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Leibnizian Organisms, Nested Individuals, and Units of *Selection*

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Summary: Leibniz developed a new notion of individuality, according to which individuals are nested one within another, thereby abandoning the Aristotelian formula at the heart of substantialist metaphysics, 'one body, one substance'. On this model, the level of individuality is determined by the degree of activity, and partly defined by its relations with other individuals. In this article, we show the importance of this new notion of individuality for some persisting questions in theoretical biology. Many evolutionary theorists presuppose a model of individuality that will eventually reduce to spatiotemporal mechanisms, and some still look for an exclusive level or function to determine a unit of selection. In recent years, a number of alternatives to these exclusive approaches have emereged, and no consensus can be foreseen. It is for this reason that we propose the model of nested individuals. This model supports pluralistic multi-level selection and rejects an exclusive level or function for a unit of selection. Since activity is essential to the unity of an individual, this model focuses on integrating processes of interaction and replication instead of choosing between them. In addition, the model of nested individuals may also be seen as a distinct perspective among the various alternative models for the unit of selection. This model stresses activity and pluralism: it accepts simultaneuous co-existence of individuals at different levels, nested one within the other. Our aim in this article is to show how a chapter of the history of metaphysics may be fruitfully brought to bear on the current debate over the unit of selection in evolutionary biology.

1. **Iiltroductiot1**

As David Hull writes, "[T]he first thing a biologist does in arguing that an entity can or cannot function as a unit of selection is to argue that it is or is not an individual." (Hull 1980, 314). In this article, we hope to illuminate some interesting aspects of the concept of unit of selection by looking

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at it In relation to one of the richer and more subtle theories of individuality put forth in the history of modern philosophy, namely, G. W. Leibniz's theory, articulated in the latter half of the 17th century, of what we will be calling 'nested individuality'. According to Leibniz, full individuals may at the same time function as subordinate constituents of larger individuals. For *Leibniz there is* no difficulty in conceding the reality of *Levels of individuality.* This aspect of Leibniz's theory contrasts sharply with the tendency, till evident among many who are involved in the debate concerning the unit of selection, to search for *the* unique level - be it the gene, the organism, the group, the species, the ecosystem, etc. - at which the true individual may be said to reside. Some involved in the debate concerning the unit of selection do recognize levels of individuality though most remain committed to finding *the exclusive* function - be it in replication or interaction - of a unit of selection. However, Leibniz's pluralistic theory of individuality is consistent with a number of recent non-exclusivist approaches to the unit of selection. This model supports a pluralistic multilevel selection and rejects an exclusive level or function for a unit of selection. We shall suggest that Leibniz's model of nested individuals may help to clarify some of the philosophical presuppositions of these new approaches.

In the first part of this paper, we will outline the historical background to Leibniz's theory of nested individuality. As we will suggest, Leibniz's theory may be seen, in large part, as an effort to accommodate the recent discovery of the ubiquity of microorganisms, and of their apparent constitutive function in the bodies of larger organisms. This discovery, we will argue, was to have tremendous implications for the metaphysics of substance (in terms of which the concept of individuality was still understood by many in Leibniz's day), and Leibniz was perhaps the only thinker of the era to recognize these implications and to respond to them with a sophisticated and novel model of *individuality. Further, we will contrast* Leibniz's conception of biological individuality with that of Denis Diderot, perhaps the most prominent representative of the materialistic monism that would come to dominate in the 18th century, and that remains, in some form, dominant to this day. In the second section, we will present a reconstruction of Leibniz's model. We *will show that* Leibniz's notion of nested individuality is rooted in agency, and that it is irreducible to any extended, physical or material notion of substance. Finally, in the third section, we will apply this notion of nested individuality to the contemporary debate concerning the unit of selection.

We stress at the outset that our effort to apply a theory from the history of philosophy to a problem in the contemporary philosophy of biology can only be a very tentative one. It is neither our intention *just* to explicate Leibniz, nor to join the debate about units of selection in the usual, historical manner. The contemporary philosophical climate encourages

its participants to do one or the other. We believe that, in this case, contemporary philosophy of biology really does have something to learn from its history, and in order to show this we will have to go into some historical detail.

2. Leibniz's Theory of Nested Individuals in its Historical Context

Let us suppose that all individuals are corporeal. Any such individual has parts, and whatever consists in parts is divisible. The divisibility of an individual suggests, if only for *purely etymological* reasons, that the individual in question is not really one at all. Since whatever is divisible is a physically cohesive bit of matter, and, vice versa, any cohesive bit of matter is at least in principle divisible, philosophers throughout history have argued that inanimate portions of matter most definitely cannot be considered true individuals. There is an inherent vagueness to the identity of any entity that's thrown together from sundry parts; rocks and tables, like heaps and balding heads, fall victim to *sorites* paradoxes. But if physical cohesion is the only criterion of individuation we can find for each of the two halves of a split chunk of organic matter, oughtn't we then conclude they are on a par with rocks and tables and that each of the two halves aren't really individuals at all?

Until some time in the 18th century, the individuality of animals and plants was often explained by appeal to souls, or substantial forms, or some sort of incorporeal spiritual principle, uniting the matter that made them up and making each of them one, real substance. In Aristotle's view, the substantial form just is the soul of the animal or plant. In the Scholastic-Aristotelian tradition, a substance is understood to be a compound of matter with a substantial form, an incorporeal soul or soul-like principle making some parcel of matter the thing that it is rather than something else.

To a great extent, it was progress in empirical life science that brought about the banishment of incorporeal spiritual principles from accounts of what makes individual biological entities true individuals. In particular, it was (i) the gradual awareness that developed in the 17th century of mutual-istic symbiosis, that is, of the cohabitation of multiple individuals in what had, prior to the development of microscopy, been taken to be the body of one substantial individual; and (ii) research on parthenogenesis in freshwater polyps and earthworms, carried out in the 1740s by Abraham Trembley and Charles Bonnet, and radically interpreted by thinkers such as Diderot, that led to the most extreme formulation of the denial of biological individuals in the 1770s and 1780s. The discovery of parthenogenesis strongly suggested that biological entities are in fact no better individuated than ordinary, inanimate physical objects.

It is fair to say that before the development of microscopy in the 17th century only parasitic cases of cohabitation of multiple organisms in one body were known and discussed. Parasitism is a close relationship between two organisms, *usually* of different species, in which one benefits and the other is harmed; one's increased benefits correlate with the other's reduced benefits. On Aristotle's view, for instance, the presence of a worm in another animal body never bodes well. In the *History of Animals* (611 b) he mentions dogs driven by the insatiable hunger intestinal para*sites cause* to eat the *standing corn,* thereby inconveniencing the humans who would have eaten it, and fish in which "an intestinal worm, which develops in them at the time of the dog-star, makes them surface and weakens them; and having come to the surface they are destroyed by the heat (602 b)". He also describes the misfortunes of worm-ridden sponges (548 b).

Besides Aristotle, many authors of ancient medical texts devote a great deal of attention to the causes and treatment of *sickness* due to intestinal and other parasites. Alexander of Trills, for instance, a 6th-century Byzantine physician, writes that "[t]he wide worms ultimately reach such a size that they extend throughout the entire intestine... They grow when food enters and the undigested juices turn into rottenness." Alexander recommends taking attar of roses, in order to kill the worms and "purge them through the stool, reawakening the lost and weakened appetite." He warns against trying to starve the parasites to death, since "often, out of a shortage of food", "the worms eat right through the entrails, so that they can be seen to come through the skin" (p. 1878-79).

