basis for subsequent animal evolution. With the addition of other molecular functionalities simple “basal” metazoan body plans (sponges, placozoans) engendered more complex diploblasts (cnidarians, ctenophores) and bilaterian triploblasts (arthropods, chordates, mollusks, and so forth). Self-organizing patterning processes arising within these integrated communities of cells produced segments, appendages, patterned skeletons and organs. Bioelectrical scaffolding effects and the standardizing effects of development from an egg transformed phylotypic forms into canalized, integrated individuals that exist in the biosphere as “natural purposes,” causes and effects of themselves.

## 1. Introduction

Any notion of biological identity will necessarily be a conditional one, dependent on which biological level one is considering (e.g., viruses, cells, multicellular organisms), what category within a level (e.g., phages vs. animal viruses, nucleated vs. nonnucleated cells, animals vs. plants), and how evolved from their points of origin are the entities under consideration. Assigning identity will also depend on the theory of the living state one brings to bear on the question. To take an extreme (and naïve) example, if an organism's identity is taken to be defined by the information contained in its genome, then even one mutation will change this identity, since it would be, by this definition, a quasi-continuous property. If, in contrast, the type-specificity of an organism is (as generally assumed), relatively autonomous of the details of its genome, then some genetic variation will be consistent with conserved biological identity.

To analyze identity within a category of organism and the range of variation consistent with membership in that category, it is necessary to distinguish that category from others. This is at-base an evolutionary question, since however extensive the differences may be among present-day types, each type is constituted, if only incipiently, when it first diverges from other ones. Like the question of identity itself, the origination of types is a theory-laden issue. The standard model of evolution (the Darwinian modern synthesis), for example, considers new phylogenetic lineages to arise from the same microevolutionary processes that fine-tune established ones. Other models (e.g., some versions of evolutionary developmental biology), in contrast, assert that saltational processes play a role in origination events. Although gradualist and saltationist models both recognize the existence of genealogical nodes at which clades (consisting of an ancestral form and all its lineal descendants) are established, the ontological status of such bifurcations will differ depending on the mechanism by which they occur.

For many important examples of emergent biological entities, e.g., living vs. nonliving chemical systems, archaea vs. bacteria, prokaryotes vs. eukaryotes, origination scenarios, i.e., accounts of the mode and degree of initial separation from the ensemble of progenitors are obscure. For others, such as the rise of the metazoans or animals from unicellular ancestors, key steps can be reconstructed. This chapter will address this case.

The idea that the identity of an organism can derive from its being an exemplar of a “natural kind” verges toward essentialism, a notion broadly rejected by modern philosophers of biology (Dupré, 2014, Lewens, 2012, Okasha, 2002), although there are some exceptions (Wilson et al., 2007, Devitt, 2010). Essentialism is widely seen to conflict with the reality of evolution, in which species identity is conditional and mutable. Even more alien to much of present-day thinking is the Kantian concept of “natural purpose,” which implies a recursive self-definition that seems to defy natural explanation (Moss and Newman, 2015). In this essay I argue that the concepts of natural kind, essence, and natural purpose are in fact applicable to living systems, but only if certain tenets of the modern synthesis are relinquished in favor of a “physico-genetic” perspective that emphasizes the material properties of cell assemblages and their inherent properties (Newman, 2012, Newman, 2018, Newman, 2019b). Rather than conflicting with naturalistic biological science, I propose that these concepts are necessary to it and enable an understanding of the relation between development and evolution, and organismal identity and individuality.

It may be impossible to formulate general criteria of organismal identity and individuality which would encompass cases as varied as bacterial biofilms, social amoebae, plants, and animals, or their prokaryotic and eukaryotic unicellular antecedents. However, it is reasonable to expect that intensive analysis of one example could inform consideration of others. Here I focus on the animals and the unicellular progenitors from which they arose, and the various phyla into which they have diversified. I argue that both genes and the physics of materials are causal factors in the constitution, diversification and individuation of animal bodies. Further, I provide evidence that the inception of new categories of animals was usually associated with the appearance of novel genes which enabled, and in some cases made inevitable, the generation of unprecedented morphological motifs. The association of the genes in question with unique morphogenetic capabilities suggests that animal type-identities so defined are intrinsically stable, a conclusion at odds with gradualist and adaptationist evolutionary models. An important corollary is that individuality need not be in tension with or disruptive of categorical identity but will often serve to intensify it.

## 2. The constitution of animal identity

The first animals to emerge on Earth arose within a population of single-celled organisms that shared ancestry with present-day choanoflagellates (reviewed in (Newman, 2016b)). The animals (metazoans), the choanoflagellates, and another unicellular group with extant members, the filastereans, are collectively termed Holozoa. Unicellular holozoan species sometimes exhibit colonial forms, but the cell masses that constitute embryos and organ primordia of animals are very different, biologically and physically, from the cell clusters or aggregates formed by unicellular holozoans. Unlike the latter's transient associations, the metazoan cells grip one another by cell attachment molecules (CAMs) that extend through their membranes and engage their internal cytoskeletons. Specifically, there was an evolutionary addition to a class of holozoan CAMs known as *cadherins* of a new cytoplasmic domain, turning them into "classical cadherins." Additionally, new genes appeared, the catenins, whose products link the cytoplasmic tails of classical cadherins to the cell's actin cytoskeleton. The classical cadherin intracellular domain and the catenins are novelties of metazoans not found in any sequenced protein of other unicellular or multicellular organisms.

