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The evolution of reproductive characters: an organismal-relational approach

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Abstract

This paper delves into the character concept as applied to reproduction. Our argument is that the prevailing functional-adaptationist perspective falls short in explaining the evolution of reproductive traits, and we propose an alternative organismal-relational approach that incorporates the developmental and interactive aspects of reproduction. To begin, we define the functional individuation of reproductive traits as evolutionary strategies aimed at enhancing fitness, and we demonstrate how this perspective influences the classification of reproductive characters and modes, the comprehension of *shared traits* as resulting from conflicts of evolutionary interest between individuals, and the explanation of reproductive diversity. After outlining the shortcomings of this framework, we introduce an organismal-relational approach grounded in evolutionary developmental studies of reproduction. This view provides a revised classification for reproductive characters and modes and offers a new understanding of *interorganismal traits* that takes into account their inherently relational nature. Lastly, we present the research agenda that emerges from this approach, which addresses the core explanatory gaps left by the adaptationist perspective, including the explanation of reproductive homologies and homoplasies, the developmental constraints associated with the evolution of reproductive modes, and the evolvability of reproductive characters.

0. Introduction

Although heredity has long been a cornerstone of evolutionary theory, the intricacies of reproduction itself, as the process by which biological individuals of a given type are produced from previous organisms, requires further elaboration (Jacob 1970). Recently, there has been an increasing interest in the field of reproduction (Fusco and Minelli 2019, 2023), denoting a growing recognition of its significance in bridging development and evolution. It is therefore crucial to examine and compare different approaches to reproduction in evolutionary biology.

The conventional understanding of evolution largely reduces reproduction to heredity. This view rests on two fundamental assumptions. Firstly, reproduction is viewed as a copying process, limiting heredity to the transmission of genetic programs. Secondly, reproductive modes (i.e., the ways by which organisms of a given kind are produced from previously existing organisms) are often conceptualized as evolutionary strategies designed to maximize fitness. These assumptions convey a functional-adaptationist interpretation of reproductive phenomena. Critics of this gene-centered view have pointed out that it overlooks the material processes integral to reproduction (Griesemer 2000, 2005, 2014; Chiu and Gilbert 2015). This has unfortunately also been the case in evolutionary developmental biology (evo-devo), where reproduction has received less attention than other processes, such as the development of morphological characters. Notable exceptions include the research on amphibian viviparity by Marvalee Wake and colleagues (Wake 2004; Buckley et al. 2007), the study of eutherian pregnancy by Günter Wagner and Mihaela Pavličev (Wagner et al. 2014), or the work by Marty Cohn on male external genitalia (Herrera and Cohn 2014).

Three conceptual biases within evo-devo explanations may account for this relative neglect (Nuño de la Rosa 2023). On the one hand, the traditional emphasis on the study of form has led to overlook function, resulting in a morphological bias. Additionally, an adult-centric bias has shaped a teleological view of development, focusing primarily on the generation of mature individuals (Minelli 2003), thereby dismissing the role of reproduction in the life cycle. Lastly, an internalist bias has contributed to the disregard of interorganismal relations, as evolutionary embryology has historically concentrated on changes within the embryo, often treating the developmental environment merely as a background condition. Although recent efforts in ecological evolutionary development (Gilbert and Epel 2009) have aimed to overcome this latter bias, the evolution of interorganismal interactions in reproduction remains largely underexplored.

Previous studies have investigated a range of reproductive phenomena from an organismal and relational approach, such as pregnancy, within the context of biological individuality (Nuño de la Rosa 2010; Nuño de la Rosa et al. 2021), agency (Nuño de la Rosa 2023), and collaborative interdependencies (Etxeberria et al. 2023; Etxeberria 2023). In this study, we examine the relational aspects of reproduction through the character concept, which allow usus to explore a broader spectrum of evolutionary reproductive relations.

The notion of character addresses the units organisms are composed of, which are integrated at different levels of organization (Wagner 2001). These units include component parts of organisms (such as feathers or limbs, but also molecules and cells), as well as developmental processes and social behaviors. The character concept is a core concept in biology, for it serves a multitude of roles, ranging from identifying cladistic groups and populations for evolutionary studies to serving as a starting point for studying developmental mechanisms. Despite its relevance in systematizing and explaining diversity, the concept of character is underdeveloped and demands further theoretical study. Here, we are interested in conceptualizing reproductive characters, including gametes, gonads, courtship behaviors, incubation methods, or embryo nourishment arrangements. We recognize as reproductive traits the morphological, developmental, physiological, or behavioral features that play a direct role in the processes leading to the production of new individuals of a given kind. They typically shape reproductive diversity across animal groups and jointly define reproductive modes or the different ways in which organisms reproduce, such as oviparity, internal fertilization, or matrotrophy.

The definition of scientific concepts and the criteria used to individuate the units these concepts refer to are theory-dependent and are deeply shaped by the epistemic goals pursued. Conversely, individuation criteria shape the epistemic range of possibilities enabled by such conceptualization Current literature provides several examples of this epistemic contextual varibility in evolutionary biology (see, e. g., Brigandt 2003 for homology; Brigandt and Love 2012 for novelty, and Villegas et al. 2021 for evolvability), and the character concept is not an exception (DiFrisco, unpublished).

This article explores the criteria used for individuating reproductive characters within two major theoretical approaches in evolutionary biology: the neo-Darwinian adaptationist framework, grounded in optimality theory, and the organismal framework, rooted in evo-devo theory and expanded to encompass the relational dimensions of reproduction. Firstly, we introduce the functional individuation of reproductive characters and critically assess how it shapes biological classifications and explanations of reproductive modes and traits (Section 1). We then present an alternative organismal-relational approach, which offers a more comprehensive and detailed taxonomy of reproductive characters and modes (Section 2). Finally, we examine the explanatory possibilities offered by our proposal, which overcomes some of the problems raised by the functional approach (Section 3).

1. The functional individuation of reproductive characters

The main research question in standard evolutionary theory centers on how evolution shapes organisms to optimize their reproductive success (Fabian and Flatt 2012). In this theoretical framework, characters are individuated by their functions, conceived in terms of adaptive design. Reproductive characters are commonly viewed as finely-tuned adaptations, a perspective consistent with life history theory (see Reznick 2014), and particularly with theories of parent-offspring conflict (Trivers 1974).

Functional definitions have been instrumental in categorizing reproductive modes and characters of diverse developmental and evolutionary origins into the same functional categories. Reproductive modes are seen as reproductive strategies, characterized by “patterns that have advantages and disadvantages that affect their evolution” (Blackburn 1999, p. 995). Such an abstraction from material reproductive relations enable generalizations such as the following: “The means by which provisioning occurs varies taxonomically, but the result is the same—significantly expanded scope for sexual, parent-offspring, and sibling conflict in multiple new arenas” (Furness et al. 2015, p. 85). For instance, viviparity is defined according to its function (namely, the production of live young), , abstracting away underlying processes and relations contributing to this outcome.The same epistemic strategy applies to reproductive characters. A prime example is the functional definition of the placenta, individuated as the intimate apposition or fusion of maternal and fetal tissues facilitating the physiological exchange of substances, including water, nutrients, wastes, and other molecules for maternal-fetal communication (Mossman 1937; Whittington et al. 2022).

1.1. A functional taxonomy of reproductive modes and reproductive characters

Functional definitions facilitate the recognition of the same reproductive patterns in different animal groups, thus “transcending taxonomic, ecological, geological, and geographical boundaries” (Blackburn 2015a, p. 961). For instance, Furness and colleagues argue that “[i]f the placenta is broadly defined as an apposition of maternal and fetal tissue specialized for the transfer of nutrients […], then such an organ has evolved not only in mammals but also in fish, sharks, and rays, reptiles, and many groups of invertebrates” (Furness et al. 2015, p. 86). This functional individuation has led to classifications of animal reproductive modes according to two parameters: (i) their mode of parity, involving either oviposition (oviparity, or egg-laying reproduction) or parturition (viviparity, or live-bearing reproduction), and (ii) their mode of nutrition, encompassing lecithotrophy (yolk-feeding) and matrotrophy (post-fertilization nourishment). Both parameters are defined according to their functional outcome, and their combination results in the categorization of animals into four distinct groups (see Table 1): lecithotrophic oviparous (e.g., birds, turtles, flies), matrotrophic oviparous (e.g., platypus), lecithotrophic viviparous (e.g., some fishes and spiders), and matrotrophic viviparous (e.g., eutherian mammals, marsupials, some salamanders). This classification is employed to systematize diversity and reconstruct phylogenies, revealing two key insights. Firstly, oviparity and lecithotrophy are the ancestral states in all major groups. Secondly, viviparity and matrotrophy have evolved independently multiple times in vertebrate and invertebrate groups.

Within this framework, an important category of reproductive characters comprises what are referred to as *shared traits*. This term was coined to encompass those characters that evolve as a result of conflictual interactions between individuals whose genetic interests are only partially aligned. Shared traits are conceptualized as the evolutionary outcome of "adaptations and counteradaptations through antagonistic selection" (Furness et al. 2015, p. 77). This broad definition comprises a wide range of traits, including developmental events and processes (e.g., embryo selection, implantation, in utero nutritional supply and growth rate, gestation length and birth size, postnatal growth rate) and behaviors (e.g., infanticide, suckling behavior, solicitation of nursing, size, date of weaning, dispersal behavior, cooperative breeding, resource sharing).

1.2. How reproductive characters are explained and used to explain

The functional individuation of reproductive traits significantly impacts their explanation and subsequent application in explaining other biological characters. Functional explanations suggest that the evolution of reproductive modes, such as viviparity, occurs when the associated benefits, like increased offspring quality or survival, outweigh the costs, such as reduced locomotor performance (Crespi and Semeniuk 2004; Furness et al. 2015; Shine 2014). Conversely, functional constraints would pervade the evolution of reproductive modes in certain circumstances. For instance, it is argued that viviparity has not evolved in birds because reverting characters such as endothermy, egg incubation, increased egg-yolk provisioning or eggshell hardening would be too energetically costly (Blackburn and Evans 1986). Similarly, viviparity is said to be prone to evolve in some lizards of the genus *Lerista* when its costs, such as locomotion reduction, are attenuated. This is the case with *Lerista buganvilli*, a semi-fossorial skink species that inhabits caves and burrows, where viviparity does not affect its locomotion (Qualls and Shine 1998).

The conflict theory of reproduction yields predictions concerning the evolution of reproductive traits, enabling targeted expectations about tissues, life history stages, and associated traits affected by conflict (Furness et al. 2015). An illustrative example is offspring size. In oviparous species such as turtles, maternal control over nutrient supply results in egg size that aligns with the mother's optimal investment, aiming to distribute resources among the maximum number of offspring (Janzen and Warner 2009). This results in eggs being smaller than would be optimal for the embryo. Conversely, in matrotrophic viviparous species embryos can exert some influence over maternal nutrient transfer. Consequently, offspring size reflects a compromise between parental and offspring interests. In eutherian pregnancy, the gene imprinting hypothesis suggests that genes inherited from each parent play a different role in determining resource allocation during pregnancy. Conditions such as maternal hypertension and alterations in insulin metabolism (Haig 1993) illustrate the predicted impact of imprinted genes on the differential distribution of resources between maternal and fetal systems.

Crucially, this functional framework enables the interconnection of diverse traits, ranging from physiological mechanisms to behavioral strategies. For instance, it predicts an evolutionary association between reproductive modes and mating strategies, despite the absence of a known direct material link between those traits. Zeh and Zeh (2001) propose that the presence of polyandry in primates serves as a compensatory mechanism for genetic incompatibility, which is estimated to be around 70% in humans.

Several issues surface when examining the functional individuation of reproductive characters. Firstly, the emphasis on the functions of reproductive characters, irrespective of their developmental constitution and functioning, often results in the oversight of both similarities and differences between such traits (Fusco and Minelli 2019). Since the selection process is blind to the mechanisms shaping a character, exclusive reliance on this perspective might result in errors in classification and phylogenetic reconstruction. Consequently, the traditional four-class classification of animal reproductive modes fails to capture the richness of natural diversity and the relevant ecological and physiological aspects of reproduction (Lodé 2012). Additionally, functional individuation of reproductive traits risks leading to flawed phylogenetic reconstructions by ignoring the material dimension of reproductive characters. A notable example is Daniel Blackburn's rejection of the hypothesis of multiple origins of oviparity in squamates (Blackburn 2015b).

Concerning explanation, this framework is arguably limited in addressing key research questions about the evolution of reproduction. On the one hand, it cannot address the shared developmental origins of homologous traits, which is crucial for understanding their evolution. A focus on development and relations is critical for accurately tracing homology and homoplasy in reproductive traits (Amundson 2005; Wake et al. 2011). For instance, the functional definition fails to distinguish between different types of placentas according to their development, as they are grouped on the basis of purely adaptive criteria. On the other hand, functional individuation overlooks developmental biases and evolvability. In confining itself to functional constraints and adaptive potential, it does not allow to examine whether reproductive modes have distinctive evolvabilities, or why certain transitions are more feasible than others.

In the following sections, we introduce an alternative framework that theorizes reproductive characters from an organismal and relational perspective, offering new individuating criteria that ground alternative classifications (Section 2) and explanations (Section 3).

2. The organismal individuation of reproductive characters

Embracing a perspective that encompasses the organismal and relational dynamics of living beings serves as a foundational framework for understanding various biological features, particularly reproductive characters (Baedke 2019; Cortés-García and Etxeberria 2023; Etxeberria 2023; Etxeberria et al. 2023; Etxeberria and Umerez 2006; Nuño de la Rosa 2023; Nuño de la Rosa et al. 2021). By adopting an organismal-relational view of reproductive characters, we aim to consider not only the materiality of reproduction but also to incorporate a functionally sensitive perspective on reproductive traits. While evo-devo is well-suited for this task, it needs to be expanded to include the study of functional relations, as it often confines the individuation of characters to body parts or morphological traits (Wagner 2001). In contrast, the organismal-relational approach also encompasses dynamic entities like processes, activities, and behaviors as reproductive traits.

This expanded view introduces new criteria for individuating processes and activities (see DiFrisco and Jaeger 2021 for process homology). As a result, it broadens the range of explanations for evolutionary questions that are often overlooked by the adaptationist framework, including novelty, modularity, integration, evolvability, homology, or homoplasy, particularly as they relate to reproduction.

In our proposal, reproductive characters are body parts, activities or behaviors that are *integrated into the organism and serve specific reproductive functions by interacting with other characters of the same organism or of other organisms*. Two aspects of this definition require further clarification. First, our perspective of functions differs from that of the adaptationist framework. Our standpoint does not accord design functions a central epistemic role in character explanation in the form of "character X evolved because it was selected for function Y". Instead, we introduce a systemic notion of organismal functions emerging from developmental processes and material relations. Hence, reproductive characters are regarded as systemically organized entities, intricately linked in such a way that they contribute to successful reproduction. Second, the relations that we identify as characterizing reproductive characters are of two kinds. *Intraorganismal relationality* concerns relations among different component parts or processes contributing to the maintenance and functioning of individual organisms across various levels of organization, from gametes to reproductive organs and extraembryonic structures. *Interorganismal relationality* relates to interactions between individual organisms, including relations between sexual partners for fertilization, and between parents and offspring for successful embryo development.

With this theoretical proposal, we aim to clarify, systematize, and expand the criteria implicitly used in some evo-devo studies of reproduction to include organismal relationships. We introduce a novel taxonomy of reproductive characters in sexually reproducing animals, grounded in an organismal-relational approach (Section 2.1). We then focus on traits that are constituted in the interplay between individual organisms, advancing the notion of interorganismal *traits* as opposed to shared traits (Section 2.2). Finally, we introduce an alternative classification of reproductive modes based on both parent-parent and parent-offspring relations (Section 2.3).