In the 17th century, for the first time, the idea began to circulate that smal*ler* organisms in the body of a *larger one are not just* inhabitants, but indeed constituents of the body in which they were found[1]. For a theorist sympathetic to this view, such as Leibniz, and at the same time committed to a metaphysics in which living beings are substances, it thus became necessary to conceive of substances as composed out of other substances. Leibniz strove to accommodate ideas from a number of different sources - scientific, philosophical, mystical - within his own system, indeed to to show how all of these ideas are in fact harmonious with one another. It is this effort that has earned him the label “conciliatory eclectic", current among scholars of Leibniz's thought. Thus, while there is no question that Leibniz was keen to accommodate the discoveries of the microscopists within his philosophical thought, it is important to bear in mind that this thought was the result of a variety of disparate interests. Important among

[1] There were other thinkers in Leibniz's period to develop theories of nested individuality independently of Leibniz, such as the Italian microscopist Malpighi. What is significant about Leibniz's theory is its metaphysical sophistication, its ability to deal with the implications for the long and venerable history of the concept of substantial individuality. For more on Mal-pighi's theory, see *Franfois Duchesneau, Lee modules dN uiuaNt de Descartes k Leibniz.*

these interests were the question concerning the infinite divisibility of matter and the problem of the mathematical continuum.
While we do not have time to discuss these concerns in any detail, some mention of Leibniz's most important conclusions is in order. Though he may initially have hoped to find some fruitful application of the infinitesimal calculus to the study of the composition of material entities, early on Leibniz became convinced that there is a fundamental difference between material, extended entities, on the one hand, and mathematical extension on the other. Namely, while a mathematical entity, such as a geometrical line or the set of real numbers, is merely ideal, bodies are real; for this reason, while mathematical entities have the property of being divisible at any arbitrarily chosen point, physical entities are, much more strongly% already actually infinitely divided. Being so divided, physical bodies are not continua, analogous to geometrical lines, but rather are collections or ensembles of units, analogous to sets of points. While, to be sure, a "worm" is not a point, it is at least, from the point of view of someone committed to a sub-stantialist metaphysics in which the worm itself is identified with the worm-soul, like a point in so far as it is absolutely discrete and unitary.
Leibniz writes to De Volder in June, 1699:

> [Y]ou ask further if an animate body has its own entelechies distinct from the soul. I reply that it has innumerable such entelechies, since it consists in turn of parts each of which is animated[2].

In correspondence with Bartholomaeus Des Bosses, Leibniz often makes explicit the nature of the substances making up the organic bodies of larger substances:

> mot, [l. e.1 Des Bosses3 ask (for example) whether the soul of a worm existing in the body of a human is a substantial part of the human body, or whether it is rather a bare requisite, and that not by metaphysical necessity but only because it is required in the course of nature[3].

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[2] G II 184. "[Q3uaeris an corpus animatum habeat proprias entelechias ab anima distinctas. Respondeo habere innumerabiles, cum rursus constet ex partibus privatim animatis". For references to the works of Leibniz we will be using the following abbreviations. References to Leibniz's writings beginning with a Roman numeral are to *Lei~niz: S~mtliche Schriften and Briefe.* ed. Deutsche Akademie der Wissenschaften (Darmstadt and Leipzig, 1923 present); AG = G. IE *Lei~niz: Philosophical Essays.* Ed. And tr. Roger Ariew and Daniel Garber (Indianapolis: Hackett, 1989); G=*Die Philosophischen Schriften won* G. IE *LeiSniz. e*d. C. I. Gerhardt. 7 volumes (Berlin, 1849-1860); GM = G. VX *Lei~niz: Mathematische Schriften.* ed. C. I. Gerhardt. 7 volumes (Halle: Schmidt, 1849-1863); L = *Gottfried Wilhelm Leibniz: Philosophical Papers and Letters. ed.* and tr. Leroy E. Loemker (Dordrecht: Reidel, 1969); Theodicy = *Essais de theodicie: sur l" bonti de Die", la liberal de l'homme, et l'origine d" mal (Paris:* Garnier-Flammarion, 1969); WBG = *Leihniz: Werke* (Darmstadt: Wissenschaft-liche Buchgesellschaft, 1959-1992).

[3] (- II 475 "[Q3uaeritur (exempli causa) an anima vermis in corpore hominis existentis sit pars substantiali humani corporis, an vero nudum requisitum et quidem non metaphysicae necessi-tatis, sed quod in cursu solum naturae requiratur".

Leibniz's response to the question he has attributed to Des Bosses is that the worm is indeed a substantial part of the human body and moreover at the same time it is itself a substance, i. e., a dominant monad with an organic body:[4]

> Some worm can be a part of my body and be subject to my dominant monad, and the same worm can have other animalcules in its body subject to its dominant monad.[5]

Leibniz writes to Arnauld, similarly, that the human

> is a being endowed with a true unity given him by his soul, in spite of the fact that the mass of his body is divided into organs, ducts, humors, and spirits and that these parts are undoubtedly filled with an infinity of other corporeal substances endowed with their own Entelechies.[6]

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[4] * François Duchesneau, in personal correspondence, has offered some very helpful comments on this paper, as well as some criticism of our version of Leibniz's model of corporeal substance. Duchesneau has been concerned to point out that machines, even organic machines, are not individuals, and that the notion of *emSoitement is a* strictly mechanical one. We agree that the bodily component of a corporeal substance, taken by itself, is strictly a machinic aggregate and not an individual. But the reason why Leibniz speaks of the *corps pris ~ part is* precisely in order to distinguish this from the *corps as* the bodily aspecl of a corporeal substance. As Glenn Hartz has quipped (see his "Why Corporeal Substances Keep popping Up in Leibniz's Later Philosophy", *British foNrnal for the History of Philosophy G* (2), 1998, pp. 192-297), surely Leibniz would not, could not, speak of corporeal substance without wishing to suggest that *corps* are substantial, at least when considered not j *part,* but as the bodies made one by the inherence of a dominant monad. Considered in itself, the organism or bodily component of a composite substance is indeed an aggregate on an ontological par with a pile of sawdust. Even though there *is never an* organism without *some incoporeal* spiritual principle uniting it, the organism can at least be conceived as something distinct from its incorporeal principle of unity. In this sense, Leibniz's concept of organicity does not concern the entire corporeal substance, as some commentators have assumed, but only its bodily component. With respect to its bodily or organic component, a corporeal substance is, like any other aggregate, the sort of thing that can be explained by appeal to mechanism alone. Duchesneau worries, further, that we are confusing the constitution of all of nature out of living organisms, with the claim that this constitution renders what would otherwise be mere aggregates full individuals. He writes: "La partie est un 6tang qui contient des poissons, mais peut-on dire que les poissons sons Dee parties de l'Etang, comme on peut parler de parties articulEes dans une machine?" We respond that the fish (and fishlike creatures) constitute the pond; so yes, they are its real parts, even though they are not articulated like the parts of an organized machine (the pond, unlike an organism, does not have articulated parts). But the organism as well *can* be analyzed down to constituent parts that constitute it in the same way that the fish constitute the pond. This claim sounds like it would contradict Leibniz's definition of the organism as that which remains machinic in its least parts. But the key thing is that Leibniz thinks the pond, as well as the organism, and as well as any other randomly chosen section of nature, is organic in this way, even though the pond does not itself as a whole constitute one organism. Thus, when Duchesneau continues that "L'Etang n'est pas de route fa~on un individu," we may respond, "of course it isn't, but that in no way damages our claim".

[5] G II 451. "Vermis aliquis potest esse part corporis mei, et sub mea monade dominance, qui idem alla animalcula in corpore suo habere potest sub sua monade dominante".

[6] L 529 "[L],homme est un estre douE d'une veritable unitE, que son ame luy donne, non obstant que la masse de son corps est divisEe en organes, vases, humeurs, esprits; et que les par ties sont pleines sans douse d'une infinitb d'autres substances corporelles douses de leur propres Enrelechies."

Leibniz's account of the composition of corporeal substances takes on a more explicitly biological character as his career progresses. As he writes in the *Entretien de Philarete et d'Ariste of* 1711:

> What does it matter if the worm that gnaws at me is within me or outside of me? Am I any the less dependent upon it? Only incorporeal substances are created independent of every other created substance.[7]

Why does Leibniz, in his later writings, begin speaking of the constitutive elements of composite substances as “worms"? Is this language merely figurative?[8] Even if Leibniz's talk of “worms" is just a figure of speech, it is a figure that at least requires a particular historical context in order to be comprehensible as such; had Aristotle spoken of his dependence on the worms inside of him, he would not have been understood as employing a vivid, somewhat gruesome figure in the aim of making a point that did not really have anything to do with worms. He simply would not have been understood. With that said, it is resonable to suggest that these are not figures of speech in Leibniz, but that they are literal.

Premodern medicine had been inclined to treat biological individuals within or upon other biological individuals as invaders. Analogously to the ancient medical position on symbiosis, we might say that Premodern philosophy adhered to the formula: one body, one animal. For thinkers such as Aristotle, who take animals to be paradigmatic substances, the formula becomes: *one Sod~, one substance.* Indeed, it would seem difficult to remain committed to a metaphysics of substance without at the same time accepting the ancient formula.