The resulting capacity of cells to extend random protrusions while remaining reversibly bound to their neighbors, enables them to move between and past one another without disrupting the cohesion of the cellular mass. This endows developing animal tissues with *liquid-like* properties (Newman, 2016a).[1] Although some other forms of multicellular life (e.g., social amoebae) have liquid-like properties (Nicol et al., 1999), none achieve it in precisely the same way as animal tissues.

In nonbiological liquids, the subunits (atoms or molecules) cohere by electrical forces while moving freely with respect to one another by random Brownian motion. Although, as indicated, cohesivity and random locomotion have entirely different bases in animal tissues, the same liquid-state physics applies. In the first place, the free exchange of cells between the periphery and interior causes these cell clusters to exhibit surface tension, and thus to assume a spherical morphology when unstressed, like non-biological liquids. Second, any interior spaces will automatically fill in with cells, since liquids do not sustain lacunae. Third, if two parcels of a

liquid tissue are fused, eventually the cells will cross the interface and mix with each other, just as in drops of non-living liquids (Foty et al., 1994).

In addition, if a liquid tissue, analogously to a binary liquid (e.g., a shaken mixture of oil and water) is composed of two different cell types, it can undergo phase separation, spontaneously sorting out (like the oil and water) into distinct layers. Such layering is the initial step in most modes of animal embryogenesis (Forgacs and Newman, 2005). For cell mixtures to sort out and form layers they must differentiate from one another. Cells in a tissue mass can be induced to differentiate by *morphogens*, secreted diffusible proteins. There are more than a dozen of these, but the most fundamental is Wnt, a molecule produced by all animal embryos but in no other known or inferred organisms. Wnt modulates the expression of genes in the cells that produce it or those nearby, leading to heterogeneous cell mixtures (Loh et al., 2016).

In cases where their cells express a few additional components, liquid tissues can mirror the more elaborate organizational effects seen in nonliving liquids composed of, or containing, asymmetric subunits. The most important of these effects are also induced by Wnt, which in addition to its influence on gene expression can mobilize internal machinery inherited from unicellular ancestors to make cells nonuniform in surface properties (“apicobasal polarity”) or anisotropic in shape (“planar polarity”) (Karner et al., 2006b, Karner et al., 2006a). When apicobasally polarized cells rearrange to surround interior tissue spaces or lumens. Here they are behaving like molecules in nonbiological liquids with polar charge distributions, which spontaneously self-organize into closed micelles or vesicles. Alternatively, like the long polymers that comprise liquid crystals (droplets of which exhibit asymmetrical shapes), planar polarized cells can intercalate among one another and reshape tissues, causing them to narrow in one direction and elongate orthogonally to it.

Following the origination of animal life as Wnt-expressing liquid and liquid crystalline tissues, several structural motifs that characterize the metazoans emerged almost automatically due to their being inherent to this novel form of matter (Newman, 2018, Newman, 2019b). The morphologically simplest animals, marine sponges and placozoans, which are the only metazoans that lack the planar polarization mechanism induced by Wnt, are characterized by

roughly-defined cell layers and labyrinths and lumens. All the other, more complex, animal groups are termed “eumetazoans.” These have sharply defined layers, elongated bodies, appendages, and in more sophisticated forms, internal organs.

Contrary to the expectations of gradualist adaptationism, all these body plans emerged in a few time-compressed episodes (beginning in the Precambrian) (Conway Morris, 2006, Rokas et al., 2005, Shen et al., 2008). They also have defining characteristics which (like the constitution of the metazoan liquid-tissue state itself) are attributable to the harnessing of previously irrelevant physical effects by novel molecular functionalities (Newman and Bhat, 2009, Newman, 2012). The implication that the superphylum- and phylum-level features of animal life (what I refer to here as “phylotypic identity”) emerged early, in broad strokes, and not as late products of repeated cycles of microevolution of simple forms, has major implications for the notion of identity in this group of organisms.

**3. The diversification of phylotypic identity**

Identity is partly a matter of group membership. In the view of the modern evolutionary synthesis, boundaries between groups are porous, and every organismal category is only apparently stable. All types are on their way to becoming something else. The picture laid out in the previous section, however, points to constitutive physical properties that define the metazoans and make the forms they assume predictable. As evolution progressed, these properties were recruited for the elaboration of new structural motifs during body and organ development. The liquid (including liquid-crystalline)-tissue state and its inherent morphological effects are necessary and enabling for the origination and development of animals, and are generatively entrenched with respect to their subsequent evolution (Wimsatt, 2015).

The early diverging sponges and placozoans, the so-called basal metazoans, lack one or more components of the planar polarization pathway, as well as the ability to produce the stiff planar extracellular matrix, the *basal lamina*, essential for sharply separated tissue layers and complex morphogenesis (see below). However, the relevant genes may have been lost completely or in part in the evolution of these forms (one group of sponges, the homoscleromorphs, contain both

the planar polarization pathway and a basal lamina, for example, and the single extant placozoan species contains a truncated gene for the enzyme –peroxidasin – required to assemble the basal lamina) (Degnan et al., 2015, Fidler et al., 2014). The simple body plans of these animals thus may reflect a secondary paring down of the metazoan "morphogenetic toolkit" (the gene products involved in morphological development) to a near-minimal set of determinants for liquid-tissue behavior.

