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EXTENDED INHERITANCE AS RE- CONSTRUCTION OF EXTENDED ORGANI- ZATION: THE PARA- DIGMATIC CASE OF SYMBIOSIS



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The paper outlines the contours of an organizational perspective on extended inheritance. Based on theoretical studies about biological organization and extended physiology, this perspective allows for the conception of extended biological legacies while keeping a theoretically indispensable distinction between biological systems and their environment. In this context, the line of demarcation between these systems and their surroundings is modelled on an organizational criterion and on the related conceptual distinction between organizational constraints, whose specific role is to harness flows of matter and energy across generations of composite biological systems, and resources exploited by those systems. Biological legacies are restricted to persisting constitutive elements responsible for the reoccurrence of organizational constraints in a given environment. The case of symbiotic transmission is presented as a paradigmatic system illustrating the main proposed conceptual clarifications.

Key words: extended inheritance, extended organization, persisting organizational constraints, composite biological systems, symbiotic transmission

1 – Introduction

There is increasing interest in the literature regarding non-genetic mechanisms putatively involved in inheritance. Many studies are dedicated to epigenetic, ecological, social or symbiotic processes participating in the transmission of traits across generations. Besides, inclusive frameworks have been proposed to conceive of so-called extended inheritance. In this context, some leading thinkers define inheritance in terms of the stability or availability of a set of genetic and non-genetic developmental resources (Griffiths & Gray 1994; Griffiths & Stotz 2013). Others adopt an informational perspective according to which biological legacies include genetic and non-genetic information contributing to phenotypic resemblances across generations (Jablonka 2002; Danchin et al. 2011; Mesoudi et al. 2013). This paper proposes an alternative framework that is grounded on the reassessment of the boundaries of biological systems that transmit traits to offspring, and which rests on a clear distinction between the stability of these systems' constitutive elements and the stability of their environment. It argues that such a distinction is crucial for building a specific epistemic space¹ for biological inheritance.

The argument is organized as follows. In Section 2, I sketch

1 - In this paper, the expression "epistemic space" refers to a conceptual and operational framework that organizes the theoretical and empirical study of a particular phenomenon.

2 - Strictly speaking, every biological system is composite. Prokaryote unicellular organisms undergo horizontal gene transfers whereas in eukaryotes, the nucleus and the organelles (mitochondria, etc.) are thought to result from endosymbiosis. In this paper, the word "composite" characterizes more specifically biological systems whose traits are primarily explained by the presence of genetically diverse components (hosts and symbionts genes) but also by the presence of other elements such as socially transmitted representations or epigenetic marks, in a given environment. These elements do not necessarily have a common fate as opposed to nuclear and mitochondrial genes.

a brief description of extended inheritance and I evoke two existing inclusive frameworks. I then argue that building a specific epistemic space for biological inheritance, extended or not, requires keeping a clear line of demarcation between biological systems and their environment, and cannot consist in including environmental elements in biological legacies even when these elements are stabilized by previous generations. In Section 3, I outline the contours of an organizational account of extended inheritance based on conceptual tools found in studies on biological organization and extended physiology (Mossio & Moreno 2010; Turner 2004). In this view, extended inheritance is defined as *trans-generational reconstruction of extended organization*. It is underpinned by the reconstruction of constitutive heterogeneous elements responsible for the reoccurrence of a set of organizational constraints, harnessing and parceling flows of matter and energy so as to maintain specific organizational patterns within and across generations of *composite biological systems*² in given environments. The demarcation between these systems and their environment is not defined by a physical (spatial) criterion; it is rather modeled on a conceptual distinction between persisting constraints and stable resources. In Section 4, I give some flesh to this conceptual framework through the well-studied case of symbiotic inheritance.

2 – Thinking about extended inheritance: description and theoretical requirements

In this section, I briefly describe non-genetic processes that could be included into pluralistic models of inheritance. I then evoke two inclusive conceptual frameworks presented in the literature, before arguing that a theoretically consistent definition of extended inheritance should be grounded on a clear distinction between biological systems and their stable environment. In this respect, I argue that thinking about extended inheritance cannot consist in including environmental elements in biological legacies, but should rather rest upon a reassessment of the boundaries and characteristics of biological systems that transmit traits to offspring.