Leibniz, while striving to retain a metaphysics of substance, saw the incompatibility of the ancient formula with the biological evidence of his time, and chose to reject the former rather than the latter. Recognizing the multitude of factors influencing any given domain of early modern philosophy, it seems reasonable to suggest that the 17th century was compelled to rethink the philosophical problem of the concept of substance in part as a result of the epoch's microscopic discoveries of the presence of microorganisms within the bodies of macro organisms. When reproduction by budding came to the center of scientific attention toward the middle of the

[7] 'G VI 586. "Qu'imporre si le ver qui me ronge est dans moy, ou hors de moy? En serois je moins dependent? Les seules substances incorporelles sont independantes de souse autre substance criie".

[8] It was common in Leibniz's era to use the terms we today translate as "worm" (Latin "vermiculus", "vermis", French "ver") to refer to any kind of small, legless creature. While we should not be taking Leibniz to be referring to what we today would identify as worms, it is important to note that his use of this term gives some indication of the surprisingness of the discovery made by the microscopists in his time that, apparently, the basic constituents of the living world are ar least like worms to the extent that they are alive, self-contained, and relatively simple and unarticulated.

18th century~ the old formula, “one body one substance", would be decidedly lost to the scrap heap of history; indeed, the concept of substance itself would be lost, and a vague spatiotemporal 'individual' accepted as in- evatible. And so it remains to this day.

Diderot explains in his *Elements de physiologie of* 1784 that life consists in nothing more than an arrangement of organs. In so far as the organs can be separated from one another and, in some cases, continue living, what: ever there is in the animal that might be called a “soul” is not indivisible. He asks, if “[l]ife remains in the organs separated from the body; where then is the soul? What becomes of its unity, its indivisibility (p. 56)?”,[9] In so far as ensouledness is nothing more, for Diderot, than the temporary capacity for motion and sensation, any division of an animal body that results in the deprivation of this capacity to one or both of the parts of the body constitutes an empirical demonstration of the possibility of the separation of the body from the soul. “A ligature of the nerves impedes all sensation, *all movement”' he* writes, “a ligature can thus *separate* the soul from the body" (p. 56).[10]

Whereas ligature is an example of the division of an animal that results in the termination of ensouledness, in his 1784 work Diderot sees all animal reproduction as consisting in nothing more than the division of one organ from another, as the passing on of life or ensouledness from one bit of living matter to another. This communication of life does not result in the coming into being of a new individual; for Diderot generation consists in the rearrangement of matter, and, eventually in the physical separation of this matter from the larger source matter. He explains that “[t]he generation of parts occurs little by little, and not suddenly, through the arrangement of parts, and not by development', (p. 56).[11]

While in an earlier treatise Diderot had joked about humans reproducing by parthenogenesis, he later comes to see sexual generation as literally nothing more than the separation of a quantity of living matter from another quantity. He writes that he is

> tempted to assimilate the generation of man to that of the polyp that reproduces by means of division. The union of the man and the woman only gives rise to the production or the development of a new organ, which is... a being resembling one of them.[12]

[9] Diderot, *Elements de physiologic.* p. 56. "La vie resee dans les organes separis du corps, oh l'ame est-elle alors? Que devient son uniti, son indivisibilit~".

[10] Diderot, *Elements de physiologic,* p. 56. "Une ligature sur les nerfs empeche tout sentiment, tout mouvement: une ligature peut done separer l'ame du corps".

[11] []iderot, *Elements de physiologic,* p. 56. "La generation des parties se fait peu i peu, et non

[12] []iderot, *Elements de physiologic,* 190f. "ue suis] tenth de ramener la generation de l'homme i celle du polipe qui se reproduit par division. L'approche de l'homme et de la *femme ne donne lieu* qdi la production ou au *developpement* d'un nouvel organe, qui est un etre semblable i l'un des deux”

For Diderot, it would make no sense to ask whether the amputated part would be a spatially disconnected part of the same biological entity, or whether it would be a new, different biological entity. Diderot's materialist conception of nature, on which there are no real individuals, only spatially discontiguous bits of living matter, might be seen as the logical, if extreme, conclusion of the denial of an intrinsic principle of activity as the source of individuality which, in the philosophical tradition stemming from Aristotle, had been adduced as a way of explaining how it is that some bit of matter is what it is rather than something else.

"Organism", for Diderot, is more a mass noun than a count noun. Moreover, at least in his 1784 work Diderot seems to see humans as of a kind with polyps with respect to their generation and their individuality. Given the importance of the interpretation of parthenogenesis in Diderot's philosophy of biology it would be reasonable to suggest that the discovery of reproduction by division, a phenomenon which Leibniz overlooked in his metaphysics of composite substance, played an important role in the ultimate disappearance of incorporeal, individuating principles of activity in the modern account of animals, and so also a role in the emergence of biology as a science.

For Leibniz, a corporeal substance consists in the union of a soul and an organic body. In so far as a finger is divisible from the organic body the bodily component of a corporeal substance is divisible. But, because the corporeal substance as a whole is not divided as a result of this amputation, because the amputation does not yield two physically separate instances of the same substance, nor does the rest of the body without the finger, cease to be the body of the individual of which it had been the body prior to the amputation, it would be incorrect in Leibniz's view to claim that the substance itself has been divided. As Robert Sleigh (1990) comments: “[D]ivisibility is not really the vital matter here; the vital matter is whether the particular entity in question can remain the same entity over time while undergoing change of components. Leibniz's claim amounts to this: given a substantial form suitably related to various components, we have a composite entity that can pass the test of remaining the same through change of components; absent the form, we do not" (p. 126).

For Leibniz, even if both halves of a bisected composite substance go on living, the corporeal substance itself has not been divided. It survives in only one of the halves, while the other half falls under the domination of a new, previously subordinate substantial form. Without germs or dominant monads, there is no question as to which half of a bisected worm or polyp (or human) remains the same creature that the whole had been prior to the bisection. On Diderot's interpretation of parthenogenesis, the whole prior to division was not really a whole at all, but rather, in Leibnizian terms, an aggregate.

On this view, the whole animal functions as one, but has no more real unity than a team whose members may quit at any time. When a member quits, for example, or when a fetus separates from its mother, or when a bit of a worm is cut off from the rest of the worm, there is no question for Diderot as to which bit of living matter retains the soul, for soul is for him nothing more than the capacity of matter for sensation and motion. The presence of soul in living matter does not elevate this matter to the status of substance, as it does in Leibniz's composite-substance metaphysics. There is for Diderot no basis in an incorporeal principle for determining to what substance some bit of living matter belongs. Thus, for him, there is no better answer to the question, "Which part of the bisected worm is the worm that was here prior to the bisection?" than to the question "Which chunk of the cleaved block of marble is the block of marble that was here prior to its cleavage?"

It might resonably be suggested that an important factor in the fate of the concept of substance was, not the limitedness of perception, but rather the expansion of perception into new realms that began in the early modern period. Thinkers such as Diderot did not feel themselves confined to a certain level of perception, beyond or beneath which lay the imperceptible substratum giving rise to what can be perceived. The 18th-century natural philosophers who benefited from the innovations of microscopy imagined themselves to be penetrating to the very depths of perceptibility, and, in penetrating to these depths in the organic bodies of living beings, found no adequate reasons there for sustaining an ontological difference between living beings and non-living things. At the same time as the scientific knowledge of the structural difference between organic individuals and inorganic collections began to rapidly *increase, the* philosophical commitment to an ontological difference between these entities, a distinction between the substantial and the phenomenal, came to rest on fairly infirm ground, and *spatiotemporal distinctness* was left as the only criterion of individuation - thereby rendering the individuality of the organism as philosophically questionable as the individuality of inanimate *objects has* long been thought to be. As Hull (1980) writes:

> Individuals are spatiotemporally localized entities that have reasonably sharp beginnings and endings in time... [i]t is only an accident of our relative size, longevity and perceptual acuity that we can see the distances between the organisms that comprise a species but not the even *greater rela*tive distances that separate the atoms that make up an organism (p. 31).