2.1 An organismal taxonomy of reproductive characters

Sexual reproduction is an inherently relational process, as it requires syngamy (i.e., the fusion of the two gametes into the zygote)[1]. Through this lens, we propose a taxonomy of reproductive traits for sexually reproducing animals according to two parameters: the nature of the characters, namely, structural, physiological, behavioral, or temporal, and the kind of relationality they engage in, namely, intraorganismal relationality, interorganismal relationality between parents, and interorganismal relationality between

[1] In our understanding, sexual reproduction can be uniparental (i.e., self-fertilization) or biparental (i.e., amphigony) (see box 1.3. in Fusco and Minelli 2019 for a discussion on different notions of sexual and asexual reproduction).

parent and offspring (see details in Table 2). This two-dimensional categorization allows us to identify various types of reproductive characters involved in relevant reproductive processes, interacting with other reproductive or non-reproductive characters of the same or other organisms. For instance, this taxonomy allows us to identify temporal patterns related to embryo incubation, such as timing of birth or duration of brood retention, as well as physiological characteristics of parent-parent interactions for reproduction at different levels, such as sperm-egg interactions, seminal proteins' interaction with female physiology, or characteristics of implantation. While outside the scope of this paper, other kinds of relations are also important for reproductive success, particularly in social species These include playing behavior, in utero sibling cannibalism, alloparenting care, or grandmother effects. Also, reproductive relations might encompass interspecific relationships, such as the role of the vaginal microbiota in fecundation or the transfer of maternal microbiota to offspring in birthing.

Importantly, our classification of reproductive relations does not aim to deliver mutually exclusive categories. Reproductive characters often participate in multiple relations simultaneously. For instance, ovarian tubes are reproductive characters insofar as they are functionally and organizationally integrated into the organism and interact with other parts, thus allowing for successful reproduction by intervening in (i) intraorganismal relationality, as ovarian tubes are integrated into the female reproductive system, connect the ovary with the uterus and aid in the movement of ova; (ii) interorganismal relationality between sexual partners, as ovarian tubes interact with sperm and facilitate spermatozoa mobility; and (iii) interorganismal relationality between parents and offspring, as ovarian tubes are involved in fertilization and, in some cases, incubation. This same example illustrates that elements constituting a reproductive character may interact at different organizational levels, spanning from gametes, zygotes, embryos, tissues, and body parts to whole mature organisms. Both forms of relationality (i.e., intra- and interorganismal) can be identified at multiple levels (i.e., cellular, tissular, organismal, social...) and interactions among relata are not necessarily intralevel (e.g. cell-cell interactions), but also interlevel (e.g. cell-organ interaction). Reproductive traits generated in the interaction between multiple organisms hold particular significance in our analysis. This framework allows evolutionary change to be traced through relationality, not only through the genetic or morphological characters of individual organisms. For instance, in eutherians, the process of decidualization (which involves significant changes in the cells covering the uterine endometrium allowing embryo implantation) is in many groups induced by the attachment of the blastocyst, thus constituting an *interorganismal* character. However, some species (i.e. those with spontaneous ovulation) have evolved internal control of decidualization so that it occurs cyclically and is hormonally regulated. This spontaneous decidualization occurs irrespective of external stimuli, constituting an *intra*organismal character that has, nevertheless, interorganismal evolutionary origins. Thus, relationality itself is an evolving character, as some forms can change to produce others through, for example, a process of internalization and autonomization of the character (Wagner et al., 2019).

2.2. Interorganismal traits vs shared traits: relational homology

Although characters are always defined in relation to other characters, there is a significant concern about the neglect of interindividual interactions in various fields of reproductive biology (see Kekäläinen 2021 on human reproduction, Lamarins et al. 2022 on eco-evolutionary population dynamics, Oliveira and

Bshary 2021 on behavioral biology, or Wade 2022 on maternal-zygotic co-evolution). To better account for those reproductive characters that emerge from the interactions between parents and between parents and offspring, we propose the notion of *interorganismal traits* in contrast to the conventional idea of shared traits. We propose two criteria for identifying such traits.

Firstly, interorganismal traits cannot be ascertained by looking only at single individual organisms. On the contrary, they developmentally arise from interactions between organisms and do not constitutively belong to any one of them in isolation. Therefore, the concept of interorganismal trait is genuinely interactive, accounting for the material changes and rearrangements involved in reproductive processes as a result of relational dynamics. For instance, placentas cannot be realized without the interplay of maternal and fetal tissue dynamics. Therefore, the study of interorganismal traits cannot be reduced to their functional aspects nor their morphology, as it concerns the evolution of relations and not of individuals. Furthermore, this shift explains why the evolution of interorganismal traits cannot be reduced to co-evolved pairings, as proposed by the conflict theory. Conventional co-evolution models involve interactions between individuals (such as parent and embryo), which are the ones that are considered to evolve. However, by focusing on the relations themselves, reproductive processes appear as grounded on a series of interactive relations, to which co-evolution models are blind. In this context, reproductive relations giving rise to interorganismal traits resemble symbiotic relations more than antagonistic co-evolutionary dynamics. Thus, interorganismal traits refer to relations embodied in an emerging supra-organismal level of organization that causally affects individuals at the organismal level (i.e., parents and/or embryos).

Secondly, like any other character, interorganismal characters persist in evolutionary time, forming lineage trajectories grounded on processes of stabilization (see section 3.2). As a result, they evolve semi-independently of other traits and have their own evolutionary potential. This shift in focus from individuals to relations enables us to consider the evolvability of specific sets of relations rather than of sets of individual traits. This can be seen in characters that first evolved as interorganismal relations and later became intraorganismal in certain groups, as in the aforementioned example of decidualization.

These two criteria (interorganismal dependency and semi-independent evolution) have been already employed to individuate the reproductive characters involved in eutherian pregnancy (Nuño de la Rosa et al. 2021). However, they can be generalized to individuate reproductive characters in sexually reproducing animals, as elaborated in the next section. Furthermore, the concept of interorganismal character does not need to be restricted to reproduction. Interorganismal characters can be found in other domains of life and also in phenomena unrelated to reproduction, such symbiotic assemblies (Chiu and Gilbert 2020, Suárez and Triviño 2020). Hence, although in this article we focus on interorganismal traits in sexually reproducing animals, they can be seen as an instantiation of a more general category encompassing different kinds of interorganismal characters. In the following section, we present a classification of reproductive modes applying an organismal-relational approach.

2.3. An organismal taxonomy of reproductive modes

In this section, we offer a twofold classification of reproductive modes accounting for fertilization mode and incubation mode, respectively. Firstly, we identify patterns of parent-parent relationality, accounting for how syngamy (i.e., gamete fusion) is achieved. Secondly, we discern forms of parent-offspring relationality, addressing how embryos are incubated and nourished. These two relations impose strong material and developmental constraints upon reproductive processes and their evolution. For this reason, we use them as the foundation for our classification, which not only provides a general framework for understanding reproductive processes but also offers a basis for developing more detailed classifications tailored to specific clades. By applying these parameters at a finer level, we can incorporate additional reproductive characters to more precisely delineate similarities and differences between reproductive modes.

2.3.1. A taxonomy for parent-parent relationality

Various forms of parent-parent relationality are implicated in the conditions under which gametes meet (i.e., insemination) and merge (i.e., fertilization, syngamy). We identify two primary relational factors characterizing parent-parent relationality. Table 3 offers a taxonomy of reproductive modes in sexually reproducing animals attending to the conditions under which syngamy occurs. First, based on the site of fertilization, we distinguish external fertilization, where gametes fuse in the environment, from internal fertilization,where gametes merge inside the body. Second, we consider the specific relations between parents that facilitate the encounter of gametes and increase the chances of successful reproduction. By applying these two parameters, we can identify different reproductive modes, which include the free dispersal of gametes into the environment, where syngamy occurs (external fertilization without parent-parent interactions), free dispersal into the environment of spermatozoa that swim and reach internally retained eggs (internal fertilization without parent-parent interactions), release of sperm over previously deposited eggs (external fertilization with indirect parent-parent interactions), spermatophore uptaking (internal fertilization with indirect parent-parent interactions), close coupling for sperm release directly onto the eggs (external fertilization with direct parent-parent interactions), and direct transfer of sperm to the female genital tract (internal fertilization with direct parent-parent interactions)[2].

2.3.2. A taxonomy for parent-offspring relationality

Regarding parent-offspring relationality, we consider two aspects: incubation and post-fertilization nourishment (see Table 4). Based on these two parameters, reproductive modes can be classified into the following categories: *ovuliparity*, where there is no form of incubation or nourishment[3]; *oviparity*, with a short period of internal incubation and limited or no post-fertilization nourishment; *monotreme oviparity*, notable for substantial nutrient transfer during limited internal incubation before oviposition; *lecithotrophic viviparity*, characterized by an extended period of internal incubation without further means for nutrient transfer; *matrotrophic viviparity*, involving extended incubation accompanied by nourishment

[2] For the present taxonomy, we restrict our scope to those relations that facilitate the achievement of syngamy. Nonetheless, a similar complementary classification could be elaborated to address parent-parent relationality with respect to courtship or parental or alloparental care of offspring after birth.

[3] This form of reproduction is regarded by the rationale of the *amount of investment* in economic terms (Lodé 2012) as the least invested by the parents. However, the absence of post-fertilization care does not entail lower investment in terms of energy, time, or effort by the parents, as shown by the example of the construction of complex nests by the fish *Gasterosteus aculeatus* put forth by Lodé himself. This shows that the criteria of the amount of investment is not operative for classifying animals according to their reproductive mode.

supply; *brooding*, characterized by a secondary period of incubation after partition; and *matrotrophic brooding*, which entails nutritional supply during secondary incubation[4].

Our classification distinguishes itself from standard approaches in reproductive biology in terms of how classes are defined: within our framework, the distinction between oviparity and viviparity is not a matter of the state of the embryos at the time of partition (i.e., contained in egg coatings vs. free-living individuals), but a consequence of the extension of pre-partition incubation. Accordingly, the traditional criterion used for distinguishing oviparity and viviparity, namely the presence or absence of egg-coatings at release, is understood within our approach as secondary to the evolution of extended periods of internal incubation theorized in terms of parent-offspring relationality. Other common derived traits besides thinning or loss of egg-coatings, such as an enhancement of water supply and gas exchange, or immune rearrangements, can be identified in clades with increased embryo retention.

It is also important to note that our classification is articulated in terms of the extent of prenatal incubation and post-fertilization nourishment. In this regard, our approach makes the distinction between classes a matter of degree, allowing for the identification of intermediate states. Although reproductive relations themselves can generally be unambiguously individuated at different organizational levels, their strength varies along a continuum. This continuity resonates with current empirical practices in reproductive biology. For instance, the assessment of whether a particular species or population is either matrotrophic or lecithotrophic is quantitatively determined through egg size measuring or dry mass analysis, and the distinction is never sharp, since "[l]ecithotrophy and matrotrophy represent extremes of a continuum" (Blackburn 2015a, p. 963). However, occasionally, this continuum is marked by specific thresholds that have significant implications for reproductive modes. For instance, pregnancy is discretely delineated by the two inflammatory events of implantation and parturition (Chavan et al. 2017).

3. The explanatory role of reproductive characters in the organismal approach

By emphasizing the material and developmental dimensions of reproduction, our proposed organismal-relational individuation of reproductive characters opens up a range of explanatory possibilities. In this section, we identify three core explanatory agendas of this approach that the functional-adaptationist approach fails to address, namely the explanation of reproductive homologies and homoplasies, the constraints associated with the evolution of reproductive modes, and the evolvability of reproductive characters.

[4] This classification is restricted to post-fertilisation events (including incubation and nourishment) during the period of parental embryo retention. A complementary classification could be elaborated that addresses other forms of incubation and provision of nutrients that are excluded from this taxonomy, such as eutherian lactation, egg incubation in nests and other forms of post-partition parental care. Such further classifications open the possibility to identify fine-grained connections between, for instance, sociability and viviparity (see Nuño de la Rosa 2023). Yet, this task exceeds the scope of this paper.

3.1. The homology/homoplasy problem

Since the organismal individuation of reproductive characters examines the relations and developmental mechanisms underlying the generation of characters, it provides a more exhaustive view of similarities and differences. This approach is necessary not only for the proper traceability of relevant homologs (DiFrisco et al. 2020) but also to discover and account for instances of homoplasy in the evolution of reproduction. Thus, instead of attributing the evolution of similar reproductive characters in unrelated lineages to convergent evolution, our approach enables explanatory generalizations across different animal groups based on their relational and developmental similarities. For example, from an organismal perspective, the placenta can be recognized as an organ that shares relational similarities across various vertebrates. This recognition is based on commonalities observed, including extended areas of contact between maternal and fetal tissues, and specific mechanisms facilitating the physiological accommodation and maintenance of this interorganismal organ. Comprising contributions from both maternal and fetal materials, the placenta serves the joint purpose of ensuring successful fetal nutrition for reproduction. This approach, unlike the adaptationist approach to shared traits, incorporates relational and material criteria in the individuation of placentas, which allows for distinguishing homologies and homoplasies. In the former case, placentas have evolved through the recruitment of homologous tissue origins, as evidenced by tissular homologies in squamate and eutherian chorioallantoic placentas, and between shark and marsupial yolk sac placentas. In the latter case, however, we observe that structures and processes display relevant similarities despite different tissular origins, such as the eutherian chorioallantoic placenta versus the marsupial yolk sac placenta (Whittington et al. 2022).

When applied to reproductive modes, this approach also enables the recognition of homoplastic patterns in the physiological, morphological, and immunological relations during the evolution of prolonged internal incubation across viviparously reproducing animals, despite their group-specificities (Gao et al 2019; Recknagel et al. 2021; Blackburn 2015).

3.2. The constraints problem

In evo-devo, the constraints problem pertains to understanding the developmental reasons that explain why some characters evolve in certain groups and not in others. The evolutionary specializations of eutherians enabling the extension of intrauterine development nicely illustrate the relevance of analyzing reproductive relations for understanding how developmental constraints evolved. Pregnancy requires regulating the general immune mechanisms responsible for tissue integrity, allowing some form of maternal recognition of the embryo. This was accomplished through the repurposing of the ancestral inflammatory endometrial reaction that in marsupials leads to the early termination of internal incubation. This constraint was co-opted in eutherians for allowing sustained implantation by facilitating vascular permeability, uterine reorganization, and suppressing deleterious effects for the embryo (Chavan et al., 2017). Functionalist explanations lump all those cases into a single category and thus preclude a satisfying account of the requirements that made this particular form of viviparity possible.

Besides, the underlying developmental mechanisms of reproductive relations have evolved in a way that confers varying degrees of stability to these relations. This variability in the stability of relational characters helps explain the so-called problem of reversibility, which addresses the apparent constraints associated with reverting from one mode of reproduction to another. The most paradigmatic case is the transition from oviparity to viviparity, which very rarely occurs in the opposite direction. From an organismal-relational perspective, this can be explained by the evolution of specializations for stabilized internal incubation and nutritional provision, which involves intricate changes in the anatomy and physiology of both parent and offspring (Blackburn 2015b; King and Lee 2015). Those changes condition the relationality between them, ensuring robust developmental control (Griesemer 2014; Rosslenbroich 2014). In contrast, other traits, such as mating behaviors, do not entail such intricate relational changes and, as a consequence, are more labile over evolutionary time. Mating behaviors exhibit greater plasticity, responding to environmental cues, population density, or resource availability (Ah-King and Gowaty 2016). This distinction highlights how the stability of reproductive relations influences the evolutionary flexibility of different reproductive traits.

Failing to consider the developmental constraints involved in the evolution of reproductive relations can result in significant errors in phylogenetic reconstruction. For instance, a controversial piece of work argued that live-bearing was the ancestral state in squamate reptiles (Pyron and Burbrink 2014). The problem with this hypothesis is that it relied on a functional individuation of reproductive characters that ignored developmental evidence for the evolution of viviparity, leading to a misinterpretation of the evolutionary history of the lineage (Blackburn 2015).

The organismal and relational individuation of characters also opens explanatory possibilities for understanding the existence of unexplored regions within the reproductive space. For example, the aforementioned functionalist conjecture as to why viviparity did not evolve in birds (Blackburn and Evans 1986) could be expanded to incorporate developmental explanations. From this perspective, it might be argued that the impermeability of eggshells, and/or the nature of the oviduct as an unfavorable environment for egg retention (see e.g. Anderson et al. 1987) have served as developmental constraints for the evolution of viviparity in birds. In the case of *Lerista*, an organismal-relational approach encourages us to explore how certain conditions favor the evolution of extended internal incubation in populations with the physiological conditions for developing those traits. An approach that incorporates developmental constraints and examines the developmental changes leading to the evolution of specific reproductive traits and parental-offspring relations enables the formulation of mechanistic explanations. This approach helps us understand how certain factors, such as physiological predispositions or behaviors, facilitate the evolution of stabilized and complex reproductive modes. For instance, knowing how extended internal incubation evolves in *Lerista* at a physiological and morphological level might enhance our understanding of how certain conditions, including semi-fossorial behavior, small clutches, or single yearly egg laying facilitate the evolution of viviparity. Hence, the study of developmental constraints helps us better understand how functional constraints affect the origin of certain traits in evolution.