The cnidarians (e.g., hydra, jellyfish), a group of animals with more than 10,000 species, are the simplest forms in which a full planar polarization pathway is present, and which have basal laminae (reviewed in (Newman, 2016b)). Planar cell polarization enabled elongation of the body, and of appendages such as tentacles, while the basal lamina was essential for the formation of true tissues, which differ from the transient and provisional cell layers of sponges and placozoans. The cnidarians are termed "diploblasts" because of their having two apposed *epithelial* tissue layers (epithelia being tissues composed of cells directly attached to one another via CAMs) with an intervening extracellular matrix composed in part of fused basal laminae produced by the respective layers. The enigmatic ctenophores (e.g., comb jellies) are similarly diploblastic but might in fact be a sister clade to all the metazoans rather than just to the cnidarians. Their many unique morphological features, apparent loss of ancestral genes and unusually rapid evolution of others, and functional substitutions (e.g., Wnt, though encoded by the genome is not employed during embryogenesis), make them difficult to place phylogenetically (King and Rokas, 2017).

The ability to form and reshape sharply defined layers of tissue allowed diploblasts to develop in a determinate fashion, generating body plans with more stereotypical architectures than those of the basal metazoans. Arnellos and Moreno (2016) propose that the capacity to generate epithelia, which distinguishes the eumetazoans from the basal metazoans, is the hallmark of organismal identity in the animals, enabling the demarcation of inside and outside (and thus organism and environment), and providing the necessary cellular conditions for the fomation of a nervous system.

Based on a unique phenomenon of electrical field-based consolidation and integration of pattern and form (see below), it is plausible that the tissues of diploblasts and the more complex triploblasts that evolved from them are a novel form of matter within, but beyond, the basic liquid-tissue state. In this sense, the cell-based materials that develop into these organisms constitute a subkind of matter within the liquid tissues that form the animals. This is analogous to asserting that the metals constitute a subkind of matter within the natural kind that collectively consists of the chemical elements. Of course, philosophers who deny the ascription of natural kinds to the category of chemical elements, or to any individual element or subset of them, are likely also to reject these biological attributions.

The evolution of about 30 metazoan phylotypes in addition to the basal metazoans and diploblasts was based on the innovation of a third tissue or "germ layer" interposed between the two epithelial ones. Unlike the transition between unicellular holozoans and the basal metazoans + cnidarians (and possibly ctenophores), the three-layered configuration, or triploblasty, appears to have been achieved in several different ways, involving different types of extracellular matrix molecules and factors promoting formation of the dispersed-cell tissue state known as *mesenchyme* (reviewed in (Newman, 2016b)). Appearing tens of millions of years later in the fossil record than cnidarians, triploblasts are thought to have arisen from diploblastic ancestors. One of the two tissue layers of ancestral forms outpocketed, separated, or disaggregated into a third (mesodermal) germ layer. The disaggregating mode, termed *epithelial-mesenchymal transformation* (EMT), seen in the development of arthropods, chordates, and several other phyla, appears to have evolved via the addition of molecules to the extracellular matrix of the middle zone separating the two layers, where they promote cell dispersion and invasion. Some mesoderm-promoting secreted proteins (e.g., fibronectin and tenascin in chordates) are phylum-specific innovations, while others, like the thrombospondin type 1 repeat (TSR) superfamily of proteins, are common to most triploblasts and appear to have been carried over from unicellular holozoan ancestors. Some extracellular matrix proteins (e.g., collagen, dentin) are capable of mineralizing under certain conditions, adding the solid state to the physical repertoire of metazoan tissues (reviewed in (Newman, 2016b)).

Since the resulting morphologies may be analogous rather than arising from a common physical cause, the triploblasts as a group probably do not represent a single natural kind, if the criterion is taken to be a uniquely characterized material. Instead, at least some of the traditionally identified bilaterians (a term with a different sense – based on symmetry – but referring to the same group of organisms as the term "triploblasts") may individually be natural subkinds of the animals.

Multilayering provided a platform for prolific diversification of body plans. In extant animals and presumably ancestral forms it occurs in several different manners, each dependent on phase-separation behaviors of the liquid tissue state and its defining genetic toolkit, with the addition (as noted) of some phylum-specific extracellular matrix molecules. Despite their being induced and mediated by a variety of different molecules, there are just a few main mechanisms by which *gastrulation*, the embryonic process that brings about multilayering in triploblastic organisms, is achieved. They are often overlapping and jointly employed, however. In topologically solid embryos (i.e., without an early-forming lumen) (i) an internal mass of cells can acquire greater cohesivity than the surrounding layer and pull away from it ("delamination"), (ii) a less cohesive cell mass can come to envelop a more cohesive one ("epiboly") or (iii) curl in on itself over the latter ("involution"); in embryos with interior spaces (which can form spontaneously by cells with A/B polarity) (iv) inward folding of the surface layer ("invagination") or (v) migration of a subset of surface cells ("ingression") can give rise to a new layer (Newman, 2016b).

