Rethinking the Individuality of Pregnancy: Eutherian Pregnancy as an Evolved Relational Novelty

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Abstract: The question of how to conceive of the relation between the pregnant female and the embryo has become a recent focus of debate in the philosophical literature. Here we consider this problem in the context of current debates on individuality in the philosophy of biology by looking at how pregnancy is individuated in different disciplinary contexts. Firstly, we review different notions of biological individuality in the literature, examine how each of them applies to the case of pregnancy, and claim that recent work on the evolution of eutherian reproduction offers insights for new criteria for rethinking the individuality of pregnancy. Then, we reconstruct the main assumptions underlying the established biological account of pregnancy. Finally, we develop an alternative account based on the hypothesis that pregnancy is an evolved relational novelty and maintain that pregnant females are conceived as *historical reproductive individuals*. In the final section before the conclusions, we discuss how the historical reproductive biological individuality of pregnancy differs from, and coexists with, other views of individuality, and examine some of its consequences.

Keywords: evo-devo; individuality; novelty; pregnancy; reproduction; transition

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Rethinking the individuality of pregnancy:

Eutherian pregnancy as an evolved relational novelty

1. Introduction

Philosophical dissents often oblige us to question unexamined assumptions. An intriguing one concerns the individuality of pregnant females. For calculations of the number of individual specimens being fed, hunted, killed by a forest fire, voting or engaged in a game, the fact that an individual is pregnant may be just a matter of irrelevant detail. However, in biological or medical contexts in which other aspects of individuality prevail, such as the potential to be affected by a disease, live, or die, it is not uncommon to refer to the mother and fetus as different individuals.

The question of how to conceive of the relation between the pregnant female and the embryo[1] has recently become a focus of debate in the philosophical literature (Howes 2008, Kingma 2018, 2019, Young 1990). Iris M. Young (1990) observed that pregnancy deserves more philosophical attention because it constitutes a very special way of being an individual, involving an inner relation with another being which is partly identical and partly extraneous to the pregnant subject. Moira Howes (2008), elaborating on this relation from the immune system perspective, considered that both the classical model of the mother as a container, and the alternative of regarding the embryo as "the mother's flesh", fail to acknowledge the material female-embryo relations. Therefore she offered a relational, "not-one-but-not-two" alternative emphasizing the dynamic physical interactions between female and embryo. In turn, Elselijn Kingma (2018, 2019) has recently argued in favor of understanding the pregnant human female as an organismal whole, the embryo being a part of it.

Yet none of these works have considered the kind of biological individuality that pregnancy entails, in the context of current debates on individuality in the philosophy of biology. In this contribution, we ask whether the pregnant female is a biological individual of some sort, in contrast to the position that individuality can only be attributed to female and/or embryo separately, as is commonly assumed when specifically referring to human pregnancy, as well as in general reproductive biology. In discussing this problem, we address the status of pregnant females as concerning all eutherians, not only humans and, rather than analysing the formal consistency of the arguments deployed to advocate different concepts of individuality, we focus on how pregnancy is individuated under different biological perspectives and practices (Bueno et al. 2018). In particular, we will pay attention to current studies on the evolution of eutherian reproduction which challenge our received views on the individuality of pregnancy. More generally, our conclusions concerning pregnancy confirm Griesemer's suggestion that the study of individuation in scientific practices can lead us to "discover new ways to think about individuality" (2018, p. 141).

[1] Following Blackburn and Starck (2015) we use the term "embryo" in a broad sense that includes also fetuses.

The received views of reproduction as a discrete event resulting in a certain number of offspring tend to disregard the complexity and diversity of the relations involved in the process. In contrast, understanding individuality in reproduction requires examining material continuities and discontinuities, forms of multiplication, developmental interactions, as well as how those originated in evolution. Following this perspective, we suggest an alternative, relational, account of reproductive individuality for pregnancy. It is grounded on new empirical evidence on the developmental evolution of reproductive systems, showing that they have undergone significant innovations, often involving complex transformations of the relations among organismal entities. These new findings make evident that received insights on reproduction as copy-making and as a strategy for maximising fitness do not suffice to explain eutherian pregnancy, and we propose that one of the reasons is precisely that they fail to consider the relational properties of reproduction and how they have evolved historically. Thus the complex phenomenology involved in the evolutionary emergence of eutherian reproduction leads us to identify the pregnant female as a form of biological individuality which we characterise as a *historical reproductive individual*.

The structure of our argument will be as follows. First, we review distinct concepts of biological individuality in the literature (physiological, evolutionary, ecological and historical), examine how each of them applies to the case of eutherian pregnancy, and propose the concept of *historical reproductive individuality* for the individuality emerging from reproductive relations. Next, we reconstruct in detail the main assumptions underlying the established biological account of pregnancy. Then we develop an alternative account based on the hypothesis that pregnancy is an evolved relational novelty, and our proposal that pregnant females are historical reproductive individuals. In the final section, we discuss how our notion of historical reproductive individuality differs from, but also coexist with, other notions of individuality, and examine some consequences of our view of the biological individuality of pregnancy.

2. Pregnancy and biological individuality

The nature of biological individuality has been a topic of intense inquiry, in particular with respect to cases such as insect colonies, symbiotic organisms, or the Portuguese Man-O-War, which challenge the commonsense delineation of biological entities as distinct, self-enclosed, and independent individuals. The subject of biological individuality has also flourished in the recent literature in philosophy of biology (Ruiz Mirazo et al 2000; Clarke 2010; Pradeu 2016), although the case of pregnancy has only recently entered this debate. Eutherian pregnancy poses particularly challenging ontological issues as, in addition to those shared with the previous cases, the transient nature of the process and the kind of relation established in the reproductive function, require specialized attention. In this section we review the classical perspectives, along with more recent proposals, on biological individuality, in order to consider next how pregnancy is differently individuated in each of these approaches, and outline the main argument for the need of a new concept.

2.1. A brief state of the art on biological individuality: four perspectives

The notion of *physiological individuality* captures the most intuitive phenomenological view of individuals as autonomous, functionally integrated, and self-maintaining systems, separated from their environments. It underlies the classical views of 'organisms' developed by the physiological

tradition in biomedicine (see, e.g. Perlman 2000), as well as the organizational approach in recent philosophy (Maturana and Varela 1987, Moreno and Mossio 2015). In this approach, individuality stems from the part/whole dynamic patterns and processes that allow a biological system to stay alive, insofar as different functional systems are integrated and contribute to the major vital functions.