3.3. The evolvability problem

The evolvability problem refers to why characters evolve in different directions, ranges, and rates (Hansen et al. 2023). Unlike adaptationist explanations, evo-devo focuses on how differences in evolvability of different reproductive modes depend on being controlled by differently integrated parameters of variation.

For instance, in viviparous amphibians, the characters involved in nutrient supply, oxygen intake and waste elimination are separated spatially, temporally, morphologically and physiologically as compared to placental vertebrates (Wake 2015). Paying attention to the degree of integration of reproductive characters in terms of both inter- and intraorganismal relationality can illuminate their differing evolutionary potential, as modularity is a well-known determinant of the independent evolution of traits.

Studying reproductive relations also sheds light on trends in the evolution of sexual reproduction. As discussed earlier, the adaptationist framework suggests that reproductive traits co-evolve by combining evolutionary strategies to enhance fitness. For example, it has been argued that some species of poeciliid fishes retain oviparity because females rely on male skin coloring patterns to assess their fitness, while others have evolved viviparity as a mechanism for internal selection of embryos, eliminating the need for sexual dimorphism in skin coloring patterns (Reznick et al. 2021). Here, reproductive modes and secondary sexual traits are seen as different strategies to maximize fitness that can be combined at will by selection. Conversely, an organismal-relational approach focuses on evolved material relations between parents and between parents and offspring showing how some reproductive relations facilitate the evolution of others.

In this regard, the taxonomies presented in the previous section highlight the relevance of constraints in the evolution of reproductive modes, showing the interconnectedness of parent-parent and parent-offspring relationality. Consequently, modes of reproduction concerning the conditions of syngamy (Table 3) and embryo development (Table 4) appear to be mutually constrained. For instance, the evolution of the reproductive mode featuring increased post-fertilization nourishment and lack of incubation may be hindered by physiological and topological constraints, as the former requires some form of material relationality and specific mechanisms for parent-offspring accommodation to evolve. . Moreover, as ovuliparity consists of the absence of incubation and post-fertilization nourishment, it can only be achieved after external fertilization. Conversely, oviparity is constrained to evolve on the substrate of a parent-parent relationality that compromises some form of internal incubation, for which internal fertilization is a prerequisite. All forms of viviparity follow the same constraints. As for brooding, since it is characterized by secondary incubation, it can be realized in a high variety of forms, being related to any form of parent-parent relationality. Such constraints play a pivotal role in shaping the evolvability of reproductive characters and modes either by restricting certain pathways or by opening new evolutionary possibilities. A similar reasoning is employed by Laura Franklin-Hall (2021) in discussing whether anisogamy explains sex-specific characters and sex-linked trends in evolution. The standard adaptationist interpretation posits that differences in gamete size drive morphological and behavioral changes, leading to sex differentiation based on optimal parental investment. In contrast, Franklin-Hall proposes an alternative evo-devo explanation, suggesting that anisogamy triggers a sequence of evolutionary changes due to developmental factors. For example, gamete size can be associated with the fact that internal fertilization evolves in females or that small gametes are more mobile.

Additionally, an organismal-relational approach to the individuation of reproductive modes can provide insights into the evolvability of non-reproductive characters. This is exemplified by the correlation, across various animal groups, between the evolution of different forms of viviparity and increased diversification (see Helmstetter et al. 2016 for teleosts and Pincheira-Donoso et al. 2013 for squamates). Viviparous lineages generally exhibit higher rates of speciation and extinction, as well as greater species turnover over time (Pyron and Burbrink 2014). From a functional-adaptationist perspective, this phenomenon is often attributed to reproductive modes acting as key innovations that facilitate adaptive radiation. In contrast, from an organismal-relational perspective, the morphological diversification linked to the evolution of specific reproductive modes can be linked to the evolution of specific reproductive relations. For instance, the extension of intrauterine developmental time in eutherians, as enabled by the evolution of the maternal-fetal interface, ensures a highly robust developmental niche that might have fostered further opportunities for exploring the morphospace (Lillegraven 1975).

Developmental constraints influencing evolutionary transitions, as well as the varied evolvabilities discussed above, do not necessarily indicate a general trend toward increased parental investments leading to hemotrophic viviparity (see Blackburn 1999, Rosslenbroich 2024). While identifiable trajectories exist, they represent localized trends specific to certain lineages.

Finally, the organismal-relational individuation of reproductive modes might lead to the identification of novel evolutionary agents that foster new levels of internal selection, yielding significant implications for evolvability (Nuño de la Rosa 2023). For instance, the evolution of internal fertilization led to the evolution of gamete selection, while implantation led to that of oocyte selection (Kekäläinen 2021). This framework enables the recognition of the reduction in fecundity (which most often accompanies the evolution of viviparity) as an evolved trait that allows for embryo selection, instead of a trade-off in the evolution of viviparity, as suggested by the adaptationist-functional approach (Kalinka 2015).

4. Conclusions

Distinct criteria for individuation applied by different theoretical frameworks result in diverse predictions and explanations regarding the evolution of reproductive modes and characters. Within the adaptationist framework, reproductive characters are functionally individuated as strategies for enhancing fitness. This approach identifies and classifies reproductive characters on the basis of their assumed functional roles, disregarding developmental origins and organismal relations between parents, and parents and offspring. In contrast, our suggested organismal-relational individuation, informed by studies on the evo-devo of reproduction, introduces a novel framework for elaborating taxonomies of reproductive modes and characters and allows for explanations that the adaptationist perspective cannot provide. Two major theoretical innovations arise from this reinterpretation of reproduction.

On the descriptive side, our proposed framework illustrates how morphological features, processes, activities, and relations can be individuated and homologized as evolutionary units. Current empirical studies on the evolution of reproductive modes often rely on transcriptome sequencing of two or more species, followed by a comparison based on Gene Ontology Analysis. This bioinformatics method aims to describe the functions of gene products according to a selected-effect notion of biological functions (Thomas 2019). It involves identifying differentially enriched genes during a specific biological process under particular conditions, where these genes exhibit a higher transcription rate and stronger association with a particular function. While this method offers a more detailed perspective than standard DNA sequencing, it encounters significant challenges in identifying gene product-function relations, particularly in the evolution of complex traits. In contrast, our approach considers the evolution of developmental processes shaping various characters involved in reproductive functions and the relations established among them and with other organisms.

On the explanatory side, the organismal-relational individuation of reproductive modes and characters addresses both how and why questions. On the one hand, homologies and homoplasies between reproductive characters can be established on the basis of developmental and relational similarities. On the other hand, developmental constraints help understand why some reproductive regions have not been explored throughout evolution, and why some trajectories in the evolution of reproduction seem to be more likely than others. These two aspects of scientific endeavor, namely description and explanation of reproduction, are crucial in our understanding of reproductive phenomena and their evolution. While it is premature to determine whether the ideas presented in this paper might support a new empirical research program, we have shown that the proposed shift can have relevant consequences in methods used to individuate reproductive characters (including practices such as reproductive mode determination, developmental studies, or modeling), the elaboration of taxonomies, and the formulation of evolutionary explanations.

Regarding the issue of whether both approaches should be integrated or rather coexist as complementary views, we adopt a cautious and nuanced stance, distinguishing two epistemic goals. Firstly, concerning trait individuation, due to the inaccuracies in classification and phylogenetic reconstructions by the functional account, we advance that a pluralist solution is not advisable. We claim that functional accounts should be integrated with organismal and relational studies because, as we have shown, the developmental, material basis of reproductive functions is required for a proper characterisation of reproductive characters and modes. In some cases, an initial functional approach focusing on adaptive capacities can be useful, but we anticipate that, as the proposed research program advances, the organismal-relational approach will increasingly replace the functional criteria for identifying reproductive characters. Secondly, regarding evolutionary explanations of reproduction, we believe that functional and evo-devo explanations should be cross-checked against each other. For instance, in explaining why eutherians have undergone greater morphological diversification compared to marsupials, a purely adaptive explanation would suggest that both groups have the same capacity to generate variation but, due to historical contingencies, eutherians have been able to explore more niches, experiencing an adaptive radiation. This explanation would be merely adaptive, *ceteris paribus*. However, a relational and developmental view can contribute to the explanation as to why eutherians have been able to explore more niches because they have been able to explore a greater morphospace due to prolonged internal incubation. In this case, both approaches would be compatible and mutually informative.

Commented [1]: Expanded in response to R2

Although the scope of this paper is limited to reproductive characters in sexually reproducing animals, the insights provided by our view may also be relevant for understanding the evolution of other forms of reproduction, such as sexual reproduction in plants and different forms of asexual reproduction. Addressing the relational dimension of the evolution and development of reproduction in these groups would require a detailed examination dealing with specific challenges such as the fuzziness of the relata apparent in some cases[5]. However, we anticipate that applying an organismal-relational view will also lead

[5] We thank an anonymous reviewer for raising this point.

to a different understanding of reproductive relations and provide new explanatory insights into other forms of reproduction.

References

Ah-King M, Gowaty PA (2016) A conceptual review of mate choice: stochastic demography, within-sex phenotypic plasticity, and individual flexibility. Ecol Evol 6(14):4607-42 https://doi.org/10.1002/ece3.2197

Amundson R (2005) The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo. Cambridge University Press, Cambridge

Anderson DJ, Stoyan NC, Ricklefs RE (1987) Why are there no viviparous birds? A comment. Am Nat 130(6):941–947 http://dx.doi.org/10.1086/284757

Baedke J (2019) O Organism, Where Art Thou? Old and New Challenges for Organism-Centered Biology. J Hist Biol 52(2):293-324 https://doi.org/10.1007/s10739-018-9549-4

Blackburn DG (1999) Viviparity and oviparity: Evolution and reproductive strategies. In: E Knobil and J D Neill (eds) Encyclopedia of Reproduction, Volume 4, Academic Press, London, pp 994–1003

Blackburn DG (2015a) Evolution of vertebrate viviparity and specializations for fetal nutrition: A quantitative and qualitative analysis. J Morphol 276(8):961–990 https://doi.org/10.1002/jmor.20272

Blackburn DG (2015b) Evolution of viviparity in squamate reptiles: Reversibility reconsidered. J Exp Zool B Mol Dev Evol 324(6):473–486 https://doi.org/10.1002/jez.b.22625

Blackburn DG, Evans H E (1986) Why are there no viviparous birds? Am Nat 128(2):165–190 http://dx.doi.org/10.1086/284552

Brigandt I (2003) Homology in comparative, molecular, and evolutionary developmental biology: the radiation of a concept. J Exp Zool **B** Mol Dev Evo 299(1):9-17 https://doi.org/10.1002/jez.b.36

Brigandt I, Love AC (2012) Conceptualizing evolutionary novelty: moving beyond definitional debates. J Exp Zool **B** Mol Dev Evo 318(6):417-427 https://doi.org/10.1002/jez.b.22461

Buckley D, Alcobendas M, García- París M, Wake MH (2007) Heterochrony, cannibalism, and the evolution of viviparity in Salamandra salamandra. Evol Dev 9(1):105–115 https://doi.org/10.1111/j.1525-142X.2006.00141.x

Chavan, A. R., Griffith, O. W., and Wagner, G. P. (2017). The inflammation paradox in the evolution of mammalian pregnancy: turning a foe into a friend. *Current opinion in genetics & development*, *47*, 24-32. https://doi.org/10.1016/j.gde.2017.08.004

Chiu L, Gilbert SF (2020) Niche construction and the transition to herbivory: phenotype switching and the organization of new nutritional modes. In: Levine H, Jolly MK, Kulkarni P, Nanjundiah V (eds) Phenotypic switching. Academic Press, Cambridge, MA, pp 459–482 https://doi.org/10.1016/B978-0-12-817996-3.00015-3

Chiu L, Gilbert SF (2015) The Birth of the Holobiont: Multi-species Birthing Through Mutual Scaffolding and Niche Construction. Biosemiotics 8(2):191–210 https://doi.org/10.1007/s12304-

015-9232-5

Cortés-García D, Etxeberria Agiriano A (2023) Ontologies in Evolutionary Biology: The Role of the Organism in the Two Syntheses. In: Viejo JM, Sanjuán M (eds) Life and Mind: New Directions in the Philosophy of Biology and Cognitive Sciences, Springer International Publishing, pp 185–205 https://doi.org/10.1007/978-3-031-30304-3_9

Crespi B, Semeniuk C (2004) Parent-offspring conflict in the evolution of vertebrate reproductive mode. Am Nat 163(5):635–653 https://doi.org/10.1086/382734

DiFrisco, J. (unpublished). Character individuation: functional, descriptive, and developmental.

DiFrisco J, Jaeger J (2021) Homology of process: Developmental dynamics in comparative biology. Interface Focus 11(3) https://doi.org/10.1098/rsfs.2021.0007

DiFrisco J, Love AC, Wagner GP (2020) Character identity mechanisms: A conceptual model for comparative-mechanistic biology. Biol Philos 35(4):44 https://doi.org/10.1007/s10539-020-09762-2

Etxeberria A, Umerez J (2006) Organismo y Organización En la Biología Teórica ¿Vuelta Al Organicismo? Ludus Vitalis 14(26):3–38

Etxeberria A, Cortés-García D, Torres M (2023) Organisms, Life Relations, and Evolution: Inter-Dependencies after Kropotkin's Mutual Aid. ArtefaCToS. Journal of Science and Technology Studies 12(1):1 https://doi.org/10.14201/art2023121179204

Etxeberria A (2023) Jacob's Understanding of Reproduction: Challenges from an Organismic Collaborative Framework. HOPOS The International Society for the History of Philosophy of Science 13(2) https://doi.org/10.1086/726256

Fabian D, Flatt T (2012) Life history evolution. Nat Sci Educ 3(10)

Franklin-Hall L (2021) The Animal Sexes as Historical Explanatory Kinds. In: Dasgupta S, Dotan R, Weslake B (eds) Current Controversies in Philosophy of Science, Routledge, New York, pp 177-197

Furness AI, Morrison KR, Orr TJ, Arendt JD, Reznick DN (2015) Reproductive mode and the shifting arenas of evolutionary conflict. Ann N Y Acad. Sci, 1360(1):75–100 https://doi.org/10.1111/nyas.12835

Fusco G, Minelli A (2019) The Biology of Reproduction. Cambridge University Press, Cambridge

Fusco G, Minelli A (2023). Understanding Reproduction. Cambridge University Press, Cambridge

Gilbert SF, Epel D (2009) Ecological Developmental Biology: Integrating Epigenetics. Sinauer Associates, Sunderland

Griesemer J (2000) The Units of Evolutionary Transition. Selection 1(1–3):67–80 https://doi.org/10.1556/Select.1.2000.1-3.7

Griesemer J (2005) The informational gene and the substantial body: On the generalization of evolutionary theory by abstraction. In Jones MR, Cartwright N (eds) Idealization XII: Correcting the Model. Idealization and Abstraction in the Sciences, Volume 86, pp 59–115

Griesemer J (2014) Reproduction and scaffolded developmental processes: An integrated evolutionary perspective. In Minelli A, Pradeu T (eds) Towards a Theory of Development, Oxford University Press, Oxford, pp 183-201 https://doi.org/10.1093/acprof:oso/9780199671427.003.0012

Haig D (1993) Genetic Conflicts in Human Pregnancy. Q Rev Biol 68(4):495–532 https://doi.org/10.1086/418300

Hansen TF, Houle D, Pavličev M, Pélabon C (2023) Evolvability: A Unifying Concept in Evolutionary Biology? The MIT Press, Cambridge, London https://doi.org/10.7551/mitpress/14126.001.0001

Helmstetter AJ, Papadopulos AST, Igea J, Van Dooren TJM, Leroi AM, Savolainen V (2016) Viviparity stimulates diversification in an order of fish. Nat Commun 7(1) https://doi.org/10.1038/ncomms11271

Herrera AM, Cohn MJ (2014) Embryonic origin and compartmental organization of the external genitalia. Sci Rep 4(6896):1-6 https://doi.org/10.1038/srep06896

Jacob F (1970) *La logique du vivant*. Gallimard, Paris. (*The Logic of Life*, Betty E. Spillmann trans., Pantheon, New York, 1973).