Each of these morphogenetic processes is inherent to the liquid nature of metazoan tissues in conjunction with the conditional apicobasal and planar polarization of their cellular subunits, and optionally, with the EMT-inducing effects of novel matrix proteins. This makes it plausible that gastrulation had its origins in the physically based rearrangements inherent to such materials rather than in multiple cycles of natural selection (Newman, 2016a). In addition to the morphological motifs of gastrulation, triploblastic/bilaterian animals exhibit other recurrent forms – segmentation (in insect bodies, vertebrate backbones, individual tetrapod digits), branching tubes (in insect trachea and veterbrate respiratory airways, vascular trees, glands), regular two-dimensional arrays (insect bristles, hair and feather follicles, pigment spots and stripes). The next section describes how these structual motifs, like those of gastrulation, are

attributable either in their present implementation or in their origination to physical effects inherent in the materials of which the respective organisms and organs are composed.

**4. The detachment of animal identity from strict genetic determination**

Acoelamates, such as flatworms, are the morphologically simplest triploblastic animals. These organisms have an enteric cavity open at both ends but lack a second body cavity, the coelom, which surrounds a separate digestive tube in coelomate species. Acoelamate animals have a small number of organ types – ovaries and testes, and ganglia, localized clusters of neurons. In coelomates, in contrast, organ complexity is dramatically increased, since additional interfaces are available for epithelial-mesenchymal interactions during development. The morphological phenomena of organogenesis in these animals (producing, for example, circulatory systems, lungs, salivary glands), are essentially identical to those of gastrulation, utilizing the same liquid, deformable sheet, and disaggregative behaviors of the component tissues. These, in turn, are mediated by the products of the same morphogenetic toolkit genes plus some phylum-associated extracellular matrix and other molecules (Newman, 2016a).

It can be concluded that both development and evolution of animal form, at both the body and organ levels, draw (and have drawn) on inherent physico-genetic properties of tissues, played out in different geometrical and topological settings. Most genes of metazoan organisms are concerned with the conduct of subcellular activities, which evolved long before animals existed and continued to be involved in primarily single-cell functions after the emergence of multicellularity. The small number of genes (the morphogenetic toolkit) that are specifically involved in creating animal identity (i.e., multicellular holozoans with the liquid-tissue properties discussed above) and in their partitioning into superphyla, phyla, and other subgroups, appeared coincidentally with animal life. Their roles are to mobilize physical forces and effects that shape and pattern tissues into often elaborate combinations of stereotypical motifs. While these effects eventually came to be programmed and orchestrated during development by interactions among groups of cells, no amount of evolution of these spatiotemporal programs can effect a departure from the “morphospace” (the array of structural possibilities) afforded to animal tissues.

Some of the genes that evolved prior to multicellularity are involved with the requirement of all cells to store chemical and mechanical energy. Others are employed in positive and negative feedback regulation of gene expression. With the rise of multicellularity, energy storage and molecular feedback mechanisms in the context of direct and indirect cell-cell communication constituted tissues as "excitable media," spatially extended dynamical systems capable of propagating chemical and mechanical waves (Forgacs and Newman, 2005). (The early-evolved genes did not change their functions in the transition to multicellularity, but rather, with the change of scale, mediated the acquisition of tissue-level properties.) Excitability enables liquid tissues to generate ("self-organize") into regular patterns and forms, exploiting the potential that exists within the limits of metazoan morphospace.

Among the structures organized by such excitable effects during body plan development are *segmentation*, full or partial subdivision of the body axis in animal groups as diverse as annelid worms, mollusks, arthropods, and vertebrates, and *patterned skeletogenesis* in the paired appendages (fins or limbs) of jawed vertebrates. Both these developmental processes employ genes and their products not as elements of incrementally modifiable ontogenetic programs implicit in the standard evolutionary narrative, but as components of dynamical systems.

Additional evidence that the constitution of phylotypic identity is "detached" (Lenny Moss's term (Moss, 2006)) from a sequential programmatic readout of the genome comes from the potential of animals to form vegetatively. While nearly all animals develop in an apparently programmatic fashion from a single-celled zygote resulting from fertilization, marine and freshwater sponges, and colonial cnidarians such as corals, also develop from released multicellular propagules into organisms indistinguishable from ones produced from a fertilized egg. Other cnidarians, including free-living hydra, reproduce both sexually and by extending buds from the body stalk that detach as fully formed individuals (reviewed in (Newman, 2014)).

Vegetative development can also occur in morphologically more complex animals. Some tunicates (triploblasts with a larval body plan like that of vertebrates) preferentially reproduce asexually. Polyembryony, the production of multiple offspring from the blastomeres (pre-gastrula cells) of a single divided embryo, is an example of vegetative reproduction that occurs in

some mammals. But while the animals in these examples can develop vegetatively, without passing through a zygote stage, they can also develop sexually. It is therefore theoretically possible that a programmed genetic readout in a recent progenitor that developed directly from a zygote is remembered and redeployed in the vegetative propagules, buds, or polyembryonic blastomeres, so vegetative development itself is not sufficient to disconfirm the existence of genetic programs for establishment of the phylotype.