Having considered the historical context in which Leibniz's notion of individual substances developed, and which was then abandoned in the 18th century, we shall now focus our attention on fleshing out some aspects of Leibniz's notion of composite substance. In doing so we have a point: Leibniz's notion of individuality was not taken up by the rising

science we now call Biology and was basically ignored in the development of our current notion of biological individuality. It is time, we believe, that some aspects of his notion of individuality be retrieved for the sake of rethinking our current notion of biological individuality. We will attempt to do just this in the *concluding section.*

3. Leibniz's Model of Nested Individuals

For Leibniz, the world consists of individuals. All that there are in the world - living or not - are individual substances and their properties. Such individuals must be unique and have unity and identity over time. In this section, we focus on a stroking feature of Leibniz's model of individuality
- viz., its nested structure and some of the implications of this structure. For Leibniz, not only do individuals *contain* other individuals (as the bodies of animals includes worms or germs) but an individual typically consists of other individuals, organized in a hierarchical structure, nested *one* within another.
Leibniz's notion of nested individuality is nicely articulated in *Mouadology* 67-70, where he writes that:

> ... there is a world of creatures, of living beings, of animals, of entele-chies, of souls in the least part of matter. Each portion of matter can be conceived as a garden full of plants, and as a pond full of fish. But each branch of a plant, each limb of an animal, each drop of its humors, is still another such garden or pond.[13]
> ... Thus we see that each living body has a dominant entelechy, which in the animal is the soul; but the limbs of this living body are full of other living beings, plants, animals, each of which also has its entelechy or its dominant sou1.[14]

This structure of nested individuals, however, must have substantial unity, i. e., it must be united as one substance. As Leibniz writes to De *Volder* (AG 175):

> Although I said that a substance, even though corporeal, contains an infinity of machines, at the some time, I think that we must add that a substance constitutes one machine composed of them, and furthermore, that it is activated by one entelechy, without which there would be no principle of true unity in it.[15]

[13] 13 Thus there " thing fallow, sterile, or dead in the universe, no chaos and no confusion except in appearance, almost like it looks in a pond at a distance, where we might see the confused and, so to *speak,* teeming motion of the fish in the pond, without discerning the fish
Themselves". *(Monadology,* 69)

[14] *Monadology, 66, 67,* 70.

[15] see also his letter to Bernoulli, AG 167

As opposed to man-made machines, a machine of nature, for Leibniz, entails an infinity of machines which form a single unit. This very distinction seems to indicate that there is an intrinsic connection between Leibniz's notion of organic unity and this unity's nested structure. The unity of a composed substance derives from a single source of activity its entelechy, which is also its source of unity.[16] Thus a single and dominating *entelechy is* supposed to activate and dominate a hierarchy of individuals nested in it.
Leibniz's model of nested individuality may be presented more fully as including (at least) the following commitments:

1. An individual substance is Aristotelian in the *sense* that it is a hylo-morphic union of an active entelechy (or substantial form) animating and organizing its organic body;[17]
2. An individual substance requires true unity;
3. Organic, living unities (animals and plants) are paradigmatic examples of such substantial unity, and are distinguished from aggregates, such as rocks, lakes, flocks and armies;
4. Animals and plants are individual substances which are composed of other such animals (or organic unities) nested in them;
5. The animals entailed in an individual substance are themselves complete individual substances which have similar structure; they are not mere "parts of the substance but are immediately required for it" (AG 177);[18]
6. The structure of nested individual substances involves a hierarchy of dominating and dominated substances; which is not accidental (as the example of worms noted above may suggest) but is constitutive of the nature of living individuals.

These commitments, taken togethe4 suggest a fascinating model of individuality. As Ishiguro (1998) notes a... at every level there are organisms with unity and we can still proceed another level down, "d iufiuit"m. It is a claim about the chain of dominant or unity-giving substances at every level. It is this stratified structure, the successive embedding of organisms within each organism that is insightful" (p. 550).
Since, for Leibniz, a corporeal substance is a stratified structure of infinitely many *substances, his model suggests a radical* break from the tradi-

[16] Unity is *also required* in order to distinguish a true corporeal (i. e., composed) substance from a mere *aggregate.*
[17] leibniz writes that "no entelechy ever lacks an organic body" (AG 176; see also AG 171

[18] "if you t 'be mass *(masse)* to be an aggregate containing many substances, you can, how
ever, conceive in it one substance that is preeminent, that is, one substance animated', by a primary entelechy. Furthermore, along with the entelechy, I don't put anything into the monad or the complete simple substance, but the primitive passive force, a force corresponding to *[relates a~]* the whole mass *[massa]* of the organic body. The remaining subordinate monads placed in the organs don't constitute a part of the substance, but yet they are immediately required for it, and they come together with the primary monad in a corporeal substance, that is, in an animal or plant" (AG 177).

tional formula identified in the previous section, 'cone body, one substance". Such a break has a price, though. Leibniz's model is in tension with some deeply rooted intuitions about individuality that are still alive today. In addition to the counterintuitive claim that many substances are entailed in one organism, the notion of nested individuals seems to conflict with Aristotle's logical and grammatical characterization of an individual substance as that which is "neither said of a subject nor in a subject".[19] *Aristotle's formulation of* what is essential to individuals remains extremely influential, for it provides not merely an articulation of our common intuitions about individuality but also underlies some of our scientific and *logical* notions concerning individuality. for example, in *classical* first-order logic, individuals are defined as saturated, while predicates are to be completed, so that an individual cannot take the predicate place in propositions. In other words, individuals cannot be instantiated; rather, individuals are always unique, and universal predicates are instantiated in them. This is why *Fa* and *FS* are well-formed formulas and a~ is not. In first-order logic there is a structural asymmetry between the notion of individual and the notion of a predicate, which corresponds to the Aristotelian view that an individual cannot be attributed to other individuals.

Similarly, in the case of our current notion of biological individuality, we tend to identify *biological individuals* with multi-cellular organisms and thereby to exclude groups or parts of organisms as complete individuals. Both of the extreme cases of genes and groups - which have been proposed not only as biological individuals but also as units of selection - illustrate our intuitive response. It is hard to accept a group, say a bee-hive, as a single individual, precisely because it consists of many organisms, bees, notwithstanding the fact that they can *only multiply as a* group. It is also hard to accept genes (or even genomes, Wimsatt 1980, 1981) as individuals because they are not independent of the organisms or individuals in which they are embeded. Thus both limit-cases seem indicative of our conceptual reluctance to attribute individuals to other individuals or to see individuals as nested in others.

In Leibniz's model, however, individuals function as constituents of other individuals. According to Leibniz's model, a component of my body may be seen as a complete individual and as a constituent of me. In using Insole's notion of entelechy, Leibniz clearly thought that his model of nested individuals is reconcilable with the Aristotelian model of individual

[19] "A substance - that which is called a substance most strictly, primarily, and most of all - is that which is neither said of a subject nor in a subject, e. g., the individual man or the individual horse" (Aristotle, Categories 5 2a 11-13).

Although Aristotle's view has been *challenged seriously* by Ramsey on the grounds that the a-symmetry between predicates and subjects reflects mainly linguistic conventions (rather than ontological priority), it remains one of the most influential articulations of our common sense notion of an individual. See also Strawson's discussion of this point in his *Individuals.*

substance, and for this reason it is remarkable that he is not alarmed by the tension between his own view of nested individuals and Aristotle's criteria for individuality. Existing individuals are characterized by their inherent entelechy or inherent principle of activity, which also gives them their unity and *identity over* time. Leibniz holds that each component of an individual substance has its own *entelechy, while being* included in a body and *subordinated to* the entelechy of my substance. For example, a cell is not accidentally in me; it is a required constituent of me. Unlike some worms or viruses that may exist without a certain individual (and the individual without them), this is not the case in Leibniz's model, where the nestedness is constitutive of individuals.

Thus the *problem raised* here is more acute than the one often noted, that an individual substance is composed of many; this way of posing the question stresses that the composition of an individual substance has an inherent nested structure which is constitutive of every individual belonging to it. As Ishiguro (2001) recently put this, "if x is a constituent of body y, then it is necessarily a constituent of y" (p. 540). Thus, if a cell is a cell of me, then it is necessarily a cell of me. Taking into account the inherent nestedness of individuals might seem to make the claim that one individual substance is composed of many others nested in it even more puzzling, but, in fact, we think that this way of phrasing the question may open a way for better understanding the question of unity. For the nested structure (and not the mere plurality of substances) plays a role in the unity of organic beings.