2.1 A brief description of extended inheritance

During the major part of the 20th century, investigations regarding biological inheritance was widely dominated by a gene-centric vision, according to which the duplication of parental genes was the sole process underpinning trans-generational similarities (Mameli 2005). However, this vision has been heavily criticized over the three last decades. Indeed, increasing data on non-genetic mechanisms involved in trans-generational resemblance have recently encouraged critics to call for the adoption of multidimensional, pluralistic and inclusive models (Jablonka & Lamb 2005; Danchin et al. 2011; Bonduriansky 2012). Non-genetic inheritance would provide better insight into the diverse *explanantia* of the like-begets-like phenomenon and could fill explanatory gaps left by gene-centric accounts. For example, it could bring a solution to the problem of missing heritability in common traits and diseases (Maher 2008) or shed light on the partly unexplained emergence of complex biological individuals in evolutionary biology (Bouchard 2013, p. 259).

The most famous non-genetic channel of inheritance is probably that of epigenetics. Coined by Waddington by the middle of the 20th century to describe the causal mechanisms by which genotypes have phenotypic effects (1942), the word epigenetics refers in contemporary biology to mitotically or meiotically heritable changes in gene function that cannot be explained by changes in DNA-sequence (Richards, Bossdorf & Pigliucci 2010).³ Epigenetic mutations, such as changes in methylation patterns, can be correlated to significant phenotypic changes: a modification of symmetry in *Linaria vulgaris* (Cubas, Vincent & Coen 1999), a change of coat color in mice (Morgan and Whitelaw, 2008), or an alteration of maternal behavior in rats (Champagne 2008). Another classic example of non-genetic inheritance is ecological inheritance. Ecological inheritance mainly refers to the trans-generational

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al transmission of a constructed parental niche, namely the transmission of environmental modifications induced by organisms during their ontogenesis and altering the selection pressures that act on offspring (Odling-Smee, Laland & Feldman 2003).⁴ Beaver dams, bird nests, spider nets, mammal burrows, or chemical modifications of the soil caused by earthworms are classic examples of an ecological niche. Behavioral inheritance refers to the transmission of behaviors or preferences through social interactions (Danchin et al. 2011; Jablonka & Lamb 2005, p. 160). It can be considered as a kind of ecological inheritance since the transmission of behaviors can modify the offspring's environment and alter its adaptive landscape (Laland, Odling-Smee & Feldman 2000). Finally, symbiotic inheritance, which refers to the transmission of symbiotic microorganisms across generations of hosts (Gilbert, Sapp & Tauber 2012), can also be considered as part of ecological inheritance. Whereas epigenetic marks, like genes, are vertically transmitted through cellular processes, niches, behaviors and microorganisms can be transmitted both vertically and horizontally.⁵ Besides, non-genetic elements are usually considered to be more mutable than genes (see Richards, Bossdorf & Pigliucci 2010, for epigenetic marks; Gould 1980, for cultural variants; Rosenberg & Zilber-Rosenberg 2008, for symbiotic partners).

This brief description gives an insight into the diversified biological legacies that biologists could take into account according to their specific theoretical interests (heritable diseases, heritable fitness, etc.). More generally, increasing data about non-genetic processes putatively involved in the like-begets-like phenomenon represents a serious challenge for philosophers of biology. In this context, they are indeed required to outline a concept of biological inheritance that departs from a gene-centric perspective but is at the same time distinct from the metaphor of inheritance that broadly refers to the transmission of “goods” across generations. In other words, philosophers are required to build an inclusive but specific epistemic space to think about biological inheritance.

2.2 A few theoretical requirements for thinking about extended inheritance

Among the inclusive frameworks that have been proposed to think about extended inheritance, many include environmental items in biological legacies. For example, Bonduriansky asserts that non-genetic inheritance is about the transmission of parts of a parental “extended phenotype”, namely the “components of the parent's body, behavior or ambient environment” (2012, p.333). In a similar way, the authors who ground their approach in Developmental Systems Theory describe extended inheritance in terms of the stability or availability of a set of developmental resources (Griffiths & Gray 2004, p.412; Stotz 2010, p.487). For instance, Griffiths

3 - The word epigenetic is derived from epigenesis, a theory of generation proposed against preformationism during the 17th and 18th centuries. Waddington was concerned with linking genetics with developmental mechanisms studies in experimental biology.