The most decisive evidence that phylotypic identity does not derive from a programmatic readout of the zygotic genome comes from interfamilial (within a taxonomic order) and interordinal (within a taxonomic class) embryo chimeras. Embryonic cells from sheep (which have 54 chromosomes) and goats (with 60 chromosomes), members of distinct families of the mammalian order *Artiodactyla* which diverged 5-8 million years ago, can be mixed together and developed into a composite organism with a variable phenotype with features of each species. Even more strikingly, mixtures of embryonic stem cells from medaka and blastomeres from zebrafish (members of two different orders of ray-finned fish that diverged from one another around 320 million years ago) developed into chimeric fish, with the medaka cells accommodating themselves to the timing of zebrafish development and incorporating into several organs of the resulting organism. In both cases, the chimeric animals developed into coherent metazoan organisms from non-zygotic cells of species whose own development is strictly fertilization-dependent (reviewed in (Newman, 2014)).

If the causal basis for establishment of metazoan phylotypic identity is not the readout of a genetic program beginning at the zygotic stage, what is its basis? As described earlier in this chapter specific genes are indeed involved, but not as part of a program. Rather, the key genes are those of the morphogenetic toolkit, and their role is to constitute the material properties of metazoan tissues, including their liquid-like nature, their capacity to elicit apicobasal and planar polarity in contiguous populations of their cellular subunits, their ability to produce basal laminae or undergo EMT, to solidify. None of these functions was present in unicellular holozoan ancestors. Correspondingly, they only begin operating at the multicellular state (the blastula, blastoderm, or inner cell mass stage of development, depending on the species) when they initiate gastrulation.

The establishment of phylotypic identity is thus an inherently multicellular, mesoscopic physics-based set of processes. It makes sense (however counter to the generally accepted paradigms of developmental and evolutionary biology (Linde-Medina, 2010)) that vegetative development, which takes off from non-zygotic propagules, can produce generic phylum representatives that are indifferent to any identification with known species, which according to the standard picture are the most honed products of evolution and the leading edge of its continued occurrence.

Notwithstanding the properties that first set the animals apart from other organisms (and indeed other kinds of matter), biological systems continue to evolve. Animals, like other organisms, are under selective pressure to conserve their useful features and propagate their types, and mechanisms that have evolved for these purposes have sometimes provided more reliable ways to develop true-to-type than the inherent physico-genetic ones described above. As described in the next section, this move from generic to specific causation has intensified and consolidated differences between types and promoted individuation of species and their members.

**5. The consolidation and intensification of animal identity**

When developmental mechanisms are looked at in detail it frequently appears that evolution has yielded a “belt and suspenders” solution to the reliable formation of important structures. A case in point is the role of the proteins nanos and hunchback in the segmentation of the *Drosophila* embryo. Both play key, well-characterized roles in determining the borders of expression of other spatially expressed genes leading up to the interdigitating seven-stripe patterns of still other genes that precede overt segment formation. Nanos is stored in the egg during oogenesis and represses the activity of hunchback. In its absence segmentation is fatally perturbed. Elimination of nanos, however, can be entirely compensated for by also eliminating the (otherwise essential) maternally derived complement of hunchback. Embryos lacking both these maternal gene products are viable and can survive as fertile adults, although without the “overdetermining” circuitry the developmental system is probably more fragile (Irish et al., 1989).

A recently characterized and unexpected mode of conservation and rectification of animal morphology is the establishment of an elaborate set of electrical cues by ion channels, pumps, and communicating junctions at the plasma membranes of the cells of developing and regenerating tissues. This leads to a bioelectric scaffolding that influences proliferation, differentiation, cell shape, and apoptosis of stem, progenitor, and somatic cells. Voltage gradients appear to encode aspects of species-specific morphology that act in concert with the morphogenetic toolkit and other gene regulatory networks to facilitate embryogenesis, or the regeneration of missing structures after trauma (Levin, 2014). While bioelectricity is not a morphogenetic force independent of the described physico-genetic mechanisms, its role is not merely passive. Experimentally reshaping the voltage pattern of a regenerating Planaria of one species to that of a different one, for example, will cause the alternative morphotype to form.

Voltage gradients can form in all animals that have intercellular gap junctions or ion channels. These are mediated by gene products called innexins and their homologs the pannexins (except for echinoderms, such as sea urchins and starfish) in all diploblastic and triploblastic animals, and additionally by connexins, a novel protein family of the chordates. Sponges and the placozoans lack these channel proteins, while echinoderms have gap junctions defined by different protein families (Bloemendal and Kuck, 2013). Bioelectrical integration of morphology thus appears to be a novel material property of eumetazoans that set them apart from basal metazoans as a natural subkind within the animals.

The major arena for stabilization and reinforcement of developmental outcomes, however, is the egg. This is notwithstanding the evidence (discussed above) that an egg stage of development is not decisive for generating phylum-specific features. Eggs themselves exhibit broad morphological variability even within a phylum (compare the minuscule mammalian egg with the huge avian one) and are the loci of widely disparate pre-cleavage intracellular signaling processes even in related species (see below). Despite this, embryos of a given phylum pass through a “phylotypic stage” in which they are morphologically very similar, before they again diverge to take on their class-, order- and species-specific identities. This phenomenon of comparative developmental biology is referred to as the “embryonic hourglass” (Newman, 2011). It finds a natural interpretation in the view presented here, in which phylotypic features

depend solely on the inherent morphogenetic properties conferred by phylum-related physics-mobilizing genes, and these are only expressed starting at the multicellular stage of embryogenesis.