Let us approach this question by asking what sort of unity and what sort of nestedness Leibniz has in mind. Thinking of unity, *we are* naturally inclined to think of material unity i. e., of parts holding together as one cohesive *spatiotemporal* unit. But this is *not* the sort of unity Leibniz has in mind. He states clearly that the substances contained in an animal are not parts of the substance; rather, they belong to the necessary structure of such a complex substance as requirements. According to Leibniz, the unity of a corporeal substance is a unity of agency, which derives from the single entelechy (or source of activity) animating and organizing its organic body. In turn, the organic body of a corporeal substance consists of the individual substances nested in it. This implies a hierarchy of dominating and dominated individuals nested one within the other.

Since the unity in question is not the unity of cohesiveness of parts but the unity of agency, that is, a unity that derives from activation or animation, Leibniz's stratified model of individuals requires the domination of an en-telechy over the whole organic body and the activation of subordinate en-telechies at every level. For *all* substances have such a structure. The structure of living things in general is stratified, such that a higher organism dominates (i. e., activates, suppresses, and organizes) the organisms nested in it.

As Leibniz writes in *Principles of Nature and Grace, Based on Reason,* see. 4:

> Each monad, together with a particular body makes up a living substance. Thus, there is not only life everywhere, joined to limbs or organs, but there are also infinite degrees of life in the monads, some dominating more or less over others (AG 208).

The stratified structure of dominating and dominated substances points to the sort of nestedness Leibniz has in mind. Here too, we are inclined to think primarily of spatial nestedness on the model of Russian dolls. Although we do not deny this sense of spatial nestedness, we'd like to point out that this is not the primary or most important sense of nested-ness Leibniz has in mind. For here too, the nestedness primarily derives from considerations of activity as opposed to passivity. A substance (S') is nested in another (S) in case it is dominated by it. That is to say, a substance is nested in another if it is activated and organized by it (and thus belongs to its organic body). This, we *suggest is* the primary *sense of "a* substance is included in another substance", or is a constituent or a requirement of or is nested in another substance. Since a substance is defined by its own source of activity S' is also active in the sense that it will activate another substance, call it S", nested in it. In turn, S" will activate S"', which will activate S"", and so on. Thus it is easy to see why Leibniz thought that the structure of nested individuals, based on activity goes to infinity.

This stratified structure of organisms is intrinsically connected to two other features of Leibniz's notion of individuality:

1. The inherent hierarchy of nested individuals is ordered by degrees of complexity and this degree of complexity corresponds to different levels of individuality. Although individuals are nested and thus dominated by other individuals, they are nevertheless complete individuals and not mere parts or organs of individuals. Note that 'levels of individuality' does not mean that some individual is more an individual than another. Rather, any x is either an individual or not. The question whether x is an individual is decided on considering whether x has its own source of activity (which is *also its* source of unity and identity overtime) *or not. The* notion of *'levels of* individuality' means that an individual may be more or less active. Since an individual is defined by means of an inner source of activity it may be both entailed in a "larger" individual, (i. e., be dominated by such individual) and maintain its own source of activity. In turn, it may also dominate other individuals nested in it. Thus the notion of levels of individuality seems to be captured mainly in terms of degrees of activity, which correspond to domination and organization.
2. It follows from the hierarchical structure that individuals are partly characterized through their relations to other individuals or through their

place in the hierarchy of individuals. Since the nested hierarchy is not accidental but essential to the individuality of each individual, the relations each one bears to the others are constitutive of it. This is not a trivial point. It implies that the very individuality of a substance is fixed through its place in the space constituted by other individuals and its relations with them.[20]

Leibniz holds a notion of individuality rooted in agency and non-reducible to an extended physical or material notion of substance. In Leibniz's model, nestedness, hierarchical structure from the simple to the complex, and *inter-individual relations* are *constitutive of* individuality. Individuality and unity are defined through activity and not primarily through spatio-temporal cohesiveness. Individuals such as animals or plants are constituted by a variety of other individuals which are activated and organized by a single source of activity and a single program of activity which is organizing and uniting them.

This model of individuality has two paticularly pertinent consequences. One is that it implies a plural notion of individuality, which recognizes different levels of individuality. The other is that in this model individuality and unity are defined through activity, not primarily through spatio-temporal cohesiveness. Some individuals, say an animal or plant, are constituted by a variety of other individuals which are activated and organized by a single source of activity and a single program of action.

In concluding this section, let us note that the notion of nestedness is not foreign to current biology; rather, it is almost a commonplace. What Leibniz's model may contribute to the current biological notion of nestedness is that the organs nested, such as cells may be seen as full individuals. In addition, an adequate description of such individuals requires some metaphysical concepts such as agency, unity, and a program of action. As we *shall* try to show in the next section, this notion of individuality may have some interesting bearing on current questions concerning biological individuality and units of selection. Lest there be any misunderstanding, let us state explicitly that the model we will be using in the next section differs significantly from the one held by Leibniz. Rather, we select only certain aspects of Leibniz's notion of individuality - mainly, nestedness, agency, and inter-individual relations - and do not borrow it in its entriety. For example, Leibniz could not have accepted anything like the evolutions of individuals. Nor did he accept any causal relations between individuals - both of which are fundamental to our current conception of biological individuality.

[20] This view has a corollary with Leibniz's notion of individuation through the complete concept of an individual. To be complete, the concept of an individual must include relations to other concepts (or relational predicates). Clearly, this is not the place to develop this interesting point.

4. Nested Individuals and the Debate **over** the Unit of Selection

Our point of departure in this section is that (as Hull noted) there is a strong relation between the question of what may count as units of selection in evolution theory and what may count as biological individuals. A ‘unit of selection' is noncontroversially defined by three criteria: phenotypic variance, fitness variance and heritability of characters relating to fitness (Lewontin 1970; Brandon 1999). A biological ‘individual' is defined *“as an* entity which is systematically the target of selection Oablonka 1994, p. 301)". This concept of individual is commonly applied to the well-known debates over the unit of selection.[21] In relation to the notion of a unit of selection, the model of nested individuals allows us to consider different levels of selection - e. g. cell, multicellular organism, group, species - and different functions of a unit - interaction and replication (Hull 1980[22])
- all at once. In that sense, the model of nested individuals is pluralistic rather than exclusive. In addition, this model characterizes the biological individual in terms of its activity, in that it calls specific attention to the mechanisms that activate or suppress the reproduction and inheritance of different levels of individuality rather than treating an individual as a passive meeting point for external selective forces.
Our model of nested individuals is consistent then with Maynard Smith and Szathmiry's (1995) Jablonka's (1994) Avital and Jablonka's (2000) and Michod's (1983, 1999) attempts to locate the specific mechanisms of evolutionary transition into a new level of individuality. An evolutionary transition occurs when a... entities that were capable of independent replication before the transition can replicate only as part of a larger whole after it.. ." (Maynard Smith and Szathmiry 1995, p. 6).

[21] 21The debates over the unit of selection involve three different questions: (1) which level - e. g. gene, organism, group - is selected during the evolution of a trait? In other words, which unit interacts with other units in a way that causes fitness variance, i. e. differential replication of the trait (Wilson 1983; Sober and Lewontin 1982; c. f. Dawkins 1982; Sterelny and Kitcher 1988); (2) To which unit is the selected trait attributed as an evolutionary adaptation? (Williams 1966; Brandon 1990; Maynard Smith 1987 a, b; Sober 1987 a, b; Okasha 2001). In other words, which unit - at past or present times - benefited from altruism and still shows heritability of the altruistic trait (Lloyd 1988, 1992; Gould and Lloyd 2000); and (3), how may have new levels of individuality evolved? In other words how did evolutionary transitions from groups of genes to chromosomes, from unicellular to multicellular organisms or from solitary to sociality, occur? (Buss 1987; Maynard Smith and Szathmiry 1995; Jablonka 1994; and Michod 1983, 1999). The notions of 'levels of selection' and 'levels of individuality', and, more generally, the notions of 'individual' and 'unit of selection'; are often used interchangeably throughout discussions in all three questions regarding the unit of selection.