4 - Darwin (1882) already evoked this phenomenon through the example of earthworms.

5 - Vertical transmission is intergenerational and toward genetically related offspring; horizontal transmission can be intragenerational and is toward non genetically related offspring.

and Stotz (2013) have recently argued that the concept of the developmental niche “is the best framework to unite all the different approaches which study those aspects of heredity and development which are ‘outside the genome’” (p.129). In this view, food, habitats and territories are considered inherited (p.136); biological legacies include “a set of epigenetic, social, ecological, epistemic and symbolic legacies inherited by the organism as necessary developmental resources” (Stotz 2010, p.483). Other leading thinkers have applied the informational vocabulary developed in molecular genetics to non-genetic elements exhibiting trans-generational stability and involved in trans-generational resemblances. In this case, extended inheritance is conceived in terms of stable information (Jablonka 2002; Danchin et al. 2011; Mesoudi et al. 2013) and biological legacies include elements as heterogeneous as genes, epigenetic marks and constructed niches, be they social or ecological (Jablonka 2002, p. 597; Danchin et al. 2011, p. 478).

However, the inclusion of environmental elements in biological legacies appears problematic when one considers the project of building a specific epistemic space for biological inheritance. Indeed, such an inclusion seems to be at odds with this project insofar as stable environmental elements are already acknowledged to play a key and proper role in the re-occurrence of traits across generations. In this view, it is not clear why they should be included in biological legacies when they are stabilized by biological systems. Additionally, talking about the inheritance of environmental resources when these resources are stabilized by biological systems problematically introduces an explanatory redundancy, as the stability of environmental resources can be primarily explained by the inheritance of the systems’ traits. For example, the trans-generational stability of an environmental resource such as meat can be explained by a socially inherited farming technique in humans but it can also be explained by a genetically inherited capacity to run fast in lions. In both cases it would be highly misleading to talk about the inheritance of meat just because meat is stable across generations. Finally, the modification of selection pressures through niche construction is unquestionably a very important phenomenon in biological evolution, but it is obviously distinct from biological inheritance, which refers to the transmission of traits across generations.

In this context, I argue that building an inclusive but specific epistemic space for the study of biological inheritance requires preserving a clear conceptual distinction between the stability of the parts of biological systems and the stability of biological systems’ environments. More precisely, I argue that biological inheritance should be restricted to the reconstruction of systems’ parts. I suggest that rather than includ-

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ing environments in biological legacies, thinking about extended inheritance requires revising the line of demarcation between biological systems and their surroundings, an option that has so far been ignored in the literature.⁶ In the rest of this paper, I develop an alternative account of extended inheritance grounded on a reassessment of the boundaries of biological systems that transmit traits to their offspring. I use an organizational criterion to draw the boundaries of composite biological individuals⁷ and to further outline an organizational account of extended inheritance, suited to build a specific epistemic space for the considered phenomenon.

3 – An organizational perspective on extended inheritance

In this section, I outline an organizational perspective on extended inheritance. First, I use an organizational criterion to individualize composite biological systems. Second, I argue that only trans-generational determinants of biological organization should be considered as integral parts of successive biological systems, and therefore thought of as inherited by these systems. In this context, the bright-line between biological systems and their environment is not determined by physical (spatial) boundaries; it is modeled on an organizational criterion and on the related theoretical distinction between persisting *constraints* and stable *resources*. Although in some cases physical and organizational criteria can match, the example of symbiotic associations developed in Section 4 shows that this may not always be the case and that a physical (or spatial) criterion is neither necessary nor sufficient to think about biological individuality.