In principle (as indicated by vegetative propagation), all that is required for parcels of metazoan tissue to generate bodies of a given phylotype are the respective phylum-specific morphogenetic toolkit genes in the context of all the shared properties of metazoan cells. Moreover (as indicated by chimerism), aggregates of such cells with otherwise variant genotypes can generate bodies that reside within the phylotype but in other respects are evolutionarily unprecedented. This raises the possibility that organisms with morphological phenotypes of modern phyla (or propensities to generate them, since the phyla's origination as clades was likely not coincident with the emergence of their all body-plan characters (Budd and Jensen, 2000)) may have first arisen in clusters of non-clonal populations of cells. This implies, in turn, that programmatic development from a single cell is a derived feature (Newman, 2011).

But in fact, animals almost always develop from fertilized eggs, or have this option, and this needs to be explained. Since organisms that develop from aggregated cells will typically be genetically heterogenous, they will incur cellular competition and potential conflict (Grosberg and Strathmann, 2007, Michod and Roze, 2001). Initiating development from a zygote is a way to ensure that the cells of the embryo are clonal. The animal egg may thus have been an evolutionary innovation – appearing subsequently to the major body plan motifs – that was selected for by its capacity to originate genetically uniform phylotypic lineages and thus ensure their phylogenetic stability (Sexuality and fertilization would have evolved afterwards in this scenario) (Newman, 2011, Newman, 2014).

The egg has two properties that distinguish it from later-developing cells of the embryo and suit it to its proposed role. The first is its size, always larger than the cells derived from it. The tendency of large cells to divide incompletely promotes cleavage, rather than cytokinesis (complete separation of daughter cells) after DNA replication. The egg has a second capability that promotes clonality even in the absence of cleavage. This is the presence of an extracellular container, the egg shell in birds and other groups, the zona pellucida in mammals. Blastomeres

that fully separate from each other (as occurs during early development in some mammals) remain associated with one another and are inhibited from mixing with the cells of other embryos owing to this containment (Newman, 2014).

Development from an enlarged cell affords additional opportunities for ensuring reproducibility of developmental outcome while simultaneously promoting subphylum diversification. This set of phenomena has been reviewed at length elsewhere and will just be summarized here. Patterning processes within a large founder cell of an embryo (pre- or post-fertilization) leads to nonuniform cytoplasm and cellular progeny that are regionally specialized properties by the time morphogenesis begins at the multicellular liquid tissue stage. Even though these intra-egg patterns do not prefigure the anatomy of the developed animal, having a set of landmarks laid out ahead of time causes the morphogenetic processes to occur in a standardized context and thus contributes to the fidelity of species-specific development (Newman, 2011).

Egg prepatterns, though not occurring in all species, are important, often critically, to subsequent development in the species in which they are present. They can be highly variable, however, differing within taxonomic orders, e.g., between mice and hamsters, both rodents. Evolutionarily more distant species like medaka and zebrafish can exhibit highly disparate intra-egg patterning processes despite having similar adult morphologies, and, as we have seen, the capacity to chimerize at later embryonic stages. In nematode worms, a phylum with little morphological diversity, formation of the embryo's anteroposterior axis can depend absolutely on egg patterning in some species (in which the patterns are highly divergent) and not at all in others, with the developmental processes then going on to produce essentially the same anatomy. Among species that require egg patterning, for example, the sperm entry point at fertilization determines the head end in some nematodes and the tail end in others (reviewed in (Newman, 2011)).

The overdetermining, bioelectrical and egg-dependent mechanisms that consolidate and integrate the morphological phenotypes apparently evolved to protect established developmental outcomes from being derailed ("canalization," in Waddington's term (Waddington, 1942)). Along with stabilizing the respective phylotypes, though, they also made them tolerant to additional genetic

change. This autonomy provided an arena for within-phylotype variability and individuality. By "individuality" I mean unique (in contrast to generic, e.g., phylum, genus, species) biological, (including genetic) identity. While the standard evolutionary narrative holds that variability undermines the type-identity of individuals insofar as it contributes to incipient speciation (e.g., Okasha 2002), in the view outlined here intensified biological individuality is compatible with, and an inevitable consequence of, genetic and epigenetic variation.

**6. The elaboration of individuality**

The previous section described inherited variation within animal types (e.g., phyla, classes) that clearly promotes the reliable development of typical sub-group members under different circumstances. A great deal of variation with no obvious function is also tolerated within types. Some of this may be pleiotropic, with negative effects balanced by positive ones. Some may be "neutral" in the sense of never having encountered an environment in which it made a difference. In the conventional evolutionary narrative all of this would be included under the rubric of "standing variation" in the respective populations, ready to be mobilized for the evolution of new types of organisms when conditions change.

If some categories of organisms are natural kinds, however, it may take more to dislodge them from their type-identity than the variations described. In analogy to an example from the physical sciences (mentioned above) in which the designation of natural kind is less controversial, a chemical element can tolerate some changes (i.e., incorporation of neutrons in its nucleus) without changing its type-identity, but not others (i.e., incorporation of additional protons). Some elements are indeed more stable with neutrons present than without them, making the "variant" more survivable. This does not negate the decisive role of protons (in contrast to neutrons) in defining the element's intrinsic nature, or essence (Ellis, 2001).