Janzen FJ, Warner DA (2009) Parent–offspring conflict and selection on egg size in turtles. J Evol Biol 22(11):2222–2230 https://doi.org/10.1111/j.1420-9101.2009.01838.x

Kalinka AT (2015) How did viviparity originate and evolve? Of conflict, co-option, and cryptic choice. BioEssays 37(7):721–731 https://doi.org/10.1002/bies.201400200

Kekäläinen J (2021) Genetic incompatibility of the reproductive partners: An evolutionary perspective on infertility. Hum Reprod 36(12):3028–3035 https://doi.org/10.1093/humrep/deab221

King B, Lee MSY (2015) Ancestral State Reconstruction, Rate Heterogeneity, and the Evolution of Reptile Viviparity. Syst Biol 64(3):532–544 https://doi.org/10.1093/sysbio/syv005

Lamarins A, Fririon V, Folio D, Vernier C, Daupagne L, Labonne J, Buoro M, Lefèvre F, Piou C, Oddou-Muratorio S (2022) Importance of interindividual interactions in eco-evolutionary population dynamics: The rise of demo-genetic agent-based models. Evol Appl 15(12):1988-2001 https://doi.org/10.1111/eva.13508

Lillegraven JA (1975) Biological considerations of the marsupial-placental dichotomy. Evolution, 29: 707–722.

Lodé T (2012) Oviparity or viviparity? That is the question…. Reprod Biol 12(3):259–264 https://doi.org/10.1016/j.repbio.2012.09.001

Minelli A (2003) The Development of Animal Form: Ontogeny, Morphology, and Evolution. Cambridge University Press, Cambridge

Mossman HW (1937) Comparative morphogenesis of the fetal membranes and accessory uterine structures. Contrib Embryol 26:129 –246

Nuño de la Rosa L (2023) Agency in Reproduction. Evol Dev 25:418–429 https://doi.org/10.1111/ede.12440

Nuño de la Rosa, L. (2010). Becoming organisms: the organisation of development and the development of organisation. *History and Philosophy of the Life Sciences*, *32*(2–3), 289–315.

Nuño de la Rosa L, Pavličev M, Etxeberria A (2021) Pregnant Females as Historical Individuals: An Insight From the Philosophy of Evo-Devo. Front Psychol 11:572106 https://doi.org/10.3389/fpsyg.2020.572106

Oliveira RF, Bshary R (2021) Expanding the concept of social behavior to interspecific interactions. Ethology 127(10):758-773 https://doi.org/10.1111/eth.13194

Pyron RA, Burbrink FT (2014) Early origin of viviparity and multiple reversions to oviparity in squamate reptiles. Ecol Lett 17(1):13–21 https://doi.org/10.1111/ele.12168

Reznick DN (2014) Evolution of Life Histories. In: Losos JB (ed) The Princeton Guide to Evolution, Princeton University Press, Princeton, pp 268–275

Reznick DN, Travis J, Pollux BJ, Furness AI (2021) Reproductive mode and conflict shape the evolution of male attributes and rate of speciation in the fish family Poeciliidae. Front Ecol Evol 9:639751 https://doi.org/10.3389/fevo.2021.639751

Rosslenbroich B (2014) On the Origin of Autonomy: A New Look at the Major Transitions in Evolution. Springer International Publishing, Cham https://doi.org/10.1007/978-3-319-04141-4

Shine R (2014) Evolution of an Evolutionary Hypothesis: A History of Changing Ideas about the Adaptive Significance of Viviparity in Reptiles. J Herpetol 48(2):147–161 https://doi.org/10.1670/13-075

Stewart JR, Blackburn DG (1988) Reptilian Placentation: Structural Diversity and Terminology. Copeia, 1988(4):839–852 https://doi.org/10.2307/1445706

Suárez J, Triviño V (2020) What is a hologenomic adaptation? Emergent individuality and inter-identity in multispecies systems. Front Psychol 11:187 https://doi.org/10.3389/fpsyg.2020.00187

Thomas PD (2017) The Gene Ontology and the Meaning of Biological Function. In: Dessimoz C, Škunca N (eds) The Gene Ontology Handbook, Springer, Cham pp. 15–24 https://doi.org/10.1007/978-1-4939-3743-1_2

Trivers RL (1974) Parent-Offspring Conflict. Am Zool 14(1):249–264 https://doi.org/10.1093/icb/14.1.249

Villegas C, Love AC, Nuño de la Rosa L, Brigandt I, Wagner GP (2021) Conceptual roles of evolvability across evolutionary biology: Between diversity and unification. In: Hansen TF, Houle D, Pavličev M, Pélabon C (eds) Evolvability: A Unifying Concept in Evolutionary Biology?, The MIT Press, Cambridge, London, pp 35–54 https://doi.org/10.7551/mitpress/14126.003.0005

Wade MJ (2022) Maternal-Offspring Interactions: Reciprocally Coevolving Social Environments. J Hered 113(1):54-60 https://doi.org/10.1093/jhered/esab044

Wagner GP (2001) Characters, Units and Natural Kinds: An Introduction. In Wagner GP (ed) The Character Concept in Evolutionary Biology, Academic Press, San Diego, pp 1–10 https://doi.org/10.1016/B978-012730055-9/50008-2

Wagner GP, Kin K, Muglia L, Pavličev M (2014) Evolution of mammalian pregnancy and the origin of the decidual stromal cell. Int J Dev Biol 58(2-3-4):117-126 https://doi.org/10.1387/ijdb.130335gw

Wagner GP, Erkenbrack EM, Love AC (2019) Stress-Induced Evolutionary Innovation: A Mechanism for the Origin of Cell Types. Bioessays 41(4):1800188 https://doi.org/10.1002/bies.201800188

Wake MH (2004) Environmental effects, embryonization, and the evolution of viviparity. In Hall BK, Pearson RD, Muller GB (eds) Environment, Development, and Evolution: Towards a Synthesis. TheVienna series in Theoretical Biology, Volume 4, The MIT Press, Cambridge, pp 151–170

Wake MH (2015) Fetal adaptations for viviparity in amphibians. J Morphol 276(8):941–960 https://doi.org/10.1002/jmor.20271

Wake DB, Wake MH, Specht CD (2011) Homoplasy: From Detecting Pattern to Determining Process and Mechanism of Evolution. Science 331(6020):1032–1035 https://doi.org/10.1126/science.1188545

Whittington CM, Buddle AL, Griffith OW, Carter AM (2022) Embryonic specializations for vertebrate placentation. Philos Trans R Soc Lond B Biol Sci 377(1865):20210261 https://doi.org/10.1098/rstb.2021.0261

Zeh JA, Zeh DW (2001) Reproductive mode and the genetic benefits of polyandry. Anim Behav 61(6):1051–1063 https://doi.org/10.1006/anbe.2000.1705

	Oviparity	**Viviparity**
Lecithotrophy	Lecithotrophic and oviparous animals. E.g., birds, crocodilians, turtles, most lizards, snakes and fishes.	Lecithotrophic and viviparous animals. E.g., some amphibians, lizards, snakes and fishes.
Matrotrophy	Matrotrophy and oviparous animals. E.g., monotremes (i.e., platypus and echidna).	Matrotrophy and viviparous animals. E.g., marsupials, eutherians, some fish, lizards and amphibians.

Table 1. A functional taxonomy of reproductive modes, illustrated by examples from vertebrates. Modified from Blackburn 2015a.

	Structural	Physiological	Behavioral	Temporal
Intraorganismal relationality	Gamete traits, anatomical characteristics of reproductive organs (gonads, tubes, glands,), extraembryonic structures.	Production of gametes, physiological regulation of reproductive homeostasis, menopause, spontaneous decidualization of uterine wall.	Suckling behavior.	Time for sexual availability, estrous cycle, menstrual cycles, ovarian cycles, hormonal cycles.
Interorganismal relationality between parents	Sexual characters related to courtship (e.g., colored feathers), structures for copulation.	Sperm-egg interactions, seminal proteins' interaction with female physiology, characteristics of implantation, sperm storage/removal, mating-induced ovulation.	Courtship behaviors, mating interactions.	Timing of mating, mating duration.
Interorganismal relationality between parents and offspring	Parental structures promoting embryo incubation.	Embryo-induced decidualization of uterine wall, mechanisms for embryo selection, in utero nutritional supply, after-birth nutritional supply.	Nest building, filial cannibalism, infanticide, solicitation of nursing, aloparental care, lactation.	Timing of birth, duration of brood retention, duration of incubation.

Table 2. A taxonomy of reproductive characters attending to the nature of the character and the kind of relationality implied.

	External fertilization	Internal fertilization
Absence of parent-parent interaction	Free dispersal of gametes in the external environment. In sessile organisms that live in highly dense populations, such as some marine invertebrates.	Sperm cells are released into the water, which swim to reach the eggs that are internally retained. In sessile aquatic animals such as sponges or corals.
Indirect parent-parent interaction	Sperm is released over previously deposited eggs. In many fishes and aquatic invertebrates. Also in the rare cases where the spermatophore is uptaken from the environment by the female, and retained for subsequent releasing upon deposited eggs (in some myriapods).	Sperm is contained in a structure named a spermatophore which is transferred to the female or deposited in the substratum and later uptaken by the female. In some cases, the male interacts chemically or physically with the female before or after depositing the spermatophore. In some urodeles and many invertebrates such as crustaceans, insects, and arachnids.
Direct parent-parent interaction	Male and female actively interact to facilitate the release of sperm directly onto the eggs. Anurans' amplexus is paradigmatic of this kind of reproduction, where the male grasps the female and releases sperm directly upon the eggs as they are deposited into the water. There is also direct contact between parents for external fertilization in some marine worms, which are surrounded by a mucus sleeve for reproducing (i.e., pseudocopulation).	There is active internal insemination (i.e. copulation), in many cases facilitated by specific organs for sperm transfer, such as intromittent or copulatory organs. In most vertebrates and many invertebrates, with a high diversity of methods for direct sperm transfer, including the juxtaposition of the genital openings (e.g., some birds and snakes), dermal impregnation (e.g., marine worms), hypodermic injection through the body wall (e.g., many insects), male appendage amputation (e.g., some spiders) and, in the most extreme cases of parent-parent contact, it is the whole male that enters the female's body (e.g. some marine worms and abyssal fishes).

Table 3: A taxonomy of reproductive modes in sexually reproducing animals attending to the conditions under which syngamy is realized, according to site of fertilization and the kind of parent-parent interaction.

	Limited or no post-fertilization nourishment	**Increased post-fertilization nourishment**
Absence of incubation	**Oviliparity**. Eggs are released prior to fertilization. Fertilized eggs with little yolk are incubated in the environment. No direct contact between parents and offspring. In anurans, some fish, amphibians, and reptiles, and some aquatic invertebrates, such as annelids, and mollusks.	
Limited pre-partition incubation	**Oviparity**. Short period of internal incubation of fertilized eggs. Sometimes, post-natal incubation in nests. In all birds, turtles, crocodiles, butterflies, bees, ants, and octopuses, most fishes, lizards, beetles, crustaceans, mollusks and other invertebrates.	**Monotreme oviparity**. A particular reproductive mode only found in monotremes, in which eggs absorb oviductal secretions during development and before oviposition.
Increased pre-partition incubation	**Lecithotrophic viviparity**. Embryos are retained within the female body so that parent-offspring interaction is extended in time, which confers protection during embryonic development. Eggs either hatch within the female cavities or organs or do not develop any form of external coating. There is little to no provisioning of nutrients, although varying degrees of water and ion transport can be found. In some lizards, snakes, amphibians, fishes, and invertebrates (brachiopods and chaetognaths).	**True viviparity**. The extended period of internal incubation (usually within the female tract) is accompanied by a closer interaction between the parent and offspring in the form of more efficient transfer of substances which includes extended provision of nutrients through two different means: ● *Phagic nurturing*. Ingestion of tissues (histophagy), eggs (oophagy) or siblings (adelphophagy or embryophagy) provided by the parent. ● *Trophic nurturing*. Nutrients are absorbed directly (histotrophy) or with the mediation of specialized structures such as placentas or pseudo-placentas (placentotrophy).
Post-partition incubation or secondary incubation	**Brooding**. After partition (either oviposition or parturition), eggs and/or embryos are incubated on the surface (e.g. spider back brooding), in cavities (e.g., frog gastric intubation, and seahorse pseudo-pregnancy), or in the organs (e.g., ovarian incubation in guppy fish) of the parents.	**Matrotrophic brooding**. Secondary mechanisms can evolve that extend nurturing in brooding species, such as lactation in marsupials or other forms of milk-like provision in some insects.

Table 4. A taxonomy of reproductive modes with respect to the conditions under which embryos are developed, according to the form of incubation and the form of nourishment provision.

The evolution of reproductive characters: an organismal-relational approach

Keywords: ~~Organism-centered biology,~~ Evo-Devo, Viviparity, Reproduction, Evolvability, Homology, Relationality, Shared traits, Conflict theory

Abstract

This paper delves into the character concept as applied to reproduction. Our argument is that the prevailing functional-adaptationist perspective falls short in explaining the evolution of reproductive traits, and we propose an alternative organismal-relational approach that incorporates the developmental and interactive aspects of reproduction. To begin, we define the functional individuation of reproductive traits as evolutionary strategies aimed at enhancing fitness, and we demonstrate how this perspective influences the classification of reproductive characters and modes, the comprehension of *shared traits* as resulting from conflicts of evolutionary interest between individuals, and the explanation of reproductive diversity. After outlining the shortcomings of this framework, we introduce an organismal-relational approach grounded in evolutionary developmental studies of reproduction. This view provides a revised classification for reproductive characters and modes and offers a new understanding of *interorganismal traits* that takes into account their inherently relational nature. Lastly, we present the research agenda that emerges from this approach, which addresses the core explanatory gaps left by the adaptationist perspective, including the explanation of reproductive homologies and homoplasies, the developmental constraints associated with the evolution of reproductive modes, and the evolvability of reproductive characters.

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0. Introduction

Although heredity has long been a~~n~~ cornerstone~~important aspect~~ of evolutionary theory~~ since its early stages~~, the intricacies of reproduction itself, as the process by which biological individuals of a given type are produced from previous organisms, requires~~needs to be~~ further elaboration~~elaborated~~ (Jacob 1970). Recently~~In recent years~~, there has been an increasing interest in the field of reproduction (Fusco and Minelli 2019, 2023), denoting ~~signifying~~ a growing recognition of its significance in bridging development and evolution. It is therefore crucial to examine and compare different approaches to reproduction in evolutionary biology.

The conventional ~~neo-Darwinian~~ understanding of evolution largely reduces reproduction to heredity. This view ~~It~~ rests on two fundamental assumptions. Firstly, reproduction is ~~predominantly~~ viewed as a copying process~~tion~~, ~~essentially~~ limiting heredity to the transmission of genetic programs. Secondly, reproductive modes (i.e., the ways by which organisms of a given kind are produced from previously existing organisms) are often conceptualized as~~in terms of~~ evolutionary strategies designed to~~aimed at~~ maximiz~~e~~ing fitness. These assumptions~~two features of the theory~~ convey a functional~~ist~~-adaptationist interpretation of reproductive phenomena. Critics of this ~~the standard~~ gene-centered view have pointed out that it overlooks ~~ignores~~ the material processes integral to reproduction (Griesemer 2000, 2005, 2014; Chiu and Gilbert 2015). This has unfortunately also been the case in evolutionary developmental biology (evo-devo), where ~~the study of~~ reproduction has received less ~~been noticeably minimal compared to the~~ attention than~~paid to~~ other processes, such as the development of morphological characters. Notable exceptions include~~Exceptions would be~~ the research on amphibian viviparity by Marvalee Wake and colleagues (Wake 2004; Buckley et al. 2007), the study of eutherian pregnancy by Günter Wagner and Mihaela Pavličev (Wagner et al. 2014), or the work by Marty Cohn on male external genitalia (Herrera and Cohn 2014).