[22] Xccording to Hull (1980) the definition of a unit of selection involves two different func tions. Either any unit that *interacts* with other units in a way that causes differential reproduction is a unit of selection, or only the unit that passes on its structure directly in *replication is a* unit of selection. Dawkins (1976, 1982) argues that only replication, and hence basically the gene, is relevant as a unit of selection; Wilson and Sober (1994) on the other hand, argue that only interaction, and hence multiple levels of organization, can be units of selection.

Maynard Smith and Szathmiryss notion of individuality is based, howeve4 on replication (1995, p. 8)[23] and on separation in space (p. 7)[24] rather than on activity of processes.[25] Although Maynard Smith and Szathmiry (1995) accept multiple levels of individuality their emphasis on replication and separateness in space actually restricts pluralism, since different levels of individuality cannot exist simultaneously. An example can clarify the difference between our approach and theirs.

According to the model of nested individuals, cells within a multi-cellular organism, such as hair cells on our skin, are a level of individuality that is currently partly suppressed. According to Maynard Smith and Szathmiry's *model, these hair cells are* now a part of the *multi-cellular* organism and may have once existed (but no longer exist) as unicellular individual organisms. Both *models look for the mechanisms that* maintain *the suppression of hair* cells - for each hair carries the same genome - but the nested-individuals model also focuses on the mechanisms that will allow activation of the hair cell. For example, long exposure to the sun could bring about a dramatic change of hair color. Transfer of a variant hair color - horizontal transmission in new hair cells as *well as vertical* transmission between parent and offspring exposed to sun - describes, on our model, an individual, not a dependent part.

Maynard Smith and Szathmiry's acceptance of a plurality of levels of individuality over time is clearly distinct from accepting an active, simultaneous, plurality of levels of individuality. However Falk's (1988) notion of a *biological individual allows species, organisms, cells etc., to be* considered as coexisting individuals one within the other. Falk (1988) provides an original and radical notion of individuality where endogenous viruses - somewhat similar to Leibniz's worms - are individuals and parts of individuals, depending on the specific trait being selected:

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[23] In their 1995 book, Maynard Smith and Szathmiry *preserve* replication, not interaction, as uniquely characterizing an individual. Since replication is relevant mostly to genes, we are left with a softer version of gene selection exclusivness (ibid. p. 8. see also Sterelny et al. 1996). In a later article Szathmiry and Maynard Smith (1997) support an alternative multi-level selection model by Griesemer (1999), but not its radical conclusions (Griesemer 2000 a). The centrality of spatiotemporal cohesiveness still precludes them from accepting nested individuals as a non-exclusive alternative

[24] "It might be asked why we do not include the origin of ecosystems in our list of transitions [from replicating molecules, chromosomes, up to social groups and language]... ecosystems are not individuals, separated from others, whereas the other stages we have listed (including sexual species and insect colonies) do have a degree of individuality, and separateness from other entities of the same kind. For this reason ecosystems cannot be units of selection" (Maynard Smith and Szathmiry's 1995, p. 7).

[25] the problem of evolutionary transition is to explain the evolutionary origin of new levels of spatial organization and to characterize how the generalized functions (replication, interaction) and capacities (opportunity for selection, heritability) described by Darwin's principles are implemented at those levels. The process perspective [an active addition to the spatial organization] can aid understanding of this problem" (Griesemer 2000 a, pp. 72-73).

> There is no need to adhere to Darwin's concept of the individual organism as necessarily the only individual of the theory of evolution by natural selection, i. e., as the only indivisible entity relevant to natural selection. It is not an asolutely ‘indivisible' entity, but rather a regulative one, that serves to rationalize the descriptive processes of nature and its organization into *law-like generalizations the individuals* whose phenotypes are selected in the course of evolution may be those of cells or their components, rather than the organisms. The identification of *the individuals* that are the entities in *evolution becomes meaningless. Once* we consider individuals to be regulative entities, endogenous viruses may be conceived not as just foreign organisms parasitizing on the cell, but as entities that in one context are individuals, the phenotype of which is selected, and in another context they are parts of another individual whose phenotype is the one selected (pp. 457-458. italics in original).

According to Falk (1988), designating an entity as an individual has a regulatory function of splitting the continuum of life into discontinuous entities we can conceive of and rationalize with. For Falk (1988 p. 457, 461-2), the regulative way we cut up the world into individuals is a context-dependent device to allow [scientific] discourse. Falk (1988) does not discuss the criteria for a *context-dependent individual - e. g.* activity, seperateness in space - or the criteria for a context-dependent class, but the implications of considering individuals as regulative entities. Falk's pluralistic approach to individuals directs biological research to the context of each individual, i. e., to explore the interaction between the individual's inherited genotype and its specific environment: the norm of reaction (Falk 2000, 2001). Here is an example of how a different conceptualization of the notion of individuality can make a heurisitc difference.
The conceptual framework offered by the new-synthesis maintained a strict dichotomy between inheritance and development, and thus implied a dichotomy between interactor and replicator. The replicator is the entity the structure of which *is directly passed* from *one generation to* another while the interactor is the entity that develops and interacts with other units in a way that causes differential replication (Hull 1980). One needed to choose whether replication or interaction characterize a biological individual. Later% concerning the debate over levels of selection, several alternative models to these dichotomies have emerged (e. g. Griesemer 1998, 2000 a, b[26];

[26] Griesemer (2000 a) explicates the innovation of integrating development and inheritance processes whithin a process-oriented perspective: "[in] Dawkins' gene's eye view replicators are rare and the subjects of a fundamental process while interactors are common, hierarchically organized subjects of a derivative process. I agrue for a more radical perspecive, in which replicators are viewed as a special class of reproducers whose development is deeply dependent on many higher levels of reproductive organization... [s]uch a hypothesis, in contrast to the replicator interpretation, would suggest that evolutionary transitions are not, or need not be, *mere* "point" transitions from independent replication to dependent replication within larger wholes. Rather, they may be extended processes with several potentially identifiable stages” (p. '7 italics in *original).*

Brandon 1990, 1999; Oyama 1985, 2000; Griffiths and Gray 1994 a, b, 1997). Each of these models provides unique and important insights into the notion of a unit of selection. Unfortunately we cannot describe them here in any detail. We can only stress what the~ broadly speaking, have in common, namely, a pluralistic approach to multi-level biological units as an active integration of different processes, which cannot be reduced to one level of organization or to one function. In all these models, a *combination of* replication and interaction characterizes the individual; and biological individuals - especially organisms - are not passive "point" entities whose fitness is determined by external selective pressure, but the dynamic interplay between individuals changes both the individual and its selective environment.

As we pointed out in the second section, non-exclusive pluralism, hierarchical dependence of various degrees of activity, and relation to other individuals, all constitute the notion of an individual in Leibniz's model of *nested individuals. According to the nested-individual* model, looking for a passive “atomic" individual, ignoring heirarchical organization, and asking which is *the* unit on which selection acts - the gene, the organism, the group etc. - or *the* function of such a unit - replication or interaction - all assume a simplistic and non-biological notion of individual. The model of nested individuals offers a broad historical and logical platform to highlight the agreement among different non-exclusive models, all revising the new-synthesis in different ways.

Since Diderot in the 18th century the notion of individual as consisting in spatiotemporal cohesion has been widely accepted. For the model of nested individuals, spatiotemporal cohesion may be a necessary but not a sufficient condition for individuality. We argued in the first section that Leibniz saw the spatiotemporal body - an aggregate of infinitely many parts, and the fully defined individual - an organizing and unifying principle of activity - as conceptually distinct. Biological research in the 18th century focused on the latter. As Griesemer (1999) pointed out, the current hierarchy of units of selection is a generalization of this traditional notion of organism. It now seems that the conceptual vagueness associated with Diderot's notion of individual as a purely material and mechanistic aggregate, pertains to all levels of selection as well. In response, philosophers of biology attempt to clarify the notion of individuality for all levels of selection (Wilson 1999)[27]; or focus on the organismic level and attempt