All animal species may have "neutron equivalents" (the egg patterning processes in fish, described above, for example, or the hunchback-nanos interaction during *Drosophila* embryogenesis) that may be necessary for their survival, but not in defining their identity, particularly their identity as animals or their membership in a given phylum. It would take much

more (the loss of one or more metazoan- or phylum-defining morphogenetic toolkit genes) to alter the type-identity of an organism of animal origin. Tunicates are a famous example of animals that lose the characteristic morphological signatures of their chordate phylum as adults. But tunicates still pass through a larval stage that exhibits characteristic chordate motifs such as an elongated body and notochord. The alchemy of true phylotypic transmutation has yet to be documented.

The evolutionary "rewiring" of gene regulatory networks shows that genetic change in a phylum's member organisms can be dramatic without converting their anatomies into non-canonical forms or even blurring the phylotype's boundaries. This phenomenon, termed "developmental system drift" (True and Haag, 2001, Haag, 2014) has been studied in several metazoan phyla, with the finding that structures that were established early in evolution, such as the neural tube (Harrington et al., 2009) and segments of vertebrates (Stern and Piatkowska, 2015), or the body plan and vulva of nematodes (True and Haag, 2001), can be induced and regulated by different sets of genes in different species. At the core of these divergent developmental mechanisms, however, are the products of the metazoan morphogenetic toolkit – classical cadherins, catenins, Wnt, type IV collagen, and few others.

While the stated conclusion that "gene regulatory networks are constantly being reconfigured even when phenotypes are not" (Haag, 2014) well describes developmental system drift, its explanation requires recognition of the autonomization of phylotypic anatomy over evolution (Müller and Newman, 1999, Newman, 2019a). Animals have inherent forms which are due to their origins as extracellular matrix-enhanced liquid-tissue parcels (Newman, 2019b). The stereotypical generation (based on their unique material properties), and subsequent integration and autonomization (based on evolved consolidating and rectifying mechanisms) of the phylotypes, make them resistant to reshaping.[2]

This still leaves plenty of room for genetic variation within the confines of a phylum. This can take form of novel alleles, or entirely novel gene segments or whole genes, or gene deletions, uniquely associated with subphylum clades, including species and individuals. A famous intraphylum elaboration is the tetrapod limb, termed an anatomical "archetype" by Charles

Darwin's contemporary and rival Richard Owen (Owen, 1849). Although it appears in only a subset of species of jawed vertebrates, its basic plan is incredibly stable over evolution, as even Darwin himself had to acknowledge ("similar bones in the same relative positions"; Darwin (1872), 382) despite his own theory pointing away from morphological stasis.

The tolerance of organisms to genetic variability without losing their phylotypic identities is also manifested at the species level, where a given gene might not have the same role in different conspecific individuals. In humans, for example, most alleles that have classically been considered disabling, or even fatal, have surprisingly been found to be consistent with health in individuals from different reference populations from those in which they were first identified. On average, a human individual has 54 mutations that, based on long-standing population studies are predicted to "sicken or even kill their bearer" but do not (Check Hayden, 2016). A recent study of a cohort of Pakistani descent in London identified a woman with a nonfunctional PRDM9 gene, the product of which is essential in defining the typical recombination hotspots during meiosis. Surprisingly, she was fertile (unlike mice that lack this gene) and had a healthy child, but the meiotic crossovers inferred from the two genomes were atypical, suggesting compensation by an unknown, alternative mechanism, employing gene products that normally have other roles (Narasimhan et al., 2016). Much recent work of this sort suggests that each individual organism, despite being a member of a hierarchy of groups, is developmentally unprecedented, utilizing the genes it shares with its conspecifics in its own distinctive way.

## 7. Conclusions

The physico-genetic view of animal origins asserts that large-scale, macroevolutionary distinctions among organismal types did not originate through microevolutionary changes, but in the novel morphogenetic capacities of new kinds of biomaterials (Newman, 2016a). It is clear that the ability to draw energy from the environment, to persist, and to grow, appeared during the evolution of unicellular life, and the thousands of genes necessary for these processes were in place millions of years before the emergence of the animals. But the liquid tissues that constituted the most primitive of these organisms and their diploblastic and triploblastic descendents were not simply clusters of preexisiting cells. Moreover, natural selection of allelic

variants of the genes of unicellular ancestors had little role in the macroevolutionary steps that produced the animals. Their origination depended on the appearance of genes with no counterparts outside of the metazoans: classical cadherins, catenins, Wnt, Stb/Vang, type IV collagen, peroxidasin, fibronectin, and a handful of others. The respective protein products, in the context of multicellularity, mobilized mesoscale physical forces that were previously irrelevant to individual cells or their aggregates (Newman, 2016b).

In ontological terms, the new materials that came to constitute the developing tissues of animals were *substances*, in the sense of being particular kinds of matter, but unlike nonliving liquids and liquid crystals, they were also *processes* (Dupré, 2018). Composed of cells, they must metabolize and biosynthesize, consume energy and emit waste, in order to maintain their decisive material natures. Their capacity to manifest physically predictable behaviors is thus intrinsically tied to their living activities: they are "biogeneric" substances (Newman 2016a).

While it continues to be claimed that natural selection is "the only explanation we have for the appearance of design without a designer" (Levin et al., 2017), the theory of emergence of animal form presented here does not appeal to selection or increased fitness. Insofar as motifs such as body cavities, segments, or appendages have proved adaptive, there is no reason (since an independent expalation for their generation is now available) to reject the notion that fitness to the environment can be "after the fact" (West-Eberhard, 2005) Novel combinations of intrinsically generated motifs may not be optimal for survival in the venue where they originated, but living organisms typically exhibit ingenuity and are not locked into preordained niches (Lewontin and Levins, 1997). This undermines the Darwinian expectation (presumed to be the motor of evolution) that a multicellular form would disappear simply because a variant in its originating population did things a little bit better.