Three conceptual biases within evo-devo explanations may account for this relative neglect (Nuño de la Rosa 2023). On the one hand, the traditional emphasis on the study of form has led to overlook function, resulting in a morphological bias. Additionally~~Secondly~~~~Moreover~~, an adult-centric bias has shaped a teleological view of development, focusing primarily~~ed~~ on the generation of mature individuals (Minelli 2003), thereby dismissing the ~~its~~ role of reproduction in the life cycle~~, which encompasses reproduction~~. Lastly, an internalist bias has contributed to the disregard~~ing~~ of interorganismal relations, as evolutionary embryology has historically concentrated on changes within the embryo, often treating the developmental environment merely as a ~~mere~~ background condition. Although recent efforts in ecological evolutionary development (Gilbert and Epel 2009) have aimed to overcome this latter bias, the evolution of interorganismal~~ic~~ interactions in reproduction remains largely underexplored. ~~In this paper, we elaborate on this critical issue and propose an alternative framework for its examination.~~

Previous studies~~research~~ have investigated a range of~~has explored various~~ reproductive phenomena from an organismal and relational approach, such as pregnancy, within the context of biological individuality (Nuño de la Rosa 2010; Nuño de la Rosa et al. 2021), agency (Nuño de la Rosa 2023), and collaborative interdependencies (Etxeberria et al. 2023; Etxeberria 2023). In this study, we examine the relational ~~and interactive~~ aspects of reproduction through the ~~lens of the~~ character concept, which allow us~~. TAs we shall see, this line of research~~ ~~enables~~~~will allow~~ us to explore a ~~open up a much~~ broader spectrum of evolutionary reproductive relations.

The notion of character addresses the units organisms are composed of, which are integrated at different levels of organization (Wagner 2001). These~~is~~ units include~~s~~ component parts of organisms (such as feathers or limbs, but also molecules and cells), as well as ~~and other observable traits, such as~~ developmental processes and social behaviors. The character concept is a core concept in biology,~~the biological sciences~~ for it serves a multitude of roles, ranging from identifying cladistic groups and populations for evolutionary studies to serving as a starting point for studying ~~underlying~~ developmental mechanisms. Despite its relevance in systematizing and explaining diversity, the concept of character is underdeveloped and demands further theoretical study. Here, we are interested in conceptualizing reproductive characters, including gametes, gonads, courtship behaviors, incubation methods, or embryo nourishment arrangements. We recognize as reproductive traits the morphological, developmental, physiological, or behavioral ~~, or other~~ features that play a direct role in the processes leading to the production of new individuals of a given kind. They typically shape reproductive diversity across animal groups and jointly define reproductive modes or the different ways in which organisms reproduce, such as oviparity, internal fertilization, or matrotrophy.

TLImportantly, the definition of the character concept, like any other scientific concept, the definition of scientific concepts and the criteria used to individuate the units these concepts refer to are theory-dependent and are deeply shaped bydepends on the epistemic goals pursued. Conversely, individuation criteriathe criteria used to individuate the units scientific concepts refer to shape the epistemic range of possibilities enabled by such conceptualization is , in turn, conditioned by how the concept is defined. Both the definition and the epistemic goals are theory-dependent and hence deeply shaped by the theoretical context in which they are elaborated. Current literature providesfacilitates several examples of this epistemic contextual varibility in evolutionary biology concepts where this is made clear (see, e. g.for example, Brigandt 2003 for the homology concept; Brigandt and Love 2012 for the novelty concept, and Villegas et al. 2021 for the evolvability concept), and. tThe character concept is not an exceptionexempt from this epistemic-contextual variability (DiFrisco, unpublished 2023).

Consequently, the definition and criteria of individuation for reproductive characters conditions the shape the way in which differentcertain epistemic endeavors that are pursuedmade, framed in different theoretical approaches. This article explores the criteria used for individuating reproductive characters within two major theoretical approaches in evolutionary biology: the neo-Darwinian adaptationist framework, grounded in optimality theory, and the organismal framework, rooted in evo-devo theoryviews of evolution and expanded to encompass the relational dimensions of reproduction. Firstly, we introduce the functional -adaptationist individuation of reproductive characters and critically assessexplore how it shapes biological classifications and explanations of reproductive modes and traits, highlighting some of its limitations in both classifying and explaining diversity (Section 1). We thenThen, we present an alternative organismal-relational approach, which offers a more comprehensive and detailed thorough taxonomy of reproductive characters and modes (Section 2). Finally, we examine the explanatory possibilities offered by our proposal, which overcomes some of the problems raised by the functionalprevious approach (Section 3).

1. The functional individuation of reproductive characters

The main research question in standard evolutionary theory centers onrevolves around how evolution shapes organisms to optimize their reproductive success (Fabian and Flatt 2012). In this theoretical framework, characters are individuated by their functions, conceived in terms of adaptive design. Reproductive characters are commonly viewed perceived as finely-tuned adaptations, a perspective consistentin line with life history theory (see Reznick 2014), and particularly with theories of parent-offspring conflict the conflict theory of vivipari ty (see Haig 1993). Conflict perspectives, as delineated by the epistemic goals of the adaptationist program, have strongly influenced the understanding of reproductive relations in evolutionary biology (Trivers 1974).

Functional definitions have been instrumental in categorizing diverse reproductive modes and characters of diverse developmental and evolutionary origins into the same functional categories. RWithin this approach, reproductive modes are seen as reproductive strategies, characterized by “patterns that have advantages and disadvantages that affect their evolution” (Blackburn 1999, p. 995). Such an abstraction from material reproductive relations enable generalizations such as the following: “The means by which provisioning occurs varies taxonomically, but the result is the same—significantly expanded scope for sexual, parent-offspring, and sibling conflict in multiple new arenas" (Furness et al. 2015, p. 85). For instance, viviparity is defined according to its function (namely, the production of live young) ~~as the release of live offspring~~, ~~and costs and benefits for mothers and offsprings are examined under this light. This definition entails individuating viviparity according to its functional output (namely, the production of live young)~~, abstracting away underlying processes and relations contributing to this outcome.

The same epistemic strategy applies to reproductive characters. A prime example is the functional definition of the placenta, individuated as the intimate apposition or fusion of maternal and fetal tissues facilitating the ~~for~~ physiological exchange of substances, including water, nutrients, wastes, and other molecules for maternal-fetal communication (Mossman 1937; Whittington et al. 2022). ~~Hence, definitions of biological traits are relatively superficial insofar as they focus solely on functional characteristics.~~

1.1. A functional taxonomy of reproductive modes and reproductive characters

Functional definitions facilitate the recognition of the same reproductive ~~mode or~~ patterns ~~character~~ in different animal groups, thus "transcending taxonomic, ecological, geological, and geographical boundaries" (Blackburn 2015a, p. 961). For instance, Furness and colleagues argue that "[i]f the placenta is broadly defined as an apposition of maternal and fetal tissue specialized for the transfer of nutrients [...]~~to sustain the physiology of developing embryos~~, then such an organ has evolved not only in mammals but also in fish, sharks, and rays, reptiles, and many groups of invertebrates" (Furness et al. 2015, p. 86). This functional individuation has led to classifications of animal reproductive modes according to two ~~primary~~ parameters: (i) their mode of parity, involving either oviposition (oviparity, or egg-laying reproduction) or parturition (viviparity, or live-bearing reproduction), and (ii) their mode of nutrition, encompassing lecithotrophy (yolk-feeding) and matrotrophy (post-fertilization nourishment). Both parameters are defined according to their functional outcome, and their combination~~. Combining these two parameters~~ results in the categorization of animals into four distinct groups (see Table 1): lecithotrophic oviparous (e.g., birds, turtles, flies), matrotrophic oviparous (e.g., platypus), lecithotrophic viviparous (e.g., some fishes and spiders), and matrotrophic viviparous (e.g., eutherian mammals, marsupials, some salamanders). This classification is employed to systematize diversity and reconstruct phylogenies, revealing two key insights. Firstly, oviparity and lecithotrophy are the ancestral states in all major groups. Secondly, viviparity and matrotrophy have evolved independently multiple times in vertebrate and invertebrate groups.

Within this framework, an important category of reproductive characters comprises what are referred to as "*shared traits*". This term was coined to encompass those ~~phenotypic~~ characters that evolve as a result of conflictual interactions between individuals whose genetic interests are only partially aligned. Shared traits are conceptualized as the evolutionary outcome~~s~~ of "adaptations and counteradaptations through antagonistic selection" (Furness et al. 2015, p. 77). This broad definition comprises a wide range of traits, including developmental events and processes (e.g., embryo selection, implantation, in utero nutritional supply and growth rate, gestation length and birth size, postnatal growth rate) and behaviors (e.g., infanticide, suckling behavior, solicitation of nursing, size, date of weaning, dispersal behavior, cooperative breeding, resource sharing).

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1.2. How reproductive characters are explained and used to explain

The functional individuation of reproductive traits significantly impacts their explanation and subsequent application in explaining other biological characters. F~~In understanding the origins of these traits, f~~unctional explanations suggest that the evolution of reproductive modes, such as viviparity, occurs when the associated benefits~~ associated with it~~, like increased offspring quality or survival, outweigh the costs, such as reduced locomotor performance (Crespi and Semeniuk 2004; Furness et al. 2015; Shine 2014). Conversely, functional constraints would pervade the evolution of reproductive modes in certain circumstances. For instance, it is argued that viviparity has not evolved~~does not evolve~~ in birds because reverting ~~current evolved~~ characters such as endothermy, egg incubation, increased egg-yolk provisioning or eggshell hardening would be too energetically costly ~~in energetic terms~~ (Blackburn and Evans 1986). Similarly~~By a similar logic~~, viviparity is said to be prone to evolve in some lizards of the genus *Lerista*~~,~~ when its costs, such as locomotion reduction, are ~~somehow~~ attenuated. This is the case with~~of~~ *Lerista buganvilli*, a semi-fossorial skink species that inhabits~~dwells in~~ caves and burrows, where ~~so that the evolution of~~ viviparity does not affect its locomotion (Qualls and Shine 1998).

~~This way of functionally grouping~~ of ~~reproductive characters promotes categories of reproductive patterns that, in some cases, may not respond to common developmental and evolutionary origins. As a consequence, functional definitions enablinge generalizations such as the following: "The means by which provisioning occurs varies taxonomically, but the result is the same—significantly expanded scope for sexual, parent-offspring, and sibling conflict in multiple new arenas" (Furness et al. 2015, p. 85).~~

T~~Moreover, t~~he conflict theory of reproduction yields predictions concerning the evolution of reproductive traits, enabling targeted expectations about tissues, life history stages, and associated traits affected by conflict (Furness et al. 2015). An illustrative example is offspring size. In oviparous species such as turtles, maternal control over nutrient supply results in egg size that aligns ~~aligning~~ with the mother's optimal investment~~from the mother's perspective~~, aiming to distribute resources among the maximum number of offspring (Janzen and Warner 2009). This results in eggs being smaller than would be optimal for the embryo. Conversely, in matrotrophic viviparous species~~, especially those with matrotrophic traits,~~ embryos can exert ~~have~~ some influence over maternal nutrient transfer. Consequently, offspring size reflects ~~is anticipated to represent~~ a compromise between parental and offspring interests. In eutherian pregnancy, the gene imprinting hypothesis suggests ~~that asymmetric resource allocation strategies arise due to the conflict or cooperation between maternal and fetal genetic interests. This framework posits~~ that genes inherited from each parent play a different role in determining resource allocation during pregnancy~~, leading to disparities in resource distribution~~. Conditions such as maternal hypertension and alterations in insulin metabolism (Haig 1993) illustrate the predicted impact of imprinted genes on the differential~~functional~~ distribution of resources between maternal and fetal systems.

Crucially, this functional~~with characters being functionally individuated, this explanatory~~ framework enables the interconnection of diverse traits, ranging ~~spanning~~ from physiological mechanisms to behavioral strategies. For instance, it predicts an evolutionary association between reproductive modes and mating strategies~~ is predicted~~, despite the absence of a known direct material link between those ~~types of~~

Commented [2]: @David, esto vuelve a hablar de individuación funcional. No pega nada aquí. He subido arriba lo que añadía algo traits.~~ Thus,~~ Zeh and Zeh (2001) propose that the presence of polyandry in primates serves as a compensatory mechanism for genetic incompatibility, which is estimated to be around 70% in humans.

Several issues surface when examining the functional individuation of reproductive characters. Firstly, the emphasis on the functions of reproductive characters, irrespective ~~regardless~~ of their developmental constitution and functioning, often results in the oversight of both similarities and differences between such traits (Fusco and Minelli 2019). Since the selection process is blind to the mechanisms shaping a character, ~~an~~ exclusive reliance on this perspective might result in errors in classification and phylogenetic reconstruction. Consequently, the traditional four-class classification of animal reproductive modes fails to capture the richness of natural diversity and the relevant ecological and physiological aspects of reproduction (Lodé 2012). Additionally~~Furthermore~~, functional individuation~~the functionalist interpretation~~ of reproductive traits risks leading to flawed phylogenetic reconstructions by ignoring the material dimension of reproductive characters. A notable example is Daniel Blackburn's rejection of the hypothesis of multiple origins of oviparity in squamates ~~provides a good example of this problem~~ (Blackburn 2015b).

Concerning explanation, this framework is arguably limited in addressing key research questions about ~~on~~ the evolution of reproduction. On the one hand~~Firstly~~, it cannot address the shared developmental origins of homologous traits, which is crucial ~~has profound implications~~ for understanding their evolution. A focus on development and relations is critical for accurately ~~proper~~ tracing~~eability of~~ homology and homoplasy in reproductive traits~~on~~ (Amundson 2005; Wake et al. 2011). For instance~~example~~, the functional definition fails to distinguish between different types of placentas according to their development, as they are grouped on the basis of purely adaptive criteria. On the other hand~~Secondly~~, functional individuation overlooks developmental biases and evolvability. In confining itself to functional constraints and adaptive potential~~ity~~, it~~this perspective~~ does not allow ~~us~~ to examine whether reproductive modes have distinctive evolvabilities, or why certain transitions are more feasible~~viable~~ than others. ~~Finally, the selectionist framework struggles to explain why reproductive modes influence lineage evolution. From a functional perspective, reproductive modes are seen as innovations enabling the exploration of new niches. In contrast, an organismal-relational perspective may associate morphological diversification with the developmental evolution of specific reproductive relations.~~

In the following sections, we introduce an alternative framework that theorizes reproductive characters from an organismal and relational perspective, offering new individuating criteria that ground~~. We explain how~~ alternative classifications (Section 2) and explanations ~~explanations~~ (Section 3)~~ derive from our criteria for individuating reproductive characters~~.

2. The organismal individuation of reproductive characters

Embracing a perspective that encompasses the organismal and relational dynamics of living beings serves as a foundational framework for understanding various biological features~~traits~~, particularly reproductive characters (Baedke 2019; Cortés-García and Etxeberria 2023; Etxeberria 2023; Etxeberria et al. 2023; Etxeberria and Umerez 2006; Nuño de la Rosa 2023;~~Cortés-García and Etxeberria 2023; Etxeberria 2023;~~

~~Etxeberria et al. 2023;~~ Nuño de la Rosa et al. 2021~~; Nuño de la Rosa 2023~~). By adopting an~~adopting~~~~proposing an~~ organismal-relational view of reproductive characters, we aim to consider not only ~~to consider~~ the materiality of reproduction but also to incorporate a functionally sensitive perspective on reproductive traits. While evo-devo is well-suited~~ideal~~ for this task, it needs to be expanded to include the study of functional relations, as it often confines the individuation of characters to body parts or morphological traits (Wagner 2001). In contrast, the organismal-relational approach also~~is not limited to body parts or morphological features but~~ encompasses dynamic entities like processes, activities, and behaviors as reproductive traits.

This expanded~~In doing so, this~~ view introduces~~adds~~ new criteria for individuating processes and activities (see~~,~~ DiFrisco and Jaeger 2021 for process homology). As a result, it ~~and expands~~ broadens the range of explanations for~~of~~ evolutionary questions that are often overlooked ~~left out~~ by the adaptationist framework, including~~,~~ ~~such as~~ novelty, modularity, integration, evolvability, homology, or homoplasy, particularly as they relate to ~~in what concerns~~ reproduction.

~~According to~~ In our proposal, reproductive characters are body parts, activities or behaviors that are ~~those~~ *integrated into the organism and~~that~~ serve specific reproductive functions by interacting with other characters of the same organism or of other organisms*. Two aspects ~~components~~ of this definition require further clarification. First, our perspective of functions differs from that of the ~~it encompasses a different view of functions as compared to the~~ adaptationist framework. O~~Unlike the latter, o~~ur standpoint does not accord design functions a central epistemic role in character explanation in the form of "character X evolved because it was selected for function Y". Instead, ~~it~~we introduce~~s~~ a systemic notion of organismal functions emerging from developmental processes and material relations. Hence, reproductive characters are regarded as systemically organized entities, intricately linked in such a way that they contribute to successful reproduction. Second, the relations that we identify as characterizing reproductive characters are of two kinds. *Intraorganismal relationality* concerns relations among different component parts or processes contributing to the maintenance and functioning of individual organisms across various levels of organization, from gametes to reproductive organs and extraembryonic structures. *Interorganismal~~ic~~ relationality* relates to interactions between individual organisms, including relations between sexual partners for fertilization, and between parents and offspring for successful embryo development.

With this theoretical proposal, we aim to clarify, systematize, and expand the criteria ~~that are~~ implicitly used in some evo-devo studies of reproduction to include ~~inter~~organismal relationships. We introduce a novel taxonomy of reproductive characters in sexually reproducing animals, grounded in an organismal-relational approach (Section 2.1). ~~Then w~~We then focus on ~~those~~ traits that are constituted in the interplay between individual organisms, ~~and~~ advancinge the notion of "interorganismal *traits*" as opposed ~~in contrast~~ to ~~that of~~ "shared traits" (Section 2.2). Finally, we introduce an alternative classification of reproductive modes based on both parent-parent and parent-offspring relations~~relationalities~~ (Section 2.3).

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2.1 An organismal taxonomy of reproductive characters

Sexual reproduction is an inherentlyneeds to be a relational process, as since it requires syngamy (i.e., the fusion of the two gametes into the zygote)[1]. Through this lens, we propose a taxonomy of reproductive traits for sexually reproducing animals according to two parameters: the nature of the characters, namely, structural, physiological, behavioral, or temporal, and the kind of relationality they engage in, namely, intraorganismal relationality, interorganismal relationality between parents, and interorganismal relationality between parent and offspring (see details in Table 2). Following tThis two-dimensional categorization, allows us towe can identify various types of reproductive characters of different types involved in relevant reproductive processes, interacting with other reproductive or non-reproductive characters of the same or other organisms. For instance, this taxonomy allows us to identify temporal patterns related to embryo incubation, such as timing of birth or duration of brood retention, as well as and also physiological characteristics of parent-parent interactions for reproduction at different levels, such as sperm-egg interactions, seminal proteins' interaction with female physiology, or characteristics of implantation. While outside the scope of this paper, Oother kinds of relations are also important for reproductive success, particularly mostly in social species These include. Hence, we can identify playing behavior between siblings, in utero sibling cannibalism, alloparenting care, or grandmother effects as reproductive relations. While outside the scope of this paper, Also, reproductive relations might extend beyond classical parental relations and include encompass interspecific relationshipsones, such as the roleinfluence of the vaginal microbiota in successful fecundation or the transfer of maternal microbiota to offspring in birthing.

Importantly, our classification of reproductive relations does not aim to deliver mutually exclusive categories. Reproductive characters often participate in multiple relations simultaneously. For instance, ovarian tubes are reproductive characters insofar as they are functionally and organizationally integrated into the organism and ; they also interact with other parts, thus and allowing for successful reproduction by intervening in (i) intraorganismal relationality, as ovarian tubes are integrated into the female reproductive system, connect the ovary with the uterus and aid in the movement of ovaand facilitate ova mobility; (ii) interorganismal relationality between sexual partners, as ovarian tubes interact with sperm and facilitate spermatozoa mobility; and (iii) interorganismal relationality between parents and offspring, as ovarian tubes are involved intervene in fertilization and, in some cases, incubation. As illustrated by tThis same example illustrates ,that elements constituting a reproductive character may interact at different organizational levels, spanning from gametes, zygotes, embryos, tissues, and body parts to whole mature organisms. Both forms of relationality (i.e., intra- and interorganismal) can be identified at multiple levels (i.e., cellular, tissular, organismal, social...) and interactions among relata are not necessarily intralevel (e.g. cell-cell interactions), but also interlevel (e.g. cell-organ interaction). Reproductive traits generated in the interaction between multiple organisms hold particular significance in our analysis. TTherefore, in this framework, allows evolutionary change to can be traced throughfrom relationality, and not only through from the genetic or morphological characters of individuala separate organisms. For instance, in eutherians, the process of decidualization in eutherians (which involves significant changes in the cells

[1] In our understanding, sexual reproduction can be uniparental (i.e., self-fertilization) or biparental (i.e., amphigony) (see box 1.3. in Fusco and Minelli 2019 for a discussion on different notions of sexual and asexual reproduction).

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covering the uterine endometrium allowing embryo implantation) is in many groups induced by the attachment of the blastocyst, thus constituting an *interorganismal* character. However, some species (i.e. those with spontaneous ovulation) have evolved~~ an~~ internal control of decidualization so that it occurs cyclically and is hormonally regulated. This~~Such a form of~~ spontaneous decidualization occurs irrespective of external stimuli, ~~and~~ constituting~~es~~ an *intra*organismal~~ic~~ character that has, nevertheless, interorganismal evolutionary origins. Thus, relationality itself is an evolving character, as some forms can change to produce others through, for example, a process of internalization and autonomization of the character (Wagner et al., 2019).

2.2. Interorganismal traits vs shared traits: relational homology

Although characters are always defined in relation to other characters, there is a significant concern about the neglect of interindividual interactions in various fields of reproductive biology (see ~~, for example,~~ Kekäläinen 2021 on human reproduction, Lamarins et al. 2022 on eco-evolutionary population dynamics, Oliveira and Bshary 2021 on behavioral biology, or Wade 2022 on maternal-zygotic co-evolution). To better account for those ~~Some~~ reproductive characters that ~~in sexually reproducing animals arise~~ emerge from the interactions between parents and between parents and offspring, we propose the notion of *interorganismal traits* in contrast to the conventional idea of shared traits. W~~Instead of perceiving these reproductive relations as "shared traits" stemming from conflicting interests among individuals, we propose conceptualizing them as "interorganismal traits". However, not every reproductive trait is interorganismal, and w~~e propose two criteria for identifying such traits.

Firstly, interorganismal traits cannot be ascertained by looking only at single individual organisms. On the contrary, they developmentally arise from interactions between organisms and do not constitutively belong to any one of them in isolation. Therefore, the concept of interorganismal trait is genuinely interactive, accounting for the material changes and rearrangements involved in reproductive processes as a result of relational dynamics. For instance, placentas cannot~~placentas a placenta formed by a fetal portion and a maternal~~ ~~materials~~ ~~portion cannot~~ be realized without the interplay of maternal and fetal tissue dynamics. Therefore, the study of interorganismal traits cannot be reduced to their functional ~~or adaptive design~~ aspects nor their morphology, as it concerns the evolution of relations and not of individuals. Furthermore, this shift explains why the evolution of interorganismal traits cannot be reduced to co-evolved pairings, as proposed by the conflict theory. Conventional ~~models of~~ co-evolution models involve interactions between individuals~~discrete entities~~ (such as parent and embryo), which are the ones that are considered to evolve. However, by~~if we~~ focusing on the relations themselves, reproductive processes appear as grounded on a series of interactive relations, to which co-evolution models are blind. In this context, reproductive relations giving rise to interorganismal traits resemble symbiotic relations more than antagonistic co-evolutionary dynamics. Thus, interorganismal traits refer to relations embodied in an emerging supra-organismal level of organization that causally affects individuals at the organismal level (i.e., parents and/or embryos).

Secondly, like any other character, interorganismal characters persist in evolutionary time, forming lineage trajectories grounded on processes of stabilization (see section 3.2). As a result~~consequence~~, they evolve semi-independently of other traits and have their own evolutionary potential. This shift in focus from individuals to relations enables us to consider the evolvability of specific sets of relations rather than of sets of individual traits. This can be seen in characters that first evolved as interorganismal~~ic~~ relations and later became intraorganismal~~ic~~ in certain groups, as in the aforementioned example of ~~the evolution of~~ decidualization.

These two criteria (interorganismal~~ic~~ dependency and semi-independent evolution) have been~~were~~ already employed to individuate the reproductive characters involved in eutherian pregnancy (Nuño de la Rosa et al. 2021). However, they can ~~may~~ be generalized to individuate reproductive characters in sexually reproducing animals, as elaborated in the next section. Furthermore, the concept of interorganismal character does not need to be restricted to reproduction. Interorganismal characters can be found in other domains of life and also in phenomena unrelated to reproduction, such ~~as the aggregation of organisms in~~ symbiotic assemblies (Chiu and Gilbert 2020, Suárez and Triviño 2020). Hence, although in this article we focus on interorganismal traits in sexually reproducing animals, they can be seen as an instantiation of a more general category encompassing different kinds of interorganismal characters. In the following section, we present a classification of reproductive modes applying an organismal-relational approach.

2.3. An organismal taxonomy of reproductive modes

In this section, we offer a twofold classification of reproductive modes accounting for fertilization mode and incubation mode, respectively.~~ which we theorize in terms of the kind of relationality that is involved.~~ Firstly, we identify patterns of parent-parent relationality, accounting for how syngamy (i.e., gamete fusion) is achieved. Secondly, we discern ~~identify~~ forms of parent-offspring relationality, addressing how embryos are incubated and nourished. These two relations impose strong material and developmental constraints upon reproductive processes and their evolution. For this reason, we use them as the foundation for our classification, which not only provides a general framework for understanding reproductive processes but also offers a basis for developing more detailed classifications tailored to specific clades. By ~~This involves~~ applying these parameters at a finer level, we can ~~which may also entail~~ incorporate~~ing~~ additional ~~other~~ reproductive characters to more precisely delineate similarities and differences between~~in~~ reproductive modes.

2.3.1. A taxonomy for parent-parent relationality

Various forms of parent-parent relationality are implicated in the conditions under which gametes meet (i.e., insemination) and merge (i.e., fertilization, syngamy). We identify two primary relational factors characterizing parent-parent relationality~~ in animals~~. Table 3 offers a taxonomy of reproductive modes in sexually reproducing animals attending to the conditions under which syngamy occurs~~, site of fertilization, and kind of parent-parent interaction~~. First, based on the site of fertilization, we distinguish external fertilization, where~~in which~~ gametes fuse in the environment, from internal fertilization,where~~ in which~~ gametes merge inside the ~~female~~ body. Second, we consider the specific relations between parents that facilitate the encounter of gametes and increase the chances of successful reproduction. By applying these two parameters, we can identify different reproductive modes, which include the free dispersal of gametes into the environment, where syngamy occurs (external fertilization without parent-parent interactions), free dispersal into the environment of spermatozoa that swim and reach internally retained eggs (internal fertilization without parent-parent interactions), release of sperm over previously deposited eggs (external fertilization with indirect parent-parent interactions), spermatophore uptaking (internal fertilization with indirect parent-parent interactions), close coupling for sperm release directly onto the eggs (external fertilization with direct parent-parent interactions), and direct transfer of sperm to the female genital tract (internal fertilization with direct parent-parent interactions)[2].

2.3.2. A taxonomy for parent-offspring relationality

Regarding parent-offspring relationality, we consider two aspects: incubation and post-fertilization nourishment (see Table 4). Based on these two parameters, reproductive modes can be classified into the following categories: *ovuliparity*, where there is no form of incubation or nourishment[3]; *oviparity*, with a short period of internal incubation and limited or no post-fertilization nourishment; *monotreme oviparity*, notable for substantial nutrient transfer during limited internal incubation before oviposition; *lecithotrophic viviparity*, characterized by an extended period of internal incubation without further means for nutrient transfer; *matrotrophic viviparity*, involving extended incubation accompanied by nourishment supply; *brooding*, characterized by a secondary period of incubation after partition; and *matrotrophic brooding*, which entails ~~the evolution of mechanisms for~~ nutritional supply during secondary incubation[4].

Our classification distinguishes itself from standard approaches in reproductive biology in terms of how classes are defined: within our framework, the distinction between oviparity and viviparity is not a matter of the state of the embryos at the time of partition (i.e., contained in egg coatings vs. free-living individuals), but a consequence of the extension of pre-partition incubation. Accordingly, the traditional criterion used for distinguishing oviparity and viviparity, namely the presence or absence of egg-coatings at release, is understood within our approach as secondary to the evolution of extended periods of internal incubation theorized in terms of parent-offspring relationality. Other common derived traits besides thinning or loss of egg-coatings, such as an enhancement of water supply and gas exchange, or immune rearrangements, can be identified in clades with increased embryo retention.

It is also important to note that our classification is articulated in terms of the extent of prenatal incubation and post-fertilization nourishment. In this regard, our approach makes the distinction between classes a matter of degree, allowing for the identification of intermediate states. Although reproductive relations

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[2] For the present taxonomy, we restrict our scope to those relations that facilitate the achievement of syngamy. Nonetheless, a similar complementary classification could be elaborated to address parent-parent relationality with respect to courtship or parental or alloparental care of offspring after birth.

[3] This form of reproduction is regarded by the rationale of the *amount of investment* in economic terms (Lodé 2012) as the least invested by the parents. However, the absence of post-fertilization care does not entail lower investment in terms of energy, time, or effort by the parents, as shown by the example of the construction of complex nests by the fish *Gasterosteus aculeatus* put forth by Lodé himself. This shows that the criteria of the amount of investment is not operative for classifying animals ~~vertebrates~~ according to their reproductive mode.

[4] This classification is restricted to post-fertilisation events (including incubation and nourishment) during the period of parental embryo retention. A complementary classification could be elaborated that addresses other forms of incubation and provision of nutrients that are excluded from this taxonomy, such as eutherian lactation, egg incubation in nests and other forms of post-partition parental care. Such further classifications open the possibility to identify fine-grained connections between, for instance, sociability and viviparity (see Nuño de la Rosa 2023). Yet, this task exceeds the scope of this paper.

themselves can generally be unambiguously individuated at different organizational levels, their strength varies along a continuum. This continuity resonates with current empirical practices in reproductive biology. For instance, the assessment of whether a particular species or population is either matrotrophic or lecithotrophic is quantitatively determined through egg size measuring or dry mass analysis, and the distinction is never sharp, since "[l]ecithotrophy and matrotrophy represent extremes of a continuum" (Blackburn 2015a, p. 963). However, occasionally, this continuum is marked by specific thresholds that have significant implications for reproductive modes. For instance, pregnancy is discretely delineated by the two inflammatory events of implantation and parturition . This constitutes a specific form of parent-offspring relationality shared by marsupials and eutherians, but the evolutionary specialization originated in eutherians to overcome the "inflammation paradox" made possible the extension of intrauterine development in this class (Chavan et al. 2017), serving as a new criterion for the individuation of eutherian pregnancy.

3. The explanatory role of reproductive characters in the organismal approach

By emphasizing the material and developmental dimensions of reproduction, our proposed organismal-relational individuation of reproductive characters opens up a range of explanatory possibilities. In this section, we identify three core explanatory agendas of this approach that the functional-adaptationist approach fails to address, namely the explanation of reproductive homologies and homoplasies, the constraints associated with the evolution of reproductive modes, and the evolvability of reproductive characters.

3.1. The homology/homoplasy problem

Since the organismal individuation of reproductive characters exameslooks at the relations and developmental mechanisms underlying the generationappearance of characters, it provides a more exhaustive view of similarities and differences. This approach is necessary not only for the proper traceability of relevant homologs (DiFrisco et al. 2020) but also to discover and account for instances of homoplasy in the evolution of reproduction. Thus, instead of attributing the evolution of similar reproductive characters in unrelated lineages to convergent evolution, our approach enables explanatory generalizations across different animal groups based on their relational and developmental similarities. For example, from an organismal perspective, the placenta can be recognized as an organ that shares relational similarities across various vertebrates. This recognition is based on commonalities observed, including extended areas of contact between maternal and fetal tissues, and specific mechanisms facilitating the physiological accommodation and maintenance of this interorganismal organ. Comprising contributions from both maternal and fetal materials, the placenta serves the joint purpose of ensuring successful fetal nutrition for reproduction. This approach, unlike the adaptationist selectionist one approach toof shared traits, incorporates relational and material criteria in the individuation of placentas, which allows for distinguishing homologies and homoplasies. In the former case, placentas have evolved through the recruitment of homologous tissue origins, as evidenced by tissular homologies in squamate and eutherian chorioallantoic placentas, and between shark and marsupial yolk sac placentas. In the latter case, however, we observe that structures and processes display relevant similarities despite different tissular origins, such as the eutherian chorioallantoic placenta versus the marsupial yolk sac placenta (Whittington et al. 2022).

When applied to reproductive modes, this ~~our~~ approach also enables the recognition of homoplastic patterns in the physiological, morphological, and immunological relations~~adaptations~~ during the evolution of prolonged internal incubation across viviparously reproducing animals, despite their group-specificities (Gao et al 2019; Recknagel et al. 2021; Blackburn 2015).