3.1 Organization as a principle of individuation: toward the conceptualization of composite biological systems

Recent studies on biological organization and on extended organismality underpinned by extended physiology offer interesting conceptual tools to think about composite biological systems whose boundaries are outlined by an extended organization. More precisely, these studies open up space for thinking about systems in which individuating physiological pathways and organizational patterns are determined by heterogeneous elements, beyond genes and “gene products”⁸, at a given biological scale and in a given environment.

The concept of biological organization through closure of constraints (Mossio, Saborido & Moreno 2009; Mossio & Moreno 2010, Montévil & Mossio 2015) first appears as a relevant tool for thinking about individuated composite bio-

6 - DST proponents insist on the importance of placing a system in its environment, but do not propose to rethink the system/environment boundaries. In this respect, their contribution is radically different from mine.

7 - The question of biological individuality is very complex and many definitions are defended in the abundant literature dedicated to this topic (Clarke 2010). The neutral organizational one appears particularly relevant in the context of extended inheritance, insofar as it allows for a departure from gene- and replicator-centered biology.

8 - “Gene product” refers to traits whose presence is correlated to the presence of specific genes in a given environment. This practical concept does not downplay the very complex developmental processes needed for the production of traits.

logical systems. Initially developed to build a technical characterization of biological organization, this concept offers a general criterion for biological individuality. It is influenced by Kantian teleology, according to which the parts of an organized system are considered with respect to the whole and as reciprocally producing themselves (1993, pp. 295-296), but it also takes into account 20th century studies on general systems theory (von Bertalanffy 1968) and self-organization (Kauffman 1995; Kauffman et al. 2008).

Within this approach, biological organization refers to a causal regime distinctive to biological systems, where self-maintenance is realized through the integration of differentiated and mutually dependent parts. These parts maintain each other as well as the highly ordered whole they belong to through their interactions (Mossio, Saborido & Moreno 2009; Mossio & Moreno 2010). They are described as chemical or structural (one may add behavioral) *constraints* performing differentiated organizational functions in open systems exchanging matter and energy with their environment. More precisely, constraints collectively channel flows of matter and energy so as to maintain the adequate thermodynamic conditions required for their own maintenance and that of the system (Mossio, Saborido & Moreno 2009; Mossio & Moreno 2010).⁹ They collectively determine the opportunities and limits for a system's self-maintenance in a given environment,¹⁰ in determining this system's access to resources and the parceling of these resources among its functional parts. It is important to note that each constraint belonging to a complex network makes a specific causal contribution to the self-maintenance of this network.

The concept of biological organization through closure of constraints provides general tools to think about composite biological individuals in which functional work is performed by heterogeneous elements sharing the theoretical status of structural, chemical or behavioral constraints. Indeed, whereas enzymes and vascular systems "encoded" by genes are classic examples of constraints, a socially transmitted behavior providing access to specific nutritional resources in blue tits and great tits (Slagsvold & Wiebe 2007), or symbionts assuming part of digestive processes for their termite hosts (Turner 2004) also appear as genuine parts of a composite biological system, making a specific contribution to the channeling and parceling of flows of matter and energy through it.

9 - Biological systems are not the only thermodynamically open systems exchanging matter and energy with their environment. However, they present some specific features partially taken into account in the presented framework. For example, their parts are differentiated and each makes a specific causal contribution to the maintenance a highly ordered whole, as suggested by the present account. A full analysis of other features that distinguish biological systems from simple dissipative structures (regulation, autonomy, etc.) is beyond the scope of this paper.

10 - These constraints are distinguished from limits imposed by environment, such as scarcity of resources.

11 - Turner notes however that "any sharp distinction (between systems and environment) is thermodynamically indefensible" and that "the distinction is only of degree rather than kind" (2004, p. 333).

12 - In the case of termite mounds developed by Turner (2002; 2004), the composite organisms include many organisms.

13 - Genetic inheritance is usually thought of as the first reliable inheritance process that appeared in the history of life. In addition, it has probably enabled the evolution of other kinds of inheritance processes. Nevertheless, genetic inheritance might not have been the first mechanism to ensure a rudimentary form of trans-generational maintenance of some elementary functions, see for example (Moreno & Ruiz-Mirazo 2009).