The notion of biological natural kinds implied by the physico-genetic picture entails the metaphysical stance that Devitt terms "intrinsic essentialism." (Devitt, 2008) Biological essentialism is often seen as a remnant of pre-Darwinian typological thinking (Mayr, 1982). According to the modern synthesis, all organismal types are potentially mutable and the boundaries between all categories are permeable. Since microevolution, the driving force of

natural selection in the Darwinian theory, is a species-level phenomenon, it is unsurprising that the debate in the philosophy of biology over essentialism and natural kinds has centered on the ontological status of species (Dupré, 2014, Okasha, 2002, Wilson et al., 2007, Devitt, 2010, Lewens, 2012). It is equally unsurprising that there is little consensus on what differences between the organisms of sister species, or between individuals within a species, could stamp them as distinct types.

While similarly "intrinsic-essentialist," the view I have put forward differs from that of Devitt (2008, 2010) in that it rejects an exclusively gene-centric notion of intrinsic identity of organismal categories, focusing rather on the material properties of animal tissues (which have, of course, a genetic dimension) (Newman, 2016a). (Analogous arguments can be made with respect to multicellular plants; see Benítez et al. (2018).) Reframing morphological evolution outside the assumptions of neo-Darwinism means that the level at which essential properties enter the picture is not that of species. A focus on the essential properties of the kingdom, superphylum and phylum ranks of the taxonomic hierarchy is consistent with a shift in perspective from the microevolution-first one of Darwinism to a macroevolution-first one.

John Dupré (2002) has presented 5 criteria that need to be satisfied for something to be considered a natural kind in the classical sense: 1. Membership of the kind is determined by possession of an essential property or properties; 2. Members of a natural kind are the appropriate subjects of scientific laws; 3. The properties or behavior of the members of a natural kind can be explained by identifying the kind to which it belongs, and referring to the kind's governing laws; 4. The conformity of the kind's members to its governing laws of nature is due to an essential property or properties; 5. If a thing belongs to more than one natural kind it must be the case that the kinds to which it belongs are part of a hierarchy in which lower level members are wholly included in higher level members. Dupré marshals this set of stipulations to argue that biological species, or relatively more inclusive taxa, are not natural kinds in this sense, an argument I find compelling. But the higher-level category of metazoan organisms as a whole, and for example, the subcategory of diploblasts, described above, with the essential properties being, respectively, the liquid-tissue state and the liquid-crystalline-tissue state, satisfy criteria 1-5 above, as do some triploblastic categories derivative of the diploblasts.

The collection of inherent morphological motifs associated with the properties of liquid tissues are not themselves animal bodies. But by providing animal-specific building blocks and structural elements beyond mere genes or gene regulatory networks they both underlie and promote the evolution of characteristic bauplans. Within the confines of phylotypic identity, which would not be breached other than by loss of a phylum's defining material properties (dependent on the described toolkit genes and the physics they mobilize in the multicellular context), subtypes (not all of them natural kinds) can be elaborated, consolidated and intensified, down to the level of the individual organism. This "intensification of uniqueness" (Newman, 1995), rather than the open-ended production of overt difference predicted by the Darwinian model, may thus be the characteristic mode of animal evolution once it has moved past its initial constitution as a hierarchy of novel biological materials.

Lenny Moss and I have suggested that a flexible appropriation of Immanuel Kant's "methodology of teleology," updated in light of developments in the biological and physical sciences in the nearly two and a half centuries since the *Critique of Judgement* (1790) was published, can inform philosophical approaches to the nature of multicellular organisms (Moss and Newman 2015). In this perspective the Kantian "organized being" is an evolutionary product. Thus, there is hypothesized to have been a period during which the mesoscale physics and self-organizational dynamics of liquid and liquid-crystalline tissues inevitably caused primitive ancestral metazoans to become multilayered, segmented and otherwise patterned. Following this, as a result of stabilizing and rectifying mechanisms such as those afforded by bioelectrical integration and egg-dependent clonality and pattern standardization described above, the prototypical animal bodies evolved into modern, stable organismal "types" with canalized taxon-specific developmental programs that generate biological individuals. Thus, while we are very far from Kant's own terms of reference, the coinage of "natural purpose" for entities that are both the causes and effects of themselves seems an appropriate characterization of animal identity.

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[1] Individual cells are not liquids (notwithstanding the viscous nature of cytosol), nor are arbitrary clusters of unicellular organisms. Cells themselves have fibrous submembrane cortices and their shapes and movements are subject to mechanical forces rather than fluid flow. Clusters and aggregates of cells will only flow as liquids if there is no constraint on their entering or leaving the surface of the tissue mass to minimize its free energy. For this to occur, their cellular subunits must be able to move randomly without losing contact with one another. These requirements make the liquid tissue state exceptionally rare.

[2] Not all the accepted (i.e., based on both genetic and body plan affinity) phyla show the same degree of body-plan stereotypy. Nematodes, with very similar anatomies represent one extreme, whereas mollusks (snails, clams, octopuses) represent another.