3.2. The constraints problem

In evo-devo, the constraints problem pertains to understanding the developmental reasons that explain why some characters evolve in certain groups and not in others. The evolutionary specializations of eutherians enabling the extension of intrauterine development nicely illustrate the relevance of ~~that the~~ analyzing~~sis~~ ~~of~~ reproductive relations for understanding how ~~requires consideringnecessitates consideration of~~ ~~how associated~~ developmental constraints evolved. Pregnancy requires regulating ~~overriding~~ the general immune mechanisms responsible for tissue integrity, allowing some form of maternal recognition of the embryo. This was accomplished through the repurposing of the ancestral inflammatory endometrial reaction that in marsupials leads to the early termination of internal incubation. This constraint was co-opted in eutherians for allowing sustained ~~Whereas the ancestral response to implantationthe uterine attachment of the blastocyst was an acute endometrial inflammation~~ ~~preventing~~ ~~, which prevented pregnancy, in eutherians this developmental constraint was overcome by~~ ~~repurposing~~ ~~transforming this reaction into a novel "good inflammation" (Chavan et al. 2017, p. 24) essential for~~ implantation by facilitating ~~that causes~~ vascular permeability, uterine reorganization, and suppressing~~es~~ deleterious effects for the embryo (Chavan et al., 2017). Functionalist explanations lump all those cases into a single~~the same~~ category and thus preclude a satisfying account of the requirements that made this particular form of viviparity possible.

Besides, the underlying developmental mechanisms of reproductive relations have evolved in a way that ~~they~~ confers varying degrees of stability to these relations. This variability in the stability of relational characters helps explain the so-called problem of reversibility, which addresses the apparent constraints associated with reverting from one mode of reproduction to another. The most paradigmatic case is the transition from oviparity to viviparity, which very rarely occurs in the opposite direction. From an organismal-relational perspective, this can be explained by ~~because~~ the evolution of specializations for stabilized internal incubation and nutritional provision, which involves intricate changes in the anatomy and physiology of both parent and offspring (Blackburn 2015b; King and Lee 2015). Those changes condition the relationality between them, ~~which in turn~~ ensuringes ~~a~~ robust developmental control ~~of development~~ (Griesemer 2014; Rosslenbroich 2014). In contrast, other traits, such as mating behaviors, do not entail such intricate relational changes ~~in relationality~~ and, as a consequence, are more labile over evolutionary time. Mating behaviors exhibit greater plasticity, responding to environmental cues, population density, or resource availability (Ah-King and Gowaty 2016). This distinction highlights how the stability of reproductive relations influences the evolutionary flexibility of different reproductive traits.

Failing to consider the developmental constraints involved in the evolution of reproductive relations can result in~~lead to~~ significant errors in phylogenetic reconstruction. For instance, a controversial piece of work argued that live-bearing was the ancestral state in squamate reptiles (Pyron and Burbrink 2014). The problem with this hypothesis is that it relied on a functional individuation of reproductive characters that ignored developmental evidence for the evolution of viviparity, leading to a misinterpretation of the evolutionary history of the lineage ~~n incorrect phylogenetic reconstruction~~ (Blackburn 2015).

The organismal and relational individuation of characters also opens explanatory possibilities for understanding the existence of unexplored regions within the reproductive space. For example, the aforementioned functionalist conjecture as to why viviparity did not evolve in birds (Blackburn and Evans 1986) could be expanded to incorporate developmental explanations. From this perspective, it might~~could~~ be argued that the impermeability of eggshells, and/or the nature of the oviduct as an unfavorable environment for egg retention (see e.g.~~,~~ Anderson et al. 1987) have served as ~~strong~~ developmental constraints for the evolution of viviparity in birds. In the case of *Lerista*, an organismal-relational approach encourages us to explore~~delve into~~ how certain conditions favor the evolution of extended internal incubation in ~~species or~~ populations with~~that meet~~ the physiological conditions for developing those traits. An approach that incorporates developmental constraints and examines the ~~tissue and~~ developmental changes leading to the evolution of specific reproductive traits and ~~forms of~~ parental-offspring relations~~relationality~~ enables the formulation of mechanistic explanations. This approach helps us understand how certain factors, such as physiological predispositions or behaviors, facilitate the evolution of stabilized and complex reproductive modes. For instance, knowing ~~a deeper knowledge of~~ how extended internal incubation evolves in *Lerista* at a physiological and morphological level might ~~highly increase~~ enhance our understanding of how certain conditions~~ and predispositions~~, including semi-fossorial behavior, small clutches, or single yearly egg laying~~,~~ facilitate the evolution of viviparity. Hence, the study of ~~the dynamics of~~ developmental constraints ~~can~~ helps us better understand ~~grasp~~ how functional constraints affect the origin~~appearance~~ of certain traits in evolution.

3.3. The evolvability problem

The evolvability problem refers to why characters~~, including reproductive characters,~~ evolve in different directions, ranges, and rates (Hansen et al. 2023). Unlike~~As opposed to~~ adaptationist explanations, evo-devo ~~explanations of the distinct evolvabilities of reproductive modes~~ focuses on how differences in evolvability of different reproductive modes ~~between them, such as those between oviparity and viviparity,~~ depend on being controlled by differently integrated parameters of variation~~ (Wake 2015)~~. For instance, ~~Thus, we observe a varying degree of physiological and topological accommodation of the characters involved. Thus,~~ in viviparous amphibians, the characters involved in nutrient supply, oxygen intake and waste elimination are separated spatially, temporally, morphologically and physiologically as compared to placental vertebrates (Wake 2015). Paying attention to the degree of integration of reproductive characters in terms of both inter- and intraorganismal relationality ~~of~~ ~~how inter- and intraorganism~~al~~ic different reproductive characters are integrated~~ can illuminate their differing evolutionary potential, as modularity is a well-known determinant of the independent evolution of traits.

Studying~~Attending~~ reproductive relations also sheds light ~~helps to explain~~ on trends in the evolution of sexual reproduction. As discussed earlier, the adaptationist ~~selectionist~~ framework suggests that~~explains the~~ reproductive traits co-evolve~~ution~~ by ~~of different reproductive characters as the outcome of~~ combining evolutionary strategies to enhance fitness. For example, it has been argued that some species of poeciliid fishes retain oviparity ~~the ancestral oviparous mode of reproduction~~ because females rely on male skin coloring patterns to assess their fitness, while others ~~species~~ have evolved viviparity as a mechanism for internal selection of embryos, eliminating the need for sexual dimorphism in skin coloring patterns (Reznick et al. 2021). Here~~In this example~~, reproductive modes ~~(i.e., oviparity and viviparity)~~ and secondary sexual traits ~~(i.e., absence or presence of skin coloring patterns in males)~~ are seen as different strategies to maximize fitness that can be combined at will by selection. Conversely~~In contrast~~, an organismal-relational approach focuses on~~to the co-evolution of reproductive characters pays attention to the~~ evolved material relations between parents and between parents and offspring showing ~~and to~~ how ~~the evolution of~~ some ~~of these~~ reproductive relations facilitate the evolution of ~~makes the evolution of~~ other~~s relations more likely~~.

In this regard, the taxonomies presented in the previous section highlight ~~seem to indicate~~ the relevance of ~~evolutionary~~ constraints in the evolution of reproductive modes, showing the interconnectedness of ~~as~~ parent-parent ~~relationality~~ and parent-offspring relationality ~~are interconnected~~. Consequently, modes of reproduction concerning the conditions of syngamy (Table 3) and embryo development (Table 4) appear to be mutually constrained. For instance, ~~it is likely that~~ the evolution of the reproductive mode featuring ~~combining~~ increased post-fertilization nourishment and lack of incubation may be hindered by ~~has not evolved due to~~ physiological and topological constraints, as the former requires some form of material relationality and specific mechanisms for parent-offspring accommodation ~~in order~~ to evolve. ~~Also, modes of reproduction concerning the conditions of syngamy (Table 3) and embryo development (Table 4) seem to be mutually constrained~~. Moreover~~For instance~~, as ovuliparity consists of the ~~complete~~ absence of incubation and post-fertilization nourishment~~supply of nutrients~~, it can only be achieved after external fertilization. Conversely~~Also~~, oviparity is constrained to evolve on the substrate of a parent-parent relationality that compromises some form of internal incubation, for which internal fertilization is a prerequisite. A~~The same occurs with a~~ll forms of viviparity follow the same constraints. As for brooding, since it is characterized by secondary incubation, it can be realized in a high variety of forms, being related to any form of parent-parent relationality. Such constraints play a pivotal role in shaping~~can affect~~ the evolvability of reproductive characters and modes either by restricting certain pathways or by opening new~~a new range of~~ evolutionary possibilities. A similar reasoning is employed by Laura Franklin-Hall (2021) in discussing whether anisogamy explains sex-specific characters and sex-linked trends in evolution. The standard adaptationist~~selectionist~~ interpretation posits ~~assumes~~ that differences in gamete size drive ~~have led to a series of~~ morphological and behavioral changes, leading to ~~that justify~~ sex differentiation~~the "natural" differentiation of the sexes~~ based on optimal parental investment. In contrast, Franklin-Hall proposes an alternative evo-devo explanation, suggesting ~~positing~~ that anisogamy triggers ~~increased the likelihood of~~ a sequence~~cascade~~ of evolutionary changes due to ~~internal~~ developmental factors. For example, gamete size can be associated with the fact that internal fertilization evolves in females or that small gametes are more mobile.

Additionally, an organismal-relational approach to the individuation of reproductive modes can provide insights into~~shed light on~~ the evolvability of non-reproductive characters. This is exemplified ~~An example is provided~~ by the correlation, across various animal groups, between the evolution of different forms of viviparity and increased diversification (see Helmstetter et al. 2016 for teleosts and ~~,~~ Pincheira-Donoso et al. 2013 for squamates). ~~In general terms, ~~V~~v~~iviparous lineages generally exhibit higher rates of speciation and~~,~~ extinction, ~~and ~~as well as greater species turnover over time (Pyron and Burbrink 2014). From a functional-adaptationist perspective, this phenomenon is often attributed to ~~explained by viewing~~ reproductive modes acting as key innovations that facilitate ~~enable ~~adaptive radiations~~the exploration of new ecological niches~~. In contrast, from an organismal-relational perspective, the morphological diversification linked to the evolution of specific ~~certain ~~reproductive modes can be linked ~~attributed ~~to the evolution ~~development ~~of specific reproductive relations. For instance, the extension of intrauterine developmental time in eutherians, as enabled by the evolution of the maternal-fetal interface, ensures a highly robust developmental niche that might have fostered further opportunities for exploring the morphospace (Lillegraven 1975).

Developmental constraints influencing~~on~~ ~~specific ~~evolutionary transitions~~ in reproductive evolution~~, as well as the varied ~~distinct ~~evolvabilities discussed above~~of reproductive characters~~, do not necessarily indicate a general ~~universal ~~trend toward increased parental investments~~, such as nourishment supply in successive stages~~ leading to hemotrophic viviparity (see Blackburn 1999, Rosslenbroich 2024). While identifiable trajectories exist, they represent localized trends specific to certain lineages.

Finally, the organismal-relational individuation of reproductive modes might lead to the identification of novel ~~new ~~evolutionary agents that foster~~leading to~~ new levels of internal selection, yielding significant implications~~with crucial consequences~~ for evolvability (Nuño de la Rosa 2023). For instance, the evolution of internal fertilization led to the evolution of gamete selection, while implantation led to that~~the evolution~~ of oocyte selection (Kekäläinen 2021). This framework enables the recognition of the reduction in fecundity (which most often accompanies the evolution of viviparity) as an evolved trait that allows for embryo selection, instead of ~~an undesired consequence or ~~a trade-off in the evolution of viviparity, as suggested by the adaptationist-functional approach (Kalinka 2015).

4. Conclusions

Distinct criteria for individuation applied by different theoretical frameworks result in diverse predictions and explanations regarding the evolution of reproductive modes and characters. Within the adaptationist ~~selectionist ~~framework, ~~the functional individuation of reproduction accounts for ~~reproductive characters are functionally individuated as strategies for enhancing fitness. This approach identifies and classifies reproductive characters on the basis of their assumed functional roles, disregarding developmental origins and organismal relations between parents, and parents and offspring. In contrast, our suggested organismal-relational individuation, informed by ~~contemporary ~~studies on the evo-devo of reproduction, introduces a novel framework ~~strategy ~~for elaborating taxonomies of reproductive modes and characters and allows for ~~more precise ~~explanations that the adaptationist ~~selectionist ~~perspective cannot provide.

Two major theoretical innovations arise from this reinterpretation of~~new way of looking at~~ reproduction.

~~-~~On the descriptive side, our proposed framework~~reproductive modes~~ illustrates how morphological features, processes, activities, and relations can be individuated and homologized as evolutionary units. Current empirical studies on the evolution of reproductive modes ~~evolution ~~often rely on transcriptome sequencing of two or more species, followed by a comparison based on Gene Ontology Analysis. This bioinformatics method aims to describe the functions of gene products according to a selected-effect notion of biological functions (Thomas 2019). It involves identifying differentially ~~"~~enriched~~"~~ genes during a specific biological process under particular conditions, where these genes exhibit a higher transcription rate and stronger association with a particular function. While this method offers a more detailed perspective than standard DNA sequencing, it encounters ~~faces~~ significant challenges in identifying gene product-function relations, particularly ~~especially~~ in the evolution of complex traits~~characters~~. In contrast, our approach considers the evolution of developmental processes shaping various characters involved in reproductive functions and the relations established among them and with other organisms.

On the explanatory side, the organismal-relational individuation of reproductive modes and characters addresses ~~might answer~~ both how and why questions. On the one hand, homologies and homoplasies between reproductive characters can be established on the basis of developmental and relational similarities. On the other hand, developmental constraints help understand why some reproductive regions have not been explored throughout evolution, and why some trajectories in the evolution of reproduction seem to be more likely than others. These two aspects of scientific endeavor, namely ~~(~~description and explanation of reproduction,~~)~~ are crucial in our understanding of reproductive phenomena and their evolution. While it is premature to determine ~~Although it is still early to assess~~ whether the ideas presented in this paper might support a new empirical research program, we have shown that the proposed shift can~~might~~ have relevant consequences in methods~~empirical methodologies~~ used to individuate reproductive characters (including practices such as reproductive mode determination, developmental studies, or modeling), the elaboration of taxonomies, and the formulation of evolutionary explanations.

Regarding the issue of whether both approaches should be integrated or rather coexist as complementary views, we adopt a cautious and nuanced stance, distinguishing two epistemic goals. Firstly, concerning trait individuation, due to the inaccuracies in classification and phylogenetic reconstructions by the functional account, we advance that a pluralist solution is not advisable. We claim that functional accounts should be integrated with organismal and relational studies because, as we have shown, the developmental, material basis of reproductive functions is required for a proper characterisation of reproductive characters and modes. In some cases, an initial functional approach focusing on adaptive capacities can be useful, but we anticipate that, as the proposed research program advances, the organismal-relational approach will increasingly replace the functional criteria for identifying reproductive characters. Secondly, regarding evolutionary explanations of reproduction, we believe that functional and evo-devo explanations should be cross-checked against each other. For instance, in explaining why eutherians have undergone greater morphological diversification compared to marsupials, a purely adaptive explanation would suggest that both groups have the same capacity to generate variation but, due to historical contingencies, eutherians have been able to explore more niches, experiencing an adaptive radiation. This explanation would be merely adaptive, *ceteris paribus*. However, a relational and developmental view can contribute to the explanation as to why eutherians have been able to explore more niches because they have been able to explore a greater morphospace due to prolonged internal incubation. In this case, both approaches would be compatible and mutually informative.

Commented [3]: Expanded in response to R2

Although the scope of this paper is limited to reproductive characters in sexually reproducing animals, the insights provided by our view may also be relevant for understanding the dynamics and evolution of other forms of reproduction, such as sexual reproduction in those of sexually reproducing plants and different forms of asexual reproduction, parthenogenesis, or colony-regulated microbial multiplication[5]. Addressing the relational dimension of the evolution and development of reproduction in these groups would require a detailed examinationexamining their characteristics in detail and dealing with specific challenges such as the fuzziness of the relata apparent in some cases[6]. However, we anticipate that applying an organismal-relational view will also lead to a different understanding of reproductive relations and provide new explanatory insights into other forms of reproduction.