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These considerations echo Turner's theoretical studies on extended organismality underpinned by extended physiology (Turner 2002; 2004). Asserting that "living environments are divided from inanimate surroundings by so-called adaptive boundaries that manipulate flows of mass and energy across them" (2004, p. 329), Turner explains that "physiological function requires an orderly environment that specifies particular pathways for flows of mass and energy" (2004, p. 332).¹¹ According to him, a living environment (to be understood as a living entity) can be structured by various *specifiers* such as genetically "encoded" enzymes, fungi degrading cellulose for termites or tunnels channeling flows of air in termite mounds. In this context, physiological transactions/functions are not exclusively ordered by "gene products" but can be specified by heterogeneous arbiters (2004, pp. 348-349). They can be found beyond the traditional limits of organisms, like in the case of termite mounds.¹² The general concept of *specifier*, as well as that of *constraint*, constitutes important theoretical tools to conceive of complex biological organizations and to think about composite individuals whose boundaries are modeled on an organizational/physiological criterion.

3.2 From extended organization to extended inheritance

The evoked theoretical tools can be used to ground an organizational perspective on extended inheritance. In this view, the biological systems that transmit traits to offspring are thought of as composite organized/physiological individuals, and extended inheritance is defined as the trans-generational reconstruction of extended organization or shared physiology. The latter is thereby functionally characterized and appears as a phenomenon of trans-generational maintenance of specific organizational patterns, underpinned by the duplication of parental genes but also by the maintenance of other elements that should not be conflated with stable environmental resources.¹³

Allowing for the conception of complex biological legacies while maintaining a key distinction between the stability of a system's parts and that of its environment, an organizational perspective appears well-suited to build an inclusive but specific epistemic space for biological inheritance. In this view, only persisting *constraints* (enzymes, feeding behaviors, etc.) will be considered as inherited, along with the persisting constitutive elements underpinning their reoccurrence across

generations (parental genes, socially transmitted representations, etc). These elements must not be mistaken with stable environmental *resources*. Indeed, whereas *constraints* channel flows of matter and energy so as to allow a system to maintain itself, environmental *resources* are exploited by this system. As a result, the stable habitats or food resources that constitute integral parts of biological legacies in other approaches (see Mameli 2004, p. 41; Griffiths & Stotz 2013, p. 136) belong neither to biological legacies nor to biological systems within the outlined organizational perspective. In contrast, the genetically or socially transmitted traits that allow the systems to actively exploit these resources are clearly inherited.

Now, for the organizational framework to be relevantly applied to the concept of extended inheritance, it is essential to make a few addenda. First, the concept of self-maintenance has to be divided into mere self-maintenance and expansion through reproduction and/or growth. In this respect, organizational constraints should be thought of as making specific contributions to both the maintenance and reproduction of the biological system to which they belong.¹⁴ Besides, whereas inherited parts are mutually dependent for the trans-generational reoccurrence of specific organizational patterns, they are not necessarily fully interdependent for their own maintenance, within and across generations. For example, while genes and “gene products” such as enzymes may be dependent on socially transmitted foraging behaviors to maintain trans-generational patterns of nutrient canalization, they will not be necessarily dependent on these behaviors to be maintained within and across generations. Thus it is necessary to consider different degrees of mutual dependence between inherited constraints, and different degrees of individuality in the composite biological systems that transmit these constraints to their offspring.¹⁵ Finally, the framework does not imply that constraints are necessarily adaptive. This point is illustrated by the paradigmatic example of symbiosis, which can be both adaptive and maladaptive (see 4.1).

3.3 Limit-cases: non-functional traits and functional environments

One could object that the outlined organizational account of extended inheritance is not fully suited to build a specific epistemic space for biological inheritance. Indeed, it first seems to ignore obviously inherited morphological traits, such as eye color or chin shape, that are not directly involved in the channeling and parceling of resources in biological systems. This objection deserves a full analysis in a future paper. However, I would like to insist on the fact that an organizational account of extended inheritance, as opposed to a trait-centered framework, fully takes into account the fact that inher-

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ited traits are parts of integrated wholes. As a result, it fully takes into account the fact that while some inherited traits are genuinely functional, others result from a phenomenon of co-variation between traits, or are due to structural or developmental constraints (Gould & Lewontin 1979). Finally, some socially transmitted traits such as dialects in hominid lineages might not be involved at all in the channeling and parceling of resources in a biological system, but could play a functional role at a group scale, in channeling other kinds of flows such as genuinely informational ones (representations, beliefs, etc.).