In the late 1970s, this conception of organisms was relegated in favour of philosophical proposals for a more abstract concept of individuality inspired by the Modern Synthesis view of evolution (Hull 1978). In this classical conceptual framework, *evolutionary (Darwinian) individuals* started to be understood as theoretical entities of evolutionary biology, namely those that play a role in evolution by natural selection, their main features being variation, heritability, and differential fitness (Godfrey-Smith 2013). On the one hand, following debates on the metaphysics of evolution, the individuality notion was scaled up from the level of the organism, and was predicated of entities that appear as continuous and cohesive, spatially and temporally localised, such as species (Hull 1978). On the other hand, as a consequence of the controversy on the units of selection, entities below and above the level of the organism, such as genes and cells also started to be considered as individuals in this sense. Worried by the poverty of the ontology of population genetics, Eldredge and others proposed a double hierarchy of biological individuality: one formed by genealogical individuals or replicators (genes, organisms, demes, species…), and the other by ecological individuals or interactors (cells, organisms, populations…) (Eldredge 1985; see also Ruiz Mirazo et al 2000, Fabregas-Tejeda et al 2018). Recently, there have been repeated attempts to recover the centrality of the organism in evolutionary biology and overcome what is perceived as the excessively reductionist view of living ontologies that derive from evolutionary accounts of individuality (Ruiz Mirazo et al 2000, Nicholson 2014, Baedke 2019).

An important contribution to the debate on biological individuality has surfaced in the last decade out of the greater attention paid to how relations of organisms with the biotic and abiotic milieu challenge some of our received assumptions on individuality. What we will refer to as the *ecological approach to individuality* has been particularly influential in discussions on the status of symbiotic associations, after some of them have turned out to be essential for the development and reproduction of both plants and animals (Gilbert et al. 2012, Gilbert and Tauber 2016). So-called "holobionts" challenge the view of individuals as non problematic well-bounded entities offered by classical physiological and evolutionary perspectives with different criteria. In the most extreme view, the universality of symbiosis has been argued to disqualify any usage of (physiological) individuals in biology (see, e.g. Gilbert et al. 2012). A contrasting stance argues that some symbiotic associations can be understood as proper individuals, heterogeneity notwithstanding (Chiu and Gilbert 2015); whereas intermediate positions consider holobionts as "hybrids" made of parts of different lineages that still preserve the individuality of their components (Chiu and Eberl 2016). Nonetheless, it is important to note that ecological reflections on the status of symbionts do not attempt to replace physiological and evolutionary criteria of individuality. Rather, symbionts might be individuated differently depending on the adopted perspective. Thus, some have considered holobionts as units of selection (Roughgarden et al. 2018), while others admit that some symbionts do count as physiological individuals but not as evolutionary individuals (Godfrey-Smith 2015).

A fourth, evolutionary historical perspective on individuality, is the one which we will rely on in our argument. It encompasses a set of criteria for individuation of entities that derive from the tradition of evolutionary developmental biology, or evo-devo. Like the evolutionary account described above, historical individuality also builds on evolutionary reasoning, yet its criteria differ from the usual variation, heritability, and differential fitness. The concept of *historical individuality* encompases entities (morphological characters, but also processes, or developmental stages) recognized as evolutionary novelties as they arise, and homologies when they persist, thus the two aspects are considered sides of the same coin[2]. The criteria used in the field of developmental evolution to track both the evolutionary emergence and the historical persistence of such units enable evolutionary developmental biologists to "track" individuals in distinct ways (Griesemer 2018). Such entities are distinct "historical individuals" insofar as they "have a definite beginning and potentially an end." (Wagner 2001, p. 10). Moreover, historical individuals fulfill certain criteria that allow us to recognize them as distinct units across taxa and throughout evolutionary time, namely 1) their continuous persistence as a distinct entity in many taxa, and 2) their non-exchangeability with other such modules.

The first criterion to track historical individuals, *persistence*, does not derive from the direct replication of an entity (like in DNA), but rather derives from the historical continuity of an entity within and across species. Persistence as a module is realized by an autonomously malleable developmental basis, which manifests at the population level as somewhat modular variation of the entity (Wagner and Altenberg 1996). The consequence of this developmental autonomy is that the entity can change or remain stable somewhat independently from the changes to the rest of the entities (e.g. in an organism). The classical example is the vertebrate limb, which across vertebrates adopts different shapes and sizes, adapted to different functions, but it yet persists as a distinct developmental entity, whether it results in a bird wing or a human arm.

The second property, *non-exchangeability*, captures the much less intuitive idea that the autonomy of a newly historically individuated part or process results from an evolutionary process of compensation and accommodation of developmental and physiological interdependencies within the organism, and not from the breaking off of previous links. This may be counterintuitive if the modularity of a part is understood to mean a complete loss of developmental integration with the rest, leading to the corresponding loss of the variational integration. However, an alternative way to achieve autonomy seems to have played a major role in evolution, that is, to compensate, or accommodate the side effects on other parts of the organism, thus resulting in a new kind of evolved integration. For example, if vertebrate hind limbs can be individuated as historical individuals it is not only because they change independently of forelimbs (and of everything else), but because they are non-exchangeable. The reason is that, although they develop using shared limb genes, hindlimbs are different from forelimbs also due to their integration in the distal part of the vertebrate body. So the individualization of hindlimb from the forelimb entails both, the relative independence of development of the forelimb, and also that hindlimb evolved a new developmental integration in that particular location, which perhaps overcomes the ancestral association with forelimb. When modular parts or processes are non-exchangeable they constitute an evolved type of organic

[2] Usually evo-devo insights on the ontological status of historical units be labelled as "natural kinds" (e.g. Wagner 1996), rather than as *historical individuals* as we do here.

integration in the overall system, because the corresponding process of individuation is compensatory, rather than solely decoupling. In contrast, human hairs cannot be considered as historical individuals: while they are physically independent morphological entities, they are nonetheless "exchangeable" in the sense that the identity of each hair does not depend on their particular location in the skin. The historical persistence of biological entities (e.g., hind limb) is thus based both in their evolutionary autonomy and in their integrative capacities within the system they belong to (e.g., distal body).