References

Ah-King M, Gowaty PA (2016) A conceptual review of mate choice: stochastic demography, within-sex phenotypic plasticity, and individual flexibility. Ecol Evol 6(14):4607-42 https://doi.org/10.1002/ece3.2197

Amundson R (2005) The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo. Cambridge University Press, Cambridge

Anderson DJ, Stoyan NC, Ricklefs RE (1987) Why are there no viviparous birds? A comment. Am Nat 130(6):941–947 http://dx.doi.org/10.1086/284757

Baedke J (2019) O Organism, Where Art Thou? Old and New Challenges for Organism-Centered Biology. J Hist Biol 52(2):293-324 https://doi.org/10.1007/s10739-018-9549-4

Blackburn DG (1999) Viviparity and oviparity: Evolution and reproductive strategies. In: E Knobil and J D Neill (eds) Encyclopedia of Reproduction, Volume 4, Academic Press, London, pp 994–1003

Blackburn DG (2015a) Evolution of vertebrate viviparity and specializations for fetal nutrition: A quantitative and qualitative analysis. J Morphol 276(8):961–990 https://doi.org/10.1002/jmor.20272

Blackburn DG (2015b) Evolution of viviparity in squamate reptiles: Reversibility reconsidered. J Exp Zool B Mol Dev Evol 324(6):473–486 https://doi.org/10.1002/jez.b.22625

Blackburn DG, Evans H E (1986) Why are there no viviparous birds? Am Nat 128(2):165–190 http://dx.doi.org/10.1086/284552

Brigandt I (2003) Homology in comparative, molecular, and evolutionary developmental biology: the radiation of a concept. J Exp Zool **B** Mol Dev Evo 299(1):9-17 https://doi.org/10.1002/jez.b.36

Brigandt I, Love AC (2012) Conceptualizing evolutionary novelty: moving beyond definitional debates. J Exp Zool **B** Mol Dev Evo 318(6):417-427 https://doi.org/10.1002/jez.b.22461

Buckley D, Alcobendas M, García- París M, Wake MH (2007) Heterochrony, cannibalism, and the evolution of viviparity in Salamandra salamandra. Evol Dev 9(1):105–115

[5] We thank an anonymous reviewer for raising this point.

[6] We thank an anonymous reviewer for raising this point.

https://doi.org/10.1111/j.1525-142X.2006.00141.x

Chavan, A. R., Griffith, O. W., and Wagner, G. P. (2017). The inflammation paradox in the evolution of mammalian pregnancy: turning a foe into a friend. *Current opinion in genetics & development*, *47*, 24-32. https://doi.org/10.1016/j.gde.2017.08.004

Chiu L, Gilbert SF (2020) Niche construction and the transition to herbivory: phenotype switching and the organization of new nutritional modes. In: Levine H, Jolly MK, Kulkarni P, Nanjundiah V (eds) Phenotypic switching. Academic Press, Cambridge, MA, pp 459–482 https://doi.org/10.1016/B978-0-12-817996-3.00015-3

Chiu L, Gilbert SF (2015) The Birth of the Holobiont: Multi-species Birthing Through Mutual Scaffolding and Niche Construction. Biosemiotics 8(2):191–210 https://doi.org/10.1007/s12304-015-9232-5

Cortés-García D, Etxeberria Agiriano A (2023) Ontologies in Evolutionary Biology: The Role of the Organism in the Two Syntheses. In: Viejo JM, Sanjuán M (eds) Life and Mind: New Directions in the Philosophy of Biology and Cognitive Sciences, Springer International Publishing, pp 185–205 https://doi.org/10.1007/978-3-031-30304-3_9

Crespi B, Semeniuk C (2004) Parent-offspring conflict in the evolution of vertebrate reproductive mode. Am Nat 163(5):635–653 https://doi.org/10.1086/382734

DiFrisco, J. (unpublished). Character individuation: functional, descriptive, and developmental.

~~DiFrisco J (2023) Toward a theory of homology: development and the de-coupling of morphological and molecular evolution. Br J Philos Sci 74(3):771-810 https://doi.org/10.1086/714959~~

DiFrisco J, Jaeger J (2021) Homology of process: Developmental dynamics in comparative biology. Interface Focus 11(3) https://doi.org/10.1098/rsfs.2021.0007

DiFrisco J, Love AC, Wagner GP (2020) Character identity mechanisms: A conceptual model for comparative-mechanistic biology. Biol Philos 35(4):44 https://doi.org/10.1007/s10539-020-09762-2

Etxeberria A, Umerez J (2006) Organismo y Organización En la Biología Teórica ¿Vuelta Al Organicismo? Ludus Vitalis 14(26):3–38

Etxeberria A, Cortés-García D, Torres M (2023) Organisms, Life Relations, and Evolution: Inter-Dependencies after Kropotkin's Mutual Aid. ArtefaCToS. Journal of Science and Technology Studies 12(1):1 https://doi.org/10.14201/art2023121179204

Etxeberria A (2023) Jacob's Understanding of Reproduction: Challenges from an Organismic Collaborative Framework. HOPOS The International Society for the History of Philosophy of Science 13(2) https://doi.org/10.1086/726256

Fabian D, Flatt T (2012) Life history evolution. Nat Sci Educ 3(10)

Franklin-Hall L (2021) The Animal Sexes as Historical Explanatory Kinds. In: Dasgupta S, Dotan R, Weslake B (eds) Current Controversies in Philosophy of Science, Routledge, New York, pp 177-197

Furness AI, Morrison KR, Orr TJ, Arendt JD, Reznick DN (2015) Reproductive mode and the shifting arenas of evolutionary conflict. Ann N Y Acad. Sci, 1360(1):75–100 https://doi.org/10.1111/nyas.12835

Fusco G, Minelli A (2019) The Biology of Reproduction. Cambridge University Press, Cambridge

Fusco G, Minelli A (2023). Understanding Reproduction. Cambridge University Press, Cambridge

Gilbert SF, Epel D (2009) Ecological Developmental Biology: Integrating Epigenetics. Sinauer Associates, Sunderland

Griesemer J (2000) The Units of Evolutionary Transition. Selection 1(1–3):67–80 https://doi.org/10.1556/Select.1.2000.1-3.7

Griesemer J (2005) The informational gene and the substantial body: On the generalization of evolutionary theory by abstraction. In Jones MR, Cartwright N (eds) Idealization XII: Correcting the Model. Idealization and Abstraction in the Sciences, Volume 86, pp 59–115

Griesemer J (2014) Reproduction and scaffolded developmental processes: An integrated evolutionary perspective. In Minelli A, Pradeu T (eds) Towards a Theory of Development, Oxford University Press, Oxford, pp 183-201 https://doi.org/10.1093/acprof:oso/9780199671427.003.0012

Haig D (1993) Genetic Conflicts in Human Pregnancy. Q Rev Biol 68(4):495–532 https://doi.org/10.1086/418300

Hansen TF, Houle D, Pavličev M, Pélabon C (2023) Evolvability: A Unifying Concept in Evolutionary Biology? The MIT Press, Cambridge, London https://doi.org/10.7551/mitpress/14126.001.0001

Helmstetter AJ, Papadopulos AST, Igea J, Van Dooren TJM, Leroi AM, Savolainen V (2016) Viviparity stimulates diversification in an order of fish. Nat Commun 7(1) https://doi.org/10.1038/ncomms11271

Herrera AM, Cohn MJ (2014) Embryonic origin and compartmental organization of the external genitalia. Sci Rep 4(6896):1-6 https://doi.org/10.1038/srep06896

Jacob F (1970) *La logique du vivant*. Gallimard, Paris. (*The Logic of Life*, Betty E. Spillmann trans., Pantheon, New York, 1973).

Janzen FJ, Warner DA (2009) Parent–offspring conflict and selection on egg size in turtles. J Evol Biol 22(11):2222–2230 https://doi.org/10.1111/j.1420-9101.2009.01838.x

Kalinka AT (2015) How did viviparity originate and evolve? Of conflict, co-option, and cryptic choice. BioEssays 37(7):721–731 https://doi.org/10.1002/bies.201400200

Kekäläinen J (2021) Genetic incompatibility of the reproductive partners: An evolutionary perspective on infertility. Hum Reprod 36(12):3028–3035 https://doi.org/10.1093/humrep/deab221

King B, Lee MSY (2015) Ancestral State Reconstruction, Rate Heterogeneity, and the Evolution of Reptile Viviparity. Syst Biol 64(3):532–544 https://doi.org/10.1093/sysbio/syv005

Lamarins A, Fririon V, Folio D, Vernier C, Daupagne L, Labonne J, Buoro M, Lefèvre F, Piou C, Oddou-Muratorio S (2022) Importance of interindividual interactions in eco-evolutionary population dynamics: The rise of demo-genetic agent-based models. Evol Appl 15(12):1988-2001 https://doi.org/10.1111/eva.13508

Lillegraven JA (1975) Biological considerations of the marsupial-placental dichotomy. Evolution, 29: 707–722.

Lodé T (2012) Oviparity or viviparity? That is the question.... Reprod Biol 12(3):259–264 https://doi.org/10.1016/j.repbio.2012.09.001

Minelli A (2003) The Development of Animal Form: Ontogeny, Morphology, and Evolution. Cambridge University Press, Cambridge

Mossman HW (1937) Comparative morphogenesis of the fetal membranes and accessory uterine structures. Contrib Embryol 26:129 –246

Nuño de la Rosa L (2023) Agency in Reproduction. Evol Dev 25:418–429 https://doi.org/10.1111/ede.12440

Nuño de la Rosa, L. (2010). Becoming organisms: the organisation of development and the development of organisation. *History and Philosophy of the Life Sciences*, *32*(2–3), 289–315.

Nuño de la Rosa L, Pavličev M, Etxeberria A (2021) Pregnant Females as Historical Individuals: An Insight From the Philosophy of Evo-Devo. Front Psychol 11:572106 https://doi.org/10.3389/fpsyg.2020.572106

Oliveira RF, Bshary R (2021) Expanding the concept of social behavior to interspecific interactions. Ethology 127(10):758-773 https://doi.org/10.1111/eth.13194

Pyron RA, Burbrink FT (2014) Early origin of viviparity and multiple reversions to oviparity in squamate reptiles. Ecol Lett 17(1):13–21 https://doi.org/10.1111/ele.12168

Reznick DN (2014) Evolution of Life Histories. In: Losos JB (ed) The Princeton Guide to Evolution, Princeton University Press, Princeton, pp 268–275

Reznick DN, Travis J, Pollux BJ, Furness AI (2021) Reproductive mode and conflict shape the evolution of male attributes and rate of speciation in the fish family Poeciliidae. Front Ecol Evol 9:639751 https://doi.org/10.3389/fevo.2021.639751

Rosslenbroich B (2014) On the Origin of Autonomy: A New Look at the Major Transitions in Evolution. Springer International Publishing, Cham https://doi.org/10.1007/978-3-319-04141-4

Shine R (2014) Evolution of an Evolutionary Hypothesis: A History of Changing Ideas about the Adaptive Significance of Viviparity in Reptiles. J Herpetol 48(2):147–161 https://doi.org/10.1670/13-075

Stewart JR, Blackburn DG (1988) Reptilian Placentation: Structural Diversity and Terminology. Copeia, 1988(4):839–852 https://doi.org/10.2307/1445706

Suárez J, Triviño V (2020) What is a hologenomic adaptation? Emergent individuality and inter-identity in multispecies systems. Front Psychol 11:187 https://doi.org/10.3389/fpsyg.2020.00187

Thomas PD (2017) The Gene Ontology and the Meaning of Biological Function. In: Dessimoz C, Škunca N (eds) The Gene Ontology Handbook, Springer, Cham pp. 15–24 https://doi.org/10.1007/978-1-4939-3743-1_2

Trivers RL (1974) Parent-Offspring Conflict. Am Zool 14(1):249–264 https://doi.org/10.1093/icb/14.1.249

Villegas C, Love AC, Nuño de la Rosa L, Brigandt I, Wagner GP (2021) Conceptual roles of evolvability across evolutionary biology: Between diversity and unification. In: Hansen TF, Houle D, Pavličev M, Pélabon C (eds) Evolvability: A Unifying Concept in Evolutionary Biology?, The MIT Press, Cambridge, London, pp 35–54 https://doi.org/10.7551/mitpress/14126.003.0005

Wade MJ (2022) Maternal-Offspring Interactions: Reciprocally Coevolving Social Environments. J Hered 113(1):54-60 https://doi.org/10.1093/jhered/esab044

Wagner GP (2001) Characters, Units and Natural Kinds: An Introduction. In Wagner GP (ed) The Character Concept in Evolutionary Biology, Academic Press, San Diego, pp 1–10 https://doi.org/10.1016/B978-012730055-9/50008-2

Wagner GP, Kin K, Muglia L, Pavličev M (2014) Evolution of mammalian pregnancy and the origin of the decidual stromal cell. Int J Dev Biol 58(2-3-4):117-126 https://doi.org/10.1387/ijdb.130335gw

Wagner GP, Erkenbrack EM, Love AC (2019) Stress-Induced Evolutionary Innovation: A Mechanism for the Origin of Cell Types. Bioessays 41(4):1800188 https://doi.org/10.1002/bies.201800188

Wake MH (2004) Environmental effects, embryonization, and the evolution of viviparity. In Hall BK, Pearson RD, Muller GB (eds) Environment, Development, and Evolution: Towards a Synthesis. TheVienna series in Theoretical Biology, Volume 4, The MIT Press, Cambridge, pp 151–170

Wake MH (2015) Fetal adaptations for viviparity in amphibians. J Morphol 276(8):941–960 https://doi.org/10.1002/jmor.20271

Wake DB, Wake MH, Specht CD (2011) Homoplasy: From Detecting Pattern to Determining Process and Mechanism of Evolution. Science 331(6020):1032–1035 https://doi.org/10.1126/science.1188545

Whittington CM, Buddle AL, Griffith OW, Carter AM (2022) Embryonic specializations for vertebrate placentation. Philos Trans R Soc Lond B Biol Sci 377(1865):20210261 https://doi.org/10.1098/rstb.2021.0261

Zeh JA, Zeh DW (2001) Reproductive mode and the genetic benefits of polyandry. Anim Behav 61(6):1051–1063 https://doi.org/10.1006/anbe.2000.1705

	Oviparity	**Viviparity**
Lecithotrophy	Lecithotrophic and oviparous animals. E.g., birds, crocodilians, turtles, most lizards, snakes and fishes.	Lecithotrophic and viviparous animals. E.g., some amphibians, lizards, snakes and fishes.
Matrotrophy	Matrotrophy and oviparous animals. E.g., monotremes (i.e., platypus and echidna).	Matrotrophy and viviparous animals. E.g., marsupials, eutherians, some fish, lizards and amphibians.

Table 1. A functional taxonomy of reproductive modes, illustrated by examples from vertebrates. Modified from Blackburn 2015a.

	Structural	Physiological	Behavioral	Temporal
Intraorganismal relationality	Gamete traits, anatomical characteristics of reproductive organs (gonads, tubes, glands, ~~copulatory appendix~~), extraembryonic structures.	Production of gametes, physiological regulation of reproductive homeostasis, menopause, spontaneous decidualization of uterine wall.	Suckling behavior.	Time for sexual availability, estrous cycle, menstrual cycles, ovarian cycles, hormonal cycles.
Interorganismal relationality between parents	Sexual characters related to courtship (e.g., colored feathers), ~~further~~ structures for copulation~~s~~.	Sperm-egg interactions, seminal proteins' interaction with female physiology, characteristics of implantation, sperm storage/removal, mating-induced ovulation ~~by mating~~.	Courtship behaviors, mating interactions.	Timing of mating, mating duration.
Interorganismal relationality between parents and offspring	Parental structures promoting embryo incubation.	Embryo-induced decidualization of uterine wall, mechanisms for embryo selection, in utero nutritional supply, after-birth nutritional supply.	Nest building, filial cannibalism, infanticide, solicitation of nursing, aloparental care, lactation.	Timing of birth, duration of brood retention, duration of incubation.

Table 2. A taxonomy of reproductive characters attending to the nature of the character and the kind of relationality implied.

	External fertilization	Internal fertilization
Absence of parent-parent interaction	Free dispersal of gametes in the external environment. In sessile organisms that live in highly dense populations, such as some marine invertebrates.	Sperm cells are ~~is~~ released into the water, which swim~~s~~ to reach the eggs that are internally retained ~~by the female~~. In sessile