[27] In order to dissolve the ambiguity associated with the meaning of biological individuality, Wilson (1999) distinguishes different contexts of this question. He suggests different definitions of 'individual': a particular, historical entity, an entity sharing a common genotype, a functional unit, a product of a developmental process, an evolutionary unit. He argues that these defintions depend on the specific context of investigation. Wilson's project helps to clar-ify the various contexts of individuality, but, as a consequence, the unified individual is lost, both in the spatial sense and the causally interdependent sense. For example, monozygotic twins are treated as one (genetic) individual but two (developmental) individuals on this view. We think that this conceptual differentiation comes with a heavy price, for the unified individual which is more or less a presupposition for both scientific and everyday practice, is lost

to retrieve a dynamic notion of organism (see for example the special issue of “Theory in Biosciences" 2000: 'ccOrganism" - Historical and Philosophical Issues'[28]).
However, even if the current notion of individual is largly based on the 18th-century notion of organism as an aggregate of material mechanisms, this notion does not fully account for 20th-century evolutionary research. Indeed, EI-Hani and Emmeche (2000) convincingly argue that in modern biology organisms were never ontologically reduced to genes and mere aggregates of genes. Property emergence above the gene level and the autonomy of various levels of selection - cell, organism etc. - is not only conceptually possible but also characterizes biology as a science. They write :

> A frequent misinterpretation is the understanding of *biological* research in the first third part of the twentieth century as a fight between vital-ism and mechanicism that finally was won by the latter stance... the cresolution of the debate' between vitalism and mechanicism was not a mechanistic stance, but a sort of historical compromise in the form of what we here call *mainstream organicssm,* which ended up functioning more or less tacitly as a background philosophy of biology. Organicism takes the complexity and physical uniqueness of the organism as a sign of the autonomy of biology as a natural science, an autonomy that is grounded not only pragmatically in epistemic incapacities of the human research community but also in the special ontological distinctiveness of life processes (237. italics in original).

The autonomy of levels of selection above the genotype level in the 20th century fits well with the nested individual model, originating from Leibniz's 17th-century model. Ishiguro (2001) stresses the ontological aspect behind the striking analogy between Leibniz's metaphysics and modern biology:

> ... we do not think that the oneness of each animal or plant is just a quesion of how we perceive it, and think about it. Neither did Leibniz. That is why he invoked the notion of corporeal substance... [s]ince, it was, as I have suggested nothing but a metaphysical hypothesis that

[28] unlike the model of nested individuals, here the organism's level is treated very differently from any other level of selection. Ruiz-Mirazo et a1. (2000) seek a distinct category for the 'organism' within the hierarchy of units of selection. They argue that "... [t]the notion of organism constitutes some sort of primitive" (p. 231); while Gutmann and Neumann-Held (2000) suggests an approach "which attempts to reestablish a theory of organism that gives the organism a central place in biology" (p. 279).

Leibniz made, it is astonishing that it is compatible with the biological knowledge we acquired only recently (Proceedings of the VII. International Leibniz Congress, 2001, 539-540).

The model of nested individuals, characterized by an active hierarchy of different individuals, one within the other, although highlighting the benefits of recent models in the philosophy of biology also highlights some of the difficulties faced in fitting uniform philosophical criteria to the wealth of biological phenomena. Since every biological individual and every evolving unit of selection must show variation, inheritance and *multiplication* (Maynard Smith 1987 a, b[29]), the model faces the following severe problem: either there are not various individuals in different levels at the same time, but rather many *suppressed* parts and only one *fully reproducing* individual; or else the model uses an empirically vacant metaphor of "hierarchical degrees of activity" instead of showing various concurrently full individuals.

Let us explain the problem. If we have concurrent individuals in different levels, they must share some common features to make them all *full* individuals in the same sense. For working biologists, most of these features must be chemical, physiological or behavioral, and not metaphysical. If different meanings of individuality are assigned to different degrees of activity, can we then say that different levels are individuals in the same sense? For example, in a very broad sense my hair cells and I both multiply (my hair cells reproduce epigenetically while I also replicate genetically and copy behavioral patterns and ideas); inherent properties (with very different *degrees of fidelity, as the celPs genome is* replicated and I am obviously not) and show variance (my cells mostly show phenotypic variance whereas I show also a high genetic variance relative to other humans). In what biologically important way are they both full individuals? From a biological point of view, my cells and I function differently are structured differently and evolve through different processes. So what is the point in saying that my cells and I are full individuals simultaneously?

In light of this critique, it seems that the metaphysical model of nested individuals is either false or unhelpful for empirical or heuristic purposes. We accept this criticism. However, it may lead to two different conclusions: (a) the rejection of the nested individuals model; (b) questioning the application of uniform criteria for a unit of selection. To elaborate on (b), an evolving unit of *selection must show* variance, inheritance and multipli-

[29] maynard Smith (1987a) defines a 'unit of evolution' in terms of multiplicit% variation, and inheritance, *emphasizing the inherited response to selection. Prior to* Maynard Smith, Lewon-tin (1970) defines the 'unit of selection' by phenotypic variance, fitness variance and heritability of characters relating to fitness, emphasizing selection of fitter traits. The main difference between Lewontin and Maynard Smith is that the latter can attempt to explain how an entity has evolved, without assuming a hierarchy of established levels of selection (Griesemer 1999).

cation (Maynard Smith 1987 a). However, is it so clear that the criterion of multiplicity is applied in the same sense to all such units? For example, one can similarly ask, in what sense are a male and a female both individuals in the same sense (e. g. males reproduce by copulation and parental care while females also become pregnant and give birth), and since none can multiply completely independently in what sense is one male or one female a biological individual?

Such questions about *biological individuals* are mentioned by philosophers of biology, but not treated as serious philosophical difficulties for evolutionary biology. The model of nested individuals, which takes a radically pluralistic stance toward biological individuality, in fact sharpens these already existing difficulties over criteria for a unit of selection, though it *clearly* does not invent them. The difficulty of accepting different entities as individuals is similar to the difficulty of accepting different entities as multiplying. The difficulty of applying rigid criteria to the wealth of biological phenomena applies to the standard criteria of a unit of selection (variance, multiplication and heritability) just as it applies to the notion of biological individuality. Thus an additional heuristic value of using the nested-individuals model is that it articulates and exposes some of the costs of the philosophical discussion over the unit of selection.

Overall, we agree with EI-Hani and Emmeche (2000) that metaphysics can assist in explaining some biological phenomena, though its relevance for working scientists, looking for pragmatic answers, may not be so clear. We do not argue that the nested-individual model better explains the notion of a unit of selection than the recent non-exclusive models, nor do we claim it resolves the *philosophical debates over* the notions of *biological* individuality. However, this model does a) articulate some presuppositions common to recent models denying a single level or function of a unit of selection, and b) suggest historical connections between the notions of organism, individual and unit of selection, and, c) highlight the advantages, but not *less importantly* the problems, in using criteria that must apply to the variable biological world in the same sense. Perhaps the main contribution is the criticism of this model of nested individuals, which forces us to think more carefully about the field called philosophy of biology, and more specifically, about the philosophical criteria for a unit of selection.

5. **Conclusion**

Leibniz articulated a non-standard notion of individuality, according to which individuals are nested one within another. In abandoning the Aristotelian formula, cone substance one body', this model has some interesting implications for the notion of individuality in general, and for biological individuality, in particular. On this model, the level of individuality is

determined by the degree of activity, and partly defined by its relations with other individuals. Many evolutionary theorists presuppose a model of biological individual that will eventually reduce to spatio-temporal mechanisms, and many still look for an exclusive level or function to determine a unit of selection. In recent years, a number of alternatives to these exclusive approaches have emerged.[30] However, as of today, there is no broad platform - philosophical or historical - to *highlight some of the* common grounds for *these* tantalizing new ideas. It is partly for this reason that we propose the model of *nested individuals. This model* supports a *pluralistic multi-level* selection and rejects an exclusive level or function for a unit of selection. Since activity is essential to the unity an individual, this model focuses on integrating processes of interaction and replication instead of choosing between them.

In addition, the model of nested individuals may also count as a distinct perspective among the various alternative models for the unit of selection. This model stresses activity and pluralism: it accepts simultaneuous co-existence of individuals at different levels, nested one within the other; and, while it directs research to evolutionary transitions that activate new levels of individuality, it also points out that "previous" levels of individuality are not necessarily lost but remain biologically viable in certain contexts.

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References

Aristotle, Historia Animalium (The History of Animals). In: McKeon, R. The Basic Works of Aristotle. Random House, New-York (1941).

Aristotle, Categoriae (Categories). In: McKeon, R. The Basic Works of Aristotle. Random House, New-York (1941).

Avital, E., Jablonka, E. (2000) Animal Traditions, Cambridge Univ. Press, Cambridge.