The outlined organizational account also leaves some ambiguity regarding the status of environmental elements that are not consumed by biological systems but rather used as functional extensions, such as caves offering a protection against predators. The status of these elements is obviously problematic insofar as the division between systems and environment, in the outlined framework, is modeled on an organizational/functional criterion. However, two arguments suggest that caves and other functional environments should be considered as environmental resources. First, their maintenance is absolutely not dependent on that of biological systems using them. On the contrary, the degree of maintenance of symbionts can for example be linked to that of hosts since partners can have aligned interests (van Baalen & Jansen 2001). Besides, the trans-generational stability of caves can be exclusively explained by the trans-generational reoccurrence of genetically or socially transmitted traits allowing biological systems to use them so as to modify the energetic cost of protection against predator.

These limit-cases crucially deserve further developments in future contributions, but they already suggest two things: i) that being a functional part (or exhibiting co-variation with a functional part) is a necessary but not sufficient condition for a stable element to be considered as inherited; ii) that an organizational account of extended inheritance offers an opportunity to rethink the umbrella category of environment.

4 – Symbiotic transmission as a paradigmatic system for an organizational perspective on extended inheritance

In this last section, I propose to consider symbiotic transmission as a paradigmatic system for an organizational perspective on extended inheritance. In other words, I present

¹⁴ - In this respect, an organizational perspective on extended inheritance takes into account the issue of the trade-off between traits involved in survival and those involved in reproduction. This issue has been widely studied in the literature dedicated to life-history strategies, see (Fabian & Flatt 2012). Altruistic traits leading a parent to sacrifice itself for its offspring appear as functional when this trade-off is taken into account.

¹⁵ - Queller and Strassmann (2009) for example, suggest that organismality is a matter of degree and should be assessed with respect to a degree of cooperation and a degree of conflicts between parts.

trans-generational symbiosis as a model of persisting extended organization.¹⁶ After a brief description of trans-generational cooperation between hosts and symbionts in performing diverse functions, I develop more specifically the case of trans-generational shared metabolism. Beyond providing an example of trans-generational cooperation between heterogeneous parts of composite biological systems, this case illustrates the distinction between persisting constraints and stable resources, as well as the organizational line of demarcation between biological systems and their environment. Finally, symbiotic inheritance gives an insight into the continuum of interdependence that can exist between constraints for their maintenance across generations.

4.1 Trans-generational symbiosis as a model of reconstructed extended organization

Coined by Anton de Bary (1879), the word symbiosis traditionally refers to “the ‘living together’ of ‘dissimilar’ or ‘differently named’ organisms”, even if some critics restrict symbiosis to interactions that are globally advantageous for both partners (Margulis 1991, pp. 1-3). Defined as a “second mode of genetic inheritance” (Gilbert, Sapp & Tauber 2012, p. 325), symbiotic inheritance occurs when the interactions between hosts and symbionts are maintained across generations of hosts.

The functional integration of hosts and their symbionts is particularly well described in the literature. Appearing as “the source of novel metabolic function increasing the host capacity to exploit resources” (Dedeine et al. 2001, p. 6247), symbionts are said to complete metabolic pathways and to take responsibility for other physiological functions in the composite system they form with their host (Gilbert, Sapp & Tauber 2012, p. 325).¹⁷ In this respect, the division of physiological labor traditionally thought to occur at the scale of a genetically homogeneous organism, “can be accomplished by several species working together” (Gilbert, Sapp & Tauber 2012, p. 329). The concept of the “holobiont” was proposed to describe the persisting functionally integrated systems composed of hosts and microbial partners (Margulis 1991, p. 2; Rosenberg, Sharon & Zilber-Rosenberg 2009, p. 2960; Gilbert, Sapp & Tauber 2012, p. 328).

A key physiological function like defense in the broad sense often requires the presence of symbionts, generation after generation. The squid *Euprymna scolope*, for example, needs to be colonized by specific bacterial associates to produce a bioluminescence that allows it to hide from predators (McFall-Ngai 2002; Nyholm & McFall-Ngai 2004). In the category of immunity, *Wolbachia* can induce resistance to RNA viral infections in *Drosophila melanogaster* (Teixeira, Ferreira & Ashburner 2008) whereas gut symbionts are known

16 - The present analysis is focused on the host, namely on the pluricellular eukaryotic organism traditionally thought of as resulting from the interactions occurring between genes contained in the zygote and environmental conditions.

17 - See footnote 2 for details about the concept of composite systems in the present paper.

18 - Just like the functions that are performed by “gene products”.

19 - An interesting distinction can be made between the symbiotic microorganisms participating in the processing of food and the microorganisms used as food, even if the boundary is not always perfectly sharp (Douglas 2009, p. 39).

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to prompt the expression of genes involved in the immunity of mammals (Hooper, Littman & Macpherson 2012). Symbionts can also play a role in reproduction and act as fertility determinants (Gilbert, Sapp & Tauber 2012; Rosenberg & Zilber-Rosenberg 2008). *Wolbachia*, for example, can induce cytoplasmic incompatibility in insects (Turelli & Hoffmann 1991; Hoffmann & Turelli 1997) and may be indispensable for oogenesis (Dedeine et al. 2001).

Finally, the case of symbiosis is particularly relevant insofar as it suggests that the functions that are not performed by “gene products” are not necessarily adaptive¹⁸, provided that one adopts a general account of symbiosis including interactions going from pathogenic to beneficial ones (van Baalen & Jansen 2001; McFall-Ngai 2002).

4.2 The striking example of trans-generational shared metabolism

Trans-generational shared metabolism, which can also be described as trans-generational food processing, is an interesting example of trans-generational shared organizational function. In this specific case, microbial symbionts perform biosynthesis and nutrient degradation for hosts, and appear as key contributors to shared metabolisms in composite biological systems.

Many microorganisms are indispensable for the degradation of cellulose in herbivorous mammals (Kamra 2005; Gilbert, Sapp & Tauber 2012, p. 327), and various species of termites rely on symbiotic fungi to perform cellulolysis, be they located within the organisms’ boundaries or in the nest (Turner 2004; Margulis & Sagan 2001; Douglas 2009, p. 43). Actually, current data suggest that there is a combination of “intrinsic” and “microbial” cellulolysis in many insects feeding on wood and other cellulose-rich diets (Douglas 2009, p. 42). Biosynthesis is another important metabolic function that can be ensured by symbiotic associates. In this category, several varieties of pea aphids rely on their vertically transmitted microbial associates from the family of *Buchnera aphidicola* to synthesize essential amino acids (Hansen & Moran 2011). The collaboration between hosts and their symbionts can be so significant that some authors talk about metabolic interdependence (Zientz, Dandekar & Gross 2004; Mc Cutcheon & von Dohlen 2011).

In these examples, persisting symbiotic partners co-determine the channeling and parceling of nutrients in composite biological systems, and thereby co-determine food utilization traits (Douglas 2009, p. 44). Thus, they act as *constraints* and cannot be mistaken with the stable *resources* they harness together with other parts of the system across generations.¹⁹ The theoretical status of *constraints* can also be attributed

to other persisting elements participating in food processing across generations of composite biological systems. For example, socially transmitted foraging behaviors in blue tits and great tits (Slagsvold & Wiebe 2007) could be considered as inherited constraints insofar as they control tits' access to resources and thereby co-determine tits' food utilization traits.

4.3 Demarcation between systems and environment, and further conceptual clarifications

Within an organizational account of extended inheritance, the boundaries of composite biological systems transmitting traits to offspring are outlined by an organizational criterion and by the related theoretical distinction between persisting *constraints* and stable *resources*. The case of symbiotic inheritance illustrates this organizational line of demarcation between systems and environment. Indeed, symbionts can be transmitted either internally or externally (Rosenberg & Zilber-Rosenberg 2008; McFall-Ngai 2002). In the first case, they are located in or on the female gamete and are transmitted through reproduction. The most famous example of this first category is probably the vertical transmission of *Wolbachia* in many arthropods and nematodes (Teixeira, Ferreira & Ashburner 2008) or that of *Buchnera aphidicola* in pea aphids (Hansen & Moran 2011). When the transmission is external – or environmental –, symbionts are inherited through parental proximity or harvested in the environment. For example, mammal gut bacteria are transferred “as soon as the amnion breaks or when infants suckle or hug” (Gilbert, Sapp & Tauber 2012, p. 328) whereas the ingestion of feces constitutes a channel of symbiont transmission for termites (McFall-Ngai 2002). The community formed by the squid *Euprymna scolope* and *Vibrio fischeri* in the Hawaiian seawaters results from the recruitment of symbionts in the environment (McFall-Ngai, 2002; Nyholm & McFall-Ngai 2004). Although symbionts recruited in the environment appear *prima facie* to be environmental resources, the outlined organizational criterion of biological individuality, and the interactions existing between hosts and their associated microorganisms (van Baalen & Jansen 2001), state that they should be considered genuine parts of composite biological systems.

The diverse channels through which symbionts are transmitted from one generation to the next give further insight into the *continuum* of interdependence existing between the parts of an organized system for their own maintenance within and across generations. In the case of symbiotic transmission, one generally makes a distinction between obligate symbionts and facultative ones. Whereas the former live in specific cells (bacteriocytes), are vertically transmitted and are generally in a relationship of mutual dependence with their host for recurrence across generations, the latter are “not required for host reproduction” and can persist outside of pluricellular organisms (Moran, McCutcheon & Nakabachi 2008).

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However, some environmentally recruited symbionts, which could be identified as facultative ones, might be very important for the survival and reproduction of the host genes (think of the squid/vibrio association). Besides, symbionts can have aligned interests with their host, even if they are not fully dependent on them to reproduce (van Baalen & Jansen 2001).

As mentioned earlier, the gradual interdependence of *constraints* for their own trans-generational maintenance suggests that there are different degrees of individuality in composite biological systems transmitting traits to offspring. These considerations will be important to assess the relevance of an organizational account of extended inheritance in evolutionary biology, since the common fate of inherited parts is traditionally considered as a key requirement for cumulative evolution by natural selection (see Sterelny 2001, p. 339). Is an organizationally characterized individual an evolutionary individual? Is an organizational account of inheritance relevant for evolutionary biologists? Whereas many authors would answer “no” to both questions due to the common-fate-of-parts requirement, an organizational account of extended inheritance still appears essential in order to think about physiological selection (Turner 2004) and also to understand the partly unexplained emergence of so-called “superindividuals” (Bouchard 2013, p. 259). It might finally constitute an indispensable ingredient in order to achieve the claimed return of organismal thinking in evolutionary biology (Walsh 2010).

5 – Conclusion

In this paper, I have outlined the contours of an organizational account of extended inheritance that appears well-suited to build a specific epistemic space for the considered biological phenomenon. From this perspective, extended inheritance is defined as trans-generational reconstruction of extended organization, or trans-generational reconstruction of extended physiology. Biological legacies do not include stable or stabilized environmental *resources*, but are restricted to persisting constitutive elements responsible for the reoccurrence of a set of organizational *constraints* whose specific causal role is to harness and parcel flows of matter and energy across generations of *composite biological systems*. The characteristics of the different constraints will have to be explored in future papers. Future studies will also have to address the related and difficult issue of trans-generational boundaries between parents and offspring, in a context where biological systems are made up of heterogeneous parts whose cycles of reconstruction are not necessarily synchronized (see Sterelny and coworkers 1996 for a similar idea). For now, the organizational perspective outlined in this paper suggests that a transformation of the concept of inheritance provides new opportunities to build bridges between physiology and evolu-

tion (for a similar idea, see Danchin and Pocheville (2014)), as well as new opportunities to bring organizational thinking back to the heart of evolutionary biology.

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