While the studies of the evolutionary origin and stabilisation of organic units have classically focused on parts of the organism, such as the vertebrate limb or a cell type, they have often been extended to include developmental stages (e.g. larval stage vs. adult stage), processes (e.g., menstruation or ovulation), or functions (e.g. behaviors) (see, e.g. Gilbert and Bolker 2001, Love 2007, Scholtz 2005). As historical entities, each of these phenotypes persists and is recognizable across species and can evolve somewhat independently from the rest.

2.2. The individuality of pregnancy

Different notions of individuality depend on the perspective favoured for solving a particular problem, and are largely relative to the methods and practices used to individuate empirical processes of concern (Griesemer 2018). In this context, the purpose of this section is not to engage in definitional debates and decide on one single notion of individuality that should prevail over the others when applied to pregnancy. The role of philosophy in this regard should not consist of recommending biologists to stick to a single, true concept of individuality, but rather to consider individuation practices across disciplines (Bueno et al. 2018; Love 2018). Therefore, here we aim to show that the received notions of physiological and evolutionary individuality do not exhaust the different ways in which the process of pregnancy is individuated in the biological practice, and that new criteria of individuation used in other disciplinary contexts should lead us to regard eutherian pregnant females as a different kind of individual.

From a physiological perspective, it is generally considered that pregnancy encompasses two individuals. The developing embryo is regarded as a distinct entity with its own physiological organization independent of, although related with, the mother. Pregnancy therefore appears to be a relation between two separate physiological individuals each characterised by the maintenance of a distinct homeostasis. Nonetheless, there is no consensus concerning the stage of pregnancy at which eutherian (particularly human) embryos begin to have a separate existence as individuals. Different developmental events have been proposed, including fertilization (Damschen et al. 2006), implantation (Alvargonzález 2016), gastrulation (Smith and Brogaard 2003), or completion of organogenesis (Nuño de la Rosa 2010), to capture when the individuation of organisms is completed in the uterus. In contrast, Kingma (2018) has argued that, until birth, embryos do not fulfill the criteria traditionally used in the physiological account of individuality. Yet, she argues that her position on the mereological nature of pregnant females is independent of the individuality issue, and therefore compatible with the possibility that embryos are indeed individuals.

From the perspective of the evolutionary (Darwinian) individuality, the best-known hypothesis on the evolution of pregnancy, the so-called "conflict hypothesis", conceives of pregnancy as entailing a conflict between paternal and maternal genes, because the former will be "adapted for" obtaining

as much nutrients as they can from the mother, and the latter for limiting that transfer (Haig 1993). Accordingly, the involved parentally imprinted alleles in the fetus will realize these differing interests on resource allocation (Haig 1993). This view, to be addressed in more detail in the following section, attributes interests to the genes (alleles of maternal and paternal origin), which are "expressed" through their interactors: mothers and embryos, the latter acting as the vehicle of the interests of both the mother and the father. Under this model, pregnancy features as an epiphenomenal entity, the pregnant female being a place of negotiation of conflicting or aligned interests of separate individuals, rather than a real biological system on its own. Although modelling a phenomenon in a particular way does not necessarily entail certain metaphysical commitments, it is often the case (as is certainly the case for pregnancy) that metaphysical consequences are inferred from modelling practices.

Ecological perspectives emphasize strong interactive views of biological entities, and thus go further than the previous ones in encouraging views of interdependence also in pregnancy. Debates on the consequences of symbiotic relationships for individuality have a direct counterpart in the different positions on the individuals involved in pregnancy. One might claim that the entities involved in pregnancy are contingently engaged with others forming a heterogeneous entity, whereas from the holobiont perspective one would posit that the pregnant female is a collective individual including female and embryo(s) as same species parts, together with allospecies microbiota. Chiu and Gilbert (2015) rely on the notions of reciprocal scaffolding and niche construction to favour the latter view. In their view, the interactions between mother, fetus and symbionts during pregnancy reciprocally construct each other's experienced environments, facilitating the scaffolding of their development and reproduction.

While debates on the status of holobionts may enrich views of pregnancy, the kind of relations between the closely related mother and embryo cannot be equated to those between pregnant females and the microbiota. The literature discussing the role of scaffolds for reproduction has incidentally commented on the specific relations that enable the development and reproduction of multicellulars, including the relation between mother and embryo in pregnancy. Nonetheless, the notion of scaffolding has been conceived of in manifold ways. Sometimes scaffolds are defined as those organic resources used in development and reproduction, that, contrary to those fueling metabolism, are not incorporated into the system. In this context, pregnancy has been conceptualised as a source of nutrition for the embryo (Minelli 2016). In other cases, developmental scaffolding is interpreted as an instance of the evolutionary tendency towards exploiting increasingly organised developmental environments (Griesemer 2014a, Minelli 2016). Then pregnancy appears as providing a new 'ontogenetic niche' (i.e. the uterus) (Stotz 2008) that increases the reliability of development by removing the difficulties that might interfere with developmental processes (Chiu and Gilbert 2015). Following a further relational insight, scaffolding may include not only the physical interactions between developers and scaffolds to facilitate development, but also 'prostheses', i.e. those parts that, like nests, enhance or substitute for developed parts (Griesemer 2014). Under this view, pregnancy is one of many possible parent-offspring relations, in which some form of strong collaboration emerges, and individuality becomes a matter of degree. For instance, Griesemer (2018) discusses the example of haptic contact between a parent and her child holding hands to cross a street as a form of transient individuality.

In this section we have seen how the concepts of individuality developed in the context of the different biological disciplines are motivated by different criteria of individuation of biological entities. Next we will sketch the reasons why studies on the developmental evolution of eutherian reproduction offer criteria for the individuation of pregnancy that neither the physiological nor the evolutionary concepts can provide, and offer an alternative account of the individuality of pregnancy that incorporates some of the insights of both the ecological approach and evo-devo perspectives on historical individuality.

2.3 Rethinking pregnancy as an evolved reproductive individuality

Reproduction is a crucial feature of life and it confronts us with the fact that in the life we know all living entities are linked to other living entities. An account of reproductive individuality and in particular of the individuality of pregnancy needs to take into account the relational phenomenology that transcends organismal boundaries, and it cannot be strictly physiological nor (Darwinian) evolutionary individual.

The criteria used for the individuation of physiological individuals have to do with the way different functionalities contribute to the self-maintenance of the biological entities considered. Most of the criticisms coming from ecological considerations have to do with the found evidence that some of those functionalities are not realized in isolation but crucially require contributions from other entities. Yet, unlike the physiological systems participating in organismic maintenance (such as the digestive, circulatory or respiratory systems) reproductive functionalities are not just contributions to the self- or the scaffolded maintenance of individual organisms, but contributions to a different type of homeostasis, namely one maintained *between* organisms (Pavlicev et al 2017).

Besides, reproductive individuality cannot be equated to a form of evolutionary individuality either. Because it is a requisite for evolution as a form of transmission with heredity and variation, the neo-Darwinian evolutionary perspective tends to reduce reproduction to replication, focusing on the formal properties of copy making and dismissing, as a consequence, all the material and organizational complexities underlying the process of reproduction. In contrast to this formal understanding of reproduction as incidental, or secondary to gene replication, the call to consider the material processes involved in reproduction has intensified recently. Reproduction cannot be conceived of as a formal process of copy making, but rather as a material process which crucially involves material overlap, i.e. the transfer of parts from parents to offspring (Griesemer 2000), as well as the contribution of a variety of external developmental resources (both environmental and parentally transmitted) that enables the *reconstruction*, rather than the mere transmission of phenotypes (Gilbert and Epel 2008; Jablonka 2004). Indeed, almost all cases of reproduction are scaffolded and engage with other living entities in this sense (Griesemer 2014a,b; Minelli 2016). Under this perspective, the different modes of reproduction are no longer regarded as strategies for maximizing fitness, but rather as complex material relations among different biological entities.

Our approach understands pregnancy as an evolved reproductive individuality which constitutes a historical kind of individual. While evo-devo has classically focused on the evolution of body parts and their interactions, recent work on the evolution of mammalian reproduction allows to apply the criteria for historical individuation to reproductive relations, and enables a view of pregnancy as a historically new, semi-independently modifiable developmental stage in the life cycle of eutherian

females. This occurs not by decoupling of pregnancy from the rest of female biology, but by the evolution of pregnancy-specific mother/embryo interactions. The evolutionary reaccomodation of female biology had as a consequence, we claim, the origination of a new *historical reproductive individual* (namely, the pregnant female) with its own evolutionary history. This new notion of individuality is different from the physiological one because it transcends the functional organization of an organism, and it is different from the evolutionary one because its features cannot be accounted from the units of selection perspective. Rather, as we will see, the evolution of mammalian reproduction brings different female-embryo relations which become increasingly internalised until the emergence of eutherian pregnant females as transient reproductive individuals in which female and embryo have merged.

3. Currently established biological accounts of pregnancy

As different studies show, social representations of scientific knowledge use metaphors influenced by social stereotypes (see e.g., Wagner et al. 1995 for the topic of conception), but also scientific accounts are influenced by social, and particularly by gender biases (see Martin 1991, for the same topic). The language used in biological accounts of eutherian pregnancy is a particularly good illustration of how the social perception of a biological process has influenced its scientific interpretation, and vice versa. Biological and biomedical accounts of pregnancy present it as a conflictual relationship between two independent entities, a "battle", or a "combat" (Ashary et al. 2018) following an "invasive placentation" where the embryo adopts an active role, using "a variety of coercive tactics" (íbid) to "manipulate" the mother (Crespi and Semeniuk 2004). As a result, the maternal response is regarded as "suppressed", leading to an "immunological indolence or inertness of the mother" (Medawar 1953).

In this section, we identify the notions of containment, female provisioning, conflict, and female manipulation by embryo as those capturing the most significant features of current biological conceptualisations of eutherian reproduction, particularly in evolutionary biology.

a. Containment.- Since Aristotle, it has been observed that the generation of animal offspring occurs by hatching from eggs laid externally (oviparity), or by developing the embryos inside the maternal reproductive tract to give birth to live offspring (viviparity) (e.g. Blackburn 2000; Wake 2002). The narrative of the evolution of viviparous reproduction emphasises a form of evolutionary continuity in which structures aiming to protect and nourish the embryo in oviparous animals (the egg shell) are assumed by the physiology of the pregnant female[3]. The transition from oviparity to viviparity is sometimes considered as an evolutionary trend in which organic processes such as fertilization, oogenesis, early development and prolonged development, become increasingly independent of environmental influences, by structurally or functionally internalising them.

[3] While highly modified, the remnants of the ancestral egg formation are still apparent in the early stages of mammalian development. In birds, the maternal reproductive tract deposits albumin (i.e., egg white) and the calcified eggshell as the fertilized egg passes through. The shell is thereby produced by the shell gland, the part of bird genital tract homologous to mammalian uterus. This is similar in reptiles and monotremes (i.e., oviparous mammals), except in that here the shell is soft. In viviparous animals, albumin and egg shell are missing, yet the extraembryonic membranes of oviparous animals have evolved are maintained: as will be explained in more detail below, they evolve to form the placenta.

From an evolutionary perspective, the explanation of the transition from external to internal development weighs the costs and benefits for the female and her offspring, treating the female and offspring as different units of selection. In general, the internalization of development provided by viviparity is suggested to have major advantages to the offspring (such as increased survivorship by avoiding the vulnerable egg stage, increased birth size and offspring vigor due to prolonged maternal provisioning), while to entail a mixture of advantages and costs to females. Advantages include greater mobility and smaller eggs which are less costly to discard when unfertilized, whereas costs range from reduced foraging ability and higher susceptibility to predation during pregnancy, total brood loss upon death, higher energetic costs, lower fecundity, and lesser ability to interrupt the reproductive process and discard the offspring when conditions change abruptly (see Bainbridge 2014; Crespi and Semeniuk 2004, for reviews).

b. Pregnancy as a provisioning relation.- Along with spatial internalisation, the received account of pregnancy in evolutionary biology emphasizes the difference between oviparity and viviparity in provisioning aspects. In the frame of understanding modes of reproduction as strategies for the acquisition of nutritional resources, pregnancy is regarded mainly as a switch in patterns of embryo nutrition, from retrieving the nutrients for development from the yolk to extracting them from the mother. In viviparous mammals (marsupials and eutherians), the placenta, a temporary organ of *fetal* origin, becomes the organ mediating the nutrition by the mother. The placenta evolved from the vascularized membranes of the yolk sac and/or allantois, which in oviparous animals supply nutrients from yolk and gas exchange with external environment. In contrast, in viviparous mammals the membranes fuse with chorion to form the placenta, which attaches to the uterine wall and serves as continuous mediator of nutrients and gas exchange with the maternal blood (Ramsey 1982; Carter 2012). There is a great diversity of placental types among eutherian species with different degrees of penetration of embryonic tissues into the uterine wall, from superficial placentas, where several cell layers separate the blood supplies of mother and embryo, to highly imbricated forms of placentation (usually referred to as "invasive placentation") with close associations of fetal and maternal tissues. Since Haeckel's times, the received assumption in evolutionary biology was that superficial placentas were the ancestral state, and that deep placentation represented the result of the embryo winning the parent–offspring conflict over the degree of parental investment (see Wildman et al. 2006, for references). In turn, this understanding of the evolutionary history of the placenta seems to have been projected back to our understanding of extant pregnancy, insofar as it is depicted as a kind of recapitulation of that hypothetical ancient war.

The perception of pregnancy as directly derived from oviparity by a simple spatial internalization followed by the switch to continuous extraction of maternal nutrients by the embryo, supports an interpretation of pregnancy as a mere *superimposition* of the embryo's physiology on the maternal physiology, contributing to the treatment of mother and embryo as semi-independent entities (Abbot and Rokas 2017).

c. Conflict.- Both internalization and the view of the female as a provisioning resource tend to emphasise that pregnancy benefits individual embryos at the cost of females. This persisting conflict of interests between female and her embryos in pregnancy is then suggested to have driven its further evolution. A particularly influential formalization of interests of participating individuals in pregnancy is the conflict hypothesis briefly discussed in the previous section (Haig 1993, 1996). This

hypothesis pertains to various situations in which a parent is not genetically identical to the offspring that it provisions for and thus also applies to mother and embryo in eutherian pregnancy. It observes that in pregnancy mother and offspring can have misaligned "interests", as the offspring also consists of paternal alleles. The optimal amount of investment of the female's limited resources in current offspring is higher on average from the perspective of the paternal alleles than from the perspective of the maternal alleles. The aduced reason is that the maternal alleles will benefit from investment in further offspring as well, whereas paternal alleles may not, given that the further offspring of the mother may have a different father. It is important to note here that this evolutionary hypothesis is not about the origin of pregnancy (in contrast to internalization), but rather about the evolution of the negotiation at the maternal-fetal interface, once this interface already exists. The strongest evidence for the presence of genetic conflict are imprinted genes (i.e. those genes in which expression from the alleles depends on which parent they are inherited from) in placenta. The prediction of the hypothesis is that the paternal alleles in the fetus will follow the interest of this particular fetus only, and their effects will be to increase the maternal investment and prolong the pregnancy, whereas the effects of the maternal alleles would predictably align with maternal interests and reduce investment to the extent that maintains her ability to produce further offspring. This hypothesis is arguably often used too generously to imply overall maternal-fetal conflict, even if the authors themselves have insisted that it applies to the genes and not to the carriers of genes (Haig 2014). It is also important to note that the proposed consequences of misalignment of interests are about the *degree* of provisioning in already evolved ongoing pregnancy, not about whether the mother or fetus survives, hence, the consequences may be limited to the genes involved in provisioning.

Alternative models of maternal-fetal interaction have proposed that co-adaptation (rather than conflict) between genes expressed in mother and those expressed in offspring has played a major role in the evolution of pregnancy and may offer a complementary explanation for imprinted genes (Wolf and Hager 2006). A difference between these models is interesting for the present discussion: the treatment of maternal and offspring fitness interests separately in conflict theories implies (some degree of) independent agency of mother and embryo, or rather separate interests of maternal and paternal genes within embryo. In contrast, the coadaptation models assign fitness advantage to the interaction itself, namely pregnancy. Even if the latter does mean advantage to both mother and embryo, these advantages are interdependent, i.e. advantage to the mother of the evolutionary change, depends on the co-evolutionary change in the fetus.

d. Female passivity.- Several aspects of the received biological and biomedical accounts of pregnancy imply a passive role of the female against embryo manipulation. The use of the expression "invasive placentation" indeed bears a suggestion that the spread of fetal tissue is imposed upon females and is potentially dangerous to them. Immune response in the pregnant females would be expected for two reasons: first, because the embryo inflicts a wound in breaching physical tissue integrity during attachment and implantation, and second, because this wounding is caused by a tissue which is immunologically different from the female organism. However, as there is no maternal immune response to reject the embryo in spite of implantation and further invasion of the female's tissues by the placental cells, the mother is described as a passive agent, and the focus of attempts to understand mammalian pregnancy is often expressed as aiming to understand how the expected

maternal immune reaction to implanting embryo is *suppressed* by the fetus, for example via the *manipulation* of progesterone production, for the duration of pregnancy (Medawar 1953).

In this section we have presented some of the aspects shaping the received view of pregnancy as a conflicting and unequal relationship between relatively independent entities, examined in terms of an internalization of an ancestral oviparous reproductive mode, in continuous conflict over provisioning, and in which the female is manipulated by embryo against her interests. This view thus provides a strong sense of pregnancy as driven by a combination of antagonistic contributions to self-maintenance and survival of fetal and maternal genes, rather than the reproductive processes functioning for promoting constructive relations between mother and offspring. As we argued in the previous section, different criteria might individuate the same biological processes in different ways. In the next section, we argue that recent empirical and conceptual developments on the evolution of pregnancy support an alternative individuation of pregnancy as a single historical reproductive individual.

4. Pregnant female as a historical reproductive individual

The naming of Eutheria as "placental mammals" not only gives the wrong impression that placenta is unique to eutherians, when also marsupials have one (Renfree 2010). It also suggests that the placenta is the only key innovation that occurred in eutherian pregnancy and thus that the key innovation occurred solely on the embryo side, rather than involving the integrated evolution of the maternal-fetal unit. Importantly, the attribution of the relative importance of fetal and maternal contributions to pregnancy is often biased, or reinforced, by the unequal understanding of the biology of each, itself conditional on accessibility of the respective tissues. For example, the easy accessibility of placental (in contrast to uterine) tissue, has biased the attention to the placental morphology and factors acting towards maternal blood stream. As the placental side is thus better understood than the maternal side, the findings superficially appear as evidence of the unilateral manipulation of the mother by the fetus. Yet a closer look at the literature, in particular recent one, reveals that the interaction is two-sided and very rich, with numerous authors reporting on the bilateral nature of pregnancy regulation in terms of signaling molecules (e.g., Knoefler 2010, Erlebacher 2013, Moffet and Colucci 2014, Pavlicev et al. 2017).

Another important factor that has influenced our understanding of eutherian reproduction as a derived consequence of the evolution of the placenta has to do with the extrapolation of characteristics of the ancestral, oviparous mode, to eutherian reproduction. In contrast, and in line with physiological evidence for the inter-active maternal role, recent findings in evolutionary reproductive biology suggest that the evolution of pregnancy involved crucial innovations on the side of the female, together with a coevolution of extensive interdependencies between mother and offspring, both sides thus forming an evolving relational unit. We claim that the presence of these innovations supports a narrative that, in attributing a decisively greater importance to the evolved *active* maternal role in pregnancy, significantly differs from the one presented in the previous section. In the following we present the alternative view of the origin of pregnancy that results from new research on the emergence of new relational structures, functions, and processes on the female side.

a.- Functional integration as evolutionary reaccommodation.- In contrast with the received view of pregnancy as a superficial kind of internalization in which the mother signifies a form of a living shelter for the embryo, recent research on the evolution of eutherian reproduction has emphasized that the origin of a new kind of integration between the mother and the embryo entailed an integral rearrangement of the interactions among the main physiological systems of the female, namely the nervous (brain and neuroendocrine changes), cardiovascular (increased blood volume, decrease in hemoglobin concentration, increased coagulation), locomotor (skeletomuscular changes in backbone, pelvis, gait), immune and metabolic control systems (e.g., protein metabolism, kidney capacity), to name a few (Bainbridge 2014). From this perspective, the eutherian reproductive system is not just a separated apparatus adapted to protect and nurture an embryo, as it follows from the view of pregnancy as an internalisation of the egg, plus the evolution of the placenta from yolk sac or allantois. The most relevant novelty of pregnancy is not the emergence of a new placental organ, but rather the modification of a range of pre-existing physiological self-maintaining systems to support a distinctly new homeostatic state that incorporates the implanted embryo. This mode of evolution is not surprising. Evolution is a process in which new traits and relations emerge not by a mere addition of new developmental stages or anatomical parts on top of the preexisting, conserved ones, but by the recruitment, modification and integration of the old into a new context (Alberch 1985). The peculiarity of pregnancy lies on the fact that its evolutionary origination did not result from a local modification of a particular system only (e.g., uterine immune system), but of the whole structure and physiology of both female and embryo merged into a system of interdependencies. This relates to our view of pregnancy as a new historical individual in the sense that a new unit is very specifically integrated due to evolved novel internal interdependencies. We claim that considering the *integral reaccommodation* of all the physiological systems that make up eutherian reproduction (including the embryo) should lead us to consider the pregnant female as a single reproductive unit.

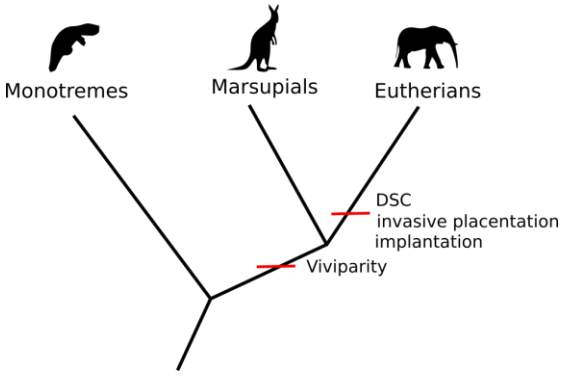

Figure 1. Viviparity is a shared derived trait of marsupials and eutherians. Embryo implantation, invasive placentation, and decidual stromal cells (DSC) occur only in the eutherian lineage (Adapted from Wagner et al 2019, Fig. 1, p. 2).

b. The relational novelties of pregnancy.- Recent research has shown that the evolution of pregnancy did not only entail the rearrangement and modification of previously existing physiological systems, but also the emergence of substantially new type of relational novelties on both the female and the embryo sides (see Figure 1).

While the placenta is not restricted to placental mammals and has originated multiple times in evolution (Renfree 2012; Roberts et al. 2016), the kind of placentation originating in the stem lineage of "placental" mammals (Eutheria) is unique, in particular with regard to the degree of maternal-fetal integration it confers (Wildman et al. 2006). Placentation in eutherians breaches maternal integrity and is associated with implantation. In stark contrast to non-mammalian viviparous animals in which the placenta is only apposed to the uterine epithelium, the maternal-

placental interface of eutherian mammals erodes the maternal uterine epithelium or even the maternal vessel walls. As we saw in the previous section, the received assumption on the evolution of the placenta has been that invasive (so-called hemochorial or endotheliochorial) placentation evolved from superficial placentas with a shallow contact between the maternal and the tissues. In contrast, phylogenetic analyses have recently shown that the invasive placental type was indeed the ancestral state of all eutherians, indicating that eutherian pregnancy arose concomitantly with the origin of highly entangled maternal-fetal interface (Wildman et al. 2006; Mess and Carter 2006).

On the maternal side, recent research has revealed that new specialized cell types, such as the decidual stromal cell, the uterine natural killer cell, and a specialized form of resident macrophages, evolved likely coincidentally with the evolution of mammalian pregnancy (Erkenbrack et al. 2018). Particularly interesting is the decidual stromal cell type, which evolved coincidentally with the evolution of invasive placentation (Chavan et al. 2016; Erkenbrack et al. 2018). These maternal novelties likely enabled implantation and therefore the evolution of eutherian pregnancy. Just like in the case of the placenta, the novelty of the uterine cells relies not only on their distinctive morphology, but on their relational abilities. Decidual cells, for example, allow the mother to "talk" to the embryo, being the main maternal cell interacting with the placenta in eutherian mammals. Indeed, impaired decidualization of endometrium has been shown to interfere with embryo-maternal interactions in humans, thus causing recurrent pregnancy loss. Thus, the maternal organism is actively involved in embryo selection at implantation, a process essential for reproductive success (Salker et al 2010).

c. The individuation of pregnancy.- Pregnancy has been traditionally described by reproductive biologists as a period between two discrete events, implantation and birth, both of which have been shown to entail inflammation (Mor 2007, Mor and Cardenas 2011). However, whereas the first contact of fertilised egg with uterus causes inflammation, this inflammation does not lead to consequent recruitment of immune cells typical of a full-fledged inflammatory response, the one that leads to expulsion (birth) in marsupials. Instead, inflammation is required for successful implantation in eutherian mammals. The inflammatory response is thus modified by the maternal decidual cells to separate the necessary inflammatory implantation from deleterious expulsion, which is delayed in eutherian mammals (Chavan et al. 2016; Griffith et al. 2017). Thus the maternal immune system is not simply suppressed, in order to accommodate pregnancy (Mor and Cardenas, 2011; Mor et al. 2017). Rather, evolution of decidual cells enabled its temporally and spatially local modification. It is important to note that the modification of the immune reaction must be local, not system-wide or persistent, because it would otherwise likely be lethal for the mother. And more importantly for the purposes of our argument, it needs to be modification, not suppression, because aspects of immune reaction are required for implantation to occur. The recognition of the positive role of inflammation in enabling implantation has led to a shift in the language depicting the immunological maternal reaction to pregnancy, from that of passivity and suppression to that of accommodation. This sequence of events in eutherians evolved after the last common ancestor with marsupials, who do not have decidual cells and react to the attachment with expulsion. The eutherian novelty hence consists of the novel cell type enabling a prolonged intrauterine developmental stage to be "inserted" between the initial attachment-related inflammation and final parturition-related inflammation (Griffith et al. 2017; Chavan 2018).

In general, two evolutionary "solutions" of a conflicting situation leading to the evolution of internal development could be considered. One might consist of removing the origin of the conflict entirely, another of integrating and modifying it. Wagner and co-authors go even a step further to suggest that stress pathway-inducing processes offer a particularly strong opportunity to generate novelties, by first internalizing, and then modifying an originally plastic stress response (Erkenbrack et al. 2018; Wagner et al 2018). Therefore, in contrast with the received understanding of pregnancy as an ongoing conflict, embryo implantation, as a disruption of tissue integrity, leads to a crisis (a disruption of physiological homeostasis), the overcoming of which, results in pregnancy.

Research on the role of inflammation in the origin of eutherian pregnancy has two important consequences for the individuality status of the pregnant female. Firstly, it shows that the origination of eutherian pregnancy entailed a major modification of the relational abilities of mammalian females, one that allowed the pregnant female to internalize the embryo as a part of a new reproductive system. Also this means that both the onset and finalization of pregnancy can be seen as coordinated relational events between mother and embryo, rather than occurring when embryo one-sidedly reaches certain stages of development or maturation. Secondly, the inflammatory events that demarcate the extended gestation characteristic of eutherian mammals, allow to individuate the process of pregnancy and identify its origination and evolutionary continuity as a historical individual.

5. The origin of pregnancy is an evolutionary transition in individuality

Major evolutionary transitions, such as the origins of chromosomes, eukaryotes or multicellulars, entail major changes in modes of reproduction (Griesemer 2000b), and often the emergence of new kinds of individuals (Buss 1987, Michod 2000). However, the origin of eutherian pregnancy has not been considered in this context (but see Rosslenbroich 2014, Ch 7, for a different view of pregnancy as a transition in autonomy). The received understanding of pregnancy as a mere evolutionary superimposition of a new reproductive apparatus on an ancestral oviparous individual probably explains this neglect. Here we argue that the evolutionary transformations reviewed in the previous section (female integral reaccomodation, emergence of a new type of placentation and cell type, and modification of inflammation) entail a form of evolutionary transition in which a new kind of historical individual--the pregnant female--emerges.

Under a reproductive perspective, major transitions entail that "entities that were capable of independent reproduction before the transition" (for instance, free living cells) "can reproduce only as parts of a larger whole after it" (as in multicellulars) (Griesemer 2000b). While eutherian mammals do not certainly need their mothers to give birth, the origin of eutherian reproduction did entail that entities that were capable of independent reproduction before the transition (namely, oviparous mammals) can only reproduce in strong association with their embryos, which, in turn, can only develop in close association with their mothers.

Concerning individuality, Richard Michod (2000) has argued major transitions involve the emergence of new levels of individuality, and he proposes conflict mediation between lower level and higher level units with different interests as the main factor allowing those transitions. As we saw above, in focusing on the gene level, mainstream evolutionary approaches to pregnancy have

tended to attribute evolutionary individuality to the genes involved, and to parents and embryos as their carriers. In contrast, we argue that the evolutionary modifications that led to the origination of pregnancy should be rather interpreted as a major transition in individuality where a new higher level of integrated unit emerged. Insofar as pregnant females and embryos are of the same kind, but, due to their differing developmental stages of a very different capacity, the origin of pregnancy can be understood as a form of fraternal-egalitarian transition in individuality[4] in which two kinds of entities previously separated in oviparous reproduction, mother and embryo, are *merged* into a single reproductive individual. In this sense, pregnancy can be considered as a last of the successive stages of female integration of reproduction: from releasing an unfertilized egg to be fertilized and developed externally, to internal fertilization followed by a largely external development (i.e. oviparity) to viviparity, in which case both fertilization as well as great part of development are incorporated within the female's body. This integration varies in extent and time: in some species (marsupials) development has evolved to become integrated with reproduction during an extremely short gestation period, while the extension of pregnancy has allowed eutherian mammals to integrate development and reproduction until a much later stage. This view aligns with Rosslenbroich's (2014) characterisation of pregnancy as instantiating the latest stage of a trend towards internalization in the evolution of mammals.

If pregnancy is considered as an evolutionary novelty it is because it, after origination, persisted as a reproductive entity in evolution, and itself became a modifiable (i.e. evolvable) unit, what we call a historical individual (see section 2). We claim that pregnancy can be inviduated in this way because it fulfills the criteria of persistence and non-exchangeability characteristic of historical individuals. The first is manifest in the form of a coordinated reproductive physiology constituting a transient, but clearly demarcated, individuality, a derived characteristic of the eutherian lineage with continuous presence since its origination (Fig. 1). As argued in the previous section, the inflammatory events following implantation and preceding birth are the two criteria used in evolutionary developmental studies of pregnancy to individuate it. The second involves the non-exchangeability of the developmental stage of pregnancy in terms of its *specific* relations within (i.e. integration with) the system in which it is embedded. This concerns the unique and specific modifications of female physiology that enable pregnancy and hence integrate it with other developmental stages in female lives. By individuation, eutherian pregnancy also obtains a certain degree of evolvability on its own, in the sense of new ways of generating potentially adaptive variation and therefore new potential to evolve. Such high evolvability is indeed reflected in the highly diverse manifestations of eutherian pregnancy realized in extant eutherian taxa.

6. Historical reproductive individuality is distinct from other forms of individuality

In this section we explain how our proposed notion of historical reproductive individuality as applied to eutherian reproduction is distinct from, while not excluding, other forms of individuality.

[4] Queller (2000) distinguishes fraternal from egalitarian transitions in evolution: the former refers to the generation of new units by the coupling of homogeneous entities, such as cells generating multicellular individuals or individuals in colonies. The latter refers to the merging of heterogeneous entities, such as nucleus and organelles forming cells.

Firstly, our concept of historical *reproductive individual* is independent from that of a physiological individual. As we argued in section 2, while physiological functions are generally understood as contributing to the self-maintenance of organisms, pregnancy does not contribute to individual viability, but to a different type of homeostasis, namely one maintained *between* organisms. Pregnancy evolves as a physiological reproductive system that generates offspring, and brings about a new form of individuality in the living realm. Insofar as the relation between female and embryo contributes to reproduction, and not merely to the self-maintenance of a higher order physiological whole, pregnancy is a *functionally integrated system*, rather than an encounter of two independent individuals, or a vehicle conferring certain advantages to an independent individual in a particular life stage. This means that there might be a lack of correspondence between the criteria used to individuate physiological individuals and those applied to individuate pregnancy. The proposed individuality is transitional, that is, it is not demarcated by birth and death. Rather it has a beginning (implantation) and the end (birth), upon which the female and embryo enter a new form of individuality. As a consequence, physiological and reproductive individuality might overlap (females do not cease to be physiological individuals during pregnancy) but they do not need to. For instance, it might be argued that embryos become fully-fledged organisms before being hatched or born, and thus that birth is not a proper marker of physiological individuation (Nuño de la Rosa 2010), insofar as it is not systematically related to the degree of developmental maturity. In contrast, birth does play a key role in the delimitation of reproductive individuality: pregnancy inaugurates a reproductive individual in which female and embryo are transiently entangled from implantation to birth. It might be argued that, given the extended period of neonatal immaturity that follows the birth in some mammals, and their dependence on lactation, birth should be considered as an arbitrary event from a reproductive perspective. In this view, the individuality of pregnant females would gradually disintegrate after birth by changing the set of maternal-offspring interdependencies to others. However, such a position would not be able to individuate pregnancy, but rather the more general kind of relationship mediating mothers and offspring among mammals, including oviparous mammals.

Secondly, our relational account reveals an important contrast to the conventional evolutionary conceptualization of pregnancy. While, from a purely genetic perspective (leaving mitochondrial genes aside), paternal and maternal roles are ontologically equivalent, from a reproductive perspective, this is not the case. The reason is that the latter account integrates in the process of reproduction the genetic, morphological, developmental and physiological processes, which affect material reproductive relations among living systems and which result in the production of a new organism with a new life history. Reproduction is thus treated less as a point event in the lifetimes, but rather as itself a developmental process, with one of its stages being formation in utero.

Thirdly, the proposed kind of reproductive relation transiently emerging in pregnancy is also distinct from other relational accounts of individuality. As we saw in section 2, the consideration of ecological interactions has led to either abandon the very notion of individuality, or to broaden it to the point of including the case of a parent and her child holding hands as a form of hybrid individual characterised by their temporary fusion (Griesemer 2018). Scaffolding has been a candidate model for understanding the pregnancy relation. Yet, we believe that in eutherian reproduction, the reproductive female is not a mere scaffold for embryonic development, either conceptualized as a stable environment, a source of nutrition, or a facilitator of development. Rather, mother and embryo participate in the co-production of the offspring, by forming a temporary reproductive

individual. The distinct status of pregnant females as compared to other forms of individuality resulting from scaffolding relationships lies in the intrinsic nature of the relation, in that it is itself an evolved entity, in which both sides of the relation are modified specifically in, and for this relation. Maternal-fetal interface evolved as an inseparable unit with the reproductive function, and this function considerably contributed to the evolvability of the groups with this new unit. As we argued in section 2, the autonomous persistence of historical individuals is not only reflected in their evolutionary continuity but also in their distinctive ability to change as compared to other historical individuals. The relative ability to evolve of eutherian mammals, or more specifically of the pregnant female as a unit, is reflected in species richness of the eutherian lineage and the characteristic diversification of the maternal-placental interface.

6. Conclusion

We have argued that Eutherian reproduction brings forth pregnant females as historical reproductive individuals. This individuality is relational because its features are associated with the way female and embryo relate in reproduction. According to our understanding, eutherian reproduction is enabled by a developmental relational system evolved as a collaborative organization. It is historical because it has evolved as a particular organization of relations in reproduction that fulfil the criteria of persistence and non exchangeability. In the case of eutherian pregnancy, offspring is generated as the result of a mutually active relation between mother and embryo. In this regard, we have contrasted widely established assumptions about pregnancy, and have explored how eutherian reproduction has evolved as a temporary merging of female and embryo involving major innovations at various organizational levels. The origin of eutherian pregnancy cannot be conceived as the simple containment of the fertilized egg followed by the loss of the shell and the origin of a new organ, the placenta, enabling a new pattern of nutrition. Rather, it entailed an integral reaccomodation of the physiological systems that made up oviparous organisation. This reaccommodation included the embryo itself which through the modification of the inflammatory response to implantation, was incorporated into the pregnant female as a part of this new individuality. The evolutionary emergence of a fundamentally new type of individual based on a myriad of maternal-embryonal relations is overlooked by existing accounts. Accordingly, we appeal to the criteria used in developmental approaches to the evolution of pregnancy in favour of considering the pregnant female as a historical form of *reproductive individual* which has evolved as a special kind of entangled relation.

Both biology and medicine have so far overlooked the reality of pregnant human females as distinct individuals, and this has had far-reaching consequences, not only for medical practices applied to pregnancy, but also for the social interpretations of reproduction. As Griesemer (2018, p.138) contends, we need "concepts of individuality in science as well as in other practices of everyday life in order to tell stories about what goes on in the world, do science, and make attributions of properties, relations, responsibility (causal or moral), and standing (e.g., epistemic, moral, legal)." Indeed, revisiting eutherian pregnancy from the perspective we have sketched here reveals a narrative of the evolution of reproductive relations in which the specificity of evolved traits and relations brings about emergent individuals. Although we only attended the case of eutherian pregnancy here, similar studies can probably be carried out for other reproductive cases.

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