Brandon, R. (1999) The units of selection revisited: the modules of selection. Biol. Philos. 14: 167-180.

Brandon, R. N. (1990) Adaptation and Environment. Princeton Univ. Press, New Jersey.

Buss, L. W. (1987) The Evolution of Individuality Princeton Univ. Press, Princeton.

Dawkins, R. (1976) The Selfish Gene. Oxford Univ. Press, Oxford.

Dawkins, R. (1982) The Extended Phenotype. Oxford Univ. Press, Oxford.

Diderot, D. Elements de Physiologic. Repr. J. Mayer. Didier (1964), Paris.

[30] The first radically pluralistic notion of individuality appeared as early as Falk, 1988

Duchesneau, F. (1998) Les Modules du Vivant de Descartes i Leibniz. Vrin, Paris.
EI-Hani, C. N., Emmeche, C. (2000) On some theoretical grounds for an organism-centered biology. Theory Biosci. 119: 234-275.
Falk, R. (1988) Species as Individuals. Biol. Philos. 3: 455--462.
Falk, R. (2000)
Falk, R. (2001)
Gould, S. J., Lloyd, E. A. (2000) Individuality and adaptation *across levels of selection: how* shall we name and generalize the unit of Darwinism? Proc. Nat. Acad. Sci. 96: 1190411909.
Griesemer, J. R. (1999) Materials for the study of evolutionary transition. Biol. and Philos. 14: 127-142.
Griesemer, J. R. (2000 a) The units of evolutionary transition. Selection 1: 67-80.
Griesemer,J. R. (2000 b) Development, culture, and the units of inheritance. Philos. Sci. 67: s 348-s 368.
Griffiths,P., Gray, R. (1994 a) Developmental systems and evolutionary explanation. J. Philos. 91: 277-304.
Griffiths,P., Gray, R. (1994b) Replicators and vehicles? or developmental systems?. Behav. Brain. Sci. 17: 622-623.
Griffiths, P., Gray, R. (1997) Replicator II - judgment day. Biol. Philos. 12: 471-492.
Gutmann, H., Neumann-Held, E. M. (2000) The theory of organism and the culturalist foundation of biology. Theory Biosci. 119: 276-317.
Hull, D. (1980) Individuality and selection. Annu. Rev. Ecol. Syst. 11: 311-332.
Ishiguro, H. (1998) Unity without simplicity. Monist 81: 534-552.
Ishiguro, H. (2001) Is there a conflict between the *logical* and metaphysical notion of unity in Leibniz? The Proceedings of the VII International Leibniz Congress, Berlin. pp. 535-542. Jablonka, E. (1994) Inheritance systems and the evolution of new levels of individuality. J. Theo. Biol. 170: 301-309.
Jablonka, E., Lamb, M. J. (1995) Epigenetic Inheritance and Evolution: The Lamarckian Dimension. Oxford Univ. Press, Oxford.
Leibniz, G. W. In: Ariew, R., Garber, D. (eds) G. W. Leibniz: Philosophical Essays, Hackett, Indianapolis. (1989).
Leibniz, G. W. In: Gerhardt, C. I. (ed) Die Philosophischen Schriften von G. W. Leibniz. Berlin. (1849-1860).
Leibniz, G. W. In: Gerhardt, C. I. (ed) Mathematische Schriften. Schmidt, Halle. (1849-1863). Leibniz, G. W. In: Leibniz: Werke. Wissenschaftliche Buchgesellschaft, Darmstadt (1959-1992). Leibniz, G. W. In: Essais de theodicie: sur la bonti de Dieu, la libertb de l'homme, et l'origine du mal. Garnier-Flammarion, Paris. (1969).
Leibniz, G. W. In: Loemker, L. E. (ed. and tr). Gottfried Wilhelm Leibniz: Philosophical Papers and Letters. Reidel, Dordrecht. (1969).
Leibniz, G. W. In: Deutsche Akademie der Wissenschaften (ed) Leibniz: Simtliche Schriften und Briefe. Darmstadt and Leipzig. (1923-present)
Lewontin, R. C. (1970) The unit of selection. Annu. Rev. Ecol. Syst. 1: 1-18.
Lloyd, E. A. (1988) The Structure and Confirmation of Evolutionary Theory. (see. ed.). Princeton University Press, Princeton (1994).
Lloyd, E. A. (1992): Unit of selection. In: Keller, E. F., Lloyd, E. A. (eds) Keywords In Evolutionary Biology. Harvard Univ. Press, Cambridge, Mass. pp. 334-340.
Maynard Smith,J. (1987a) How *to model* evolution. In: Dupri, J. *(ed) The Latest* on the Best: Essays on Evolution and Optimality. M.I.T. press, Cambridge, Mass. pp. 119-131. Maynard Smith,J. (1987b) Reply to Sober. In: Dupri,J. (ed) The Latest on the Best: Essays on Evolution and Optimality. M.I.T. Press, Cambridge, Mass. pp. 147-149.
Maynard Smith, J., Szathmiry, E. (1995) The Major Transitions in Evolution. W. fl. Freeman, Oxford.
Michod, R. E. (1983) Population biology of the first replicators: on the origin of the genotype, phenotype and organism. Am. 2oo1. 23: 5-14.
Michod, R. E. (1999) Darwinian Dynamics - Evolutionary Transitions in Fitness and Individuality. Princeton Univ. Press, Princeton, New Jersey.
Okasha, S. (2001) Why won't the group selection controversy go away? Brit. J. Phil. Sci. 52: 25-50.

Oyama, S. (1985) The Ontogeny of Information: Developmental Systems and Evolution. Cambridge Univ. Press, Cambridge.
Oyama, S. (2000) Evolution's Eye. Duke Univ. Press, Durham and London.
Ruiz-Mirazo, K., Etxeberria, A., Moreno A., Ibanez J. (2000) Organisms and their place in biology. Theory Biosci. 119: 209-233.
Sleigh, R. C. (1990) Leibniz and Arnauld: A Commentary on their Correspondence. Yale Univ. Press, New Haven.
Sober, E. (1987 a) What Is adaptationism? In Dupri, J. (ed) The Latest on the Best: Essays on Evolution and Optimality. M.I.T. Press, Cambridge, Mass, pp. 105-118.
Sober, E. (1987 b) Comments on Maynard Smith's 'How to model evolution'. In Dupr~, J. (ed) The Latest on the Best: Essays on Evolution and Optimality. M.I.T. Press, Cambridge, Mass, pp. 133-137.
Sober, E., Wilson, D. S. (1994) A critical review of philosopical work on the units of selection problem. Philos. Sci. 61: 534-555.
Sober, E., Wilson, D. S. (1998) Unto Others. Harvard Univ. Press, Cambridge, Mass.
Sober, E., Lewontin, R. (1952) Artifact, cause and genie selection. Philos. Sci. 49: 157-180.
Sterelny, K., Kitcher, P. (1988) The Return of the Gene. J. Philos. 85: 339-361.
Sterelny, K., Smith, K., Dickison, M. (1996) The *Extended Replicator. Biol.* Philos. 11:]77403.
Szathmiry, E., Maynard Smith, J. (1997) From replicators to reproducers: the first major transitions leading to life. J. Theo. Biol. 187: 555-571.
Tralles, A. von. In: Puschmann, T. (ed) Ein Beitrag zur Geschichte der Medicin, Vienna. (1878-1879).
Williams, G. C. (1966) Adaptation and Natural Selection. Princeton Univ. Press, New-Jersey. Wilson, D. S. (1983) The group selection controversy: history and current status. Annu. Rev. Ecol. Syst. 14: 159-187.
Wilson, D. S., Sober, E. (1994) Reintroducing group selection to the human behavioral sciences. Behav. Brain. Sci. 17: 585-654.
Wilson, J. (1999) Biological Individuality. Cambridge Univ. Press, USA.
Wimsatt, W. C. (1980) Reductionistic research strategies and their biases in the units of selection controversy. In Nickles, T. (ed) Scientific Discovery: Case Studies. vol. II, Reidel, Dordrecht. pp. 213-259.
Wimsatt, W. C. (1981) Units of selection and the structure of the multi-level genome. In As-quith, P., Giere, R. (eds) Proc. Philos. Sci. Assoc vol. 2, Philosophy of Science Association, East Lansing. pp. 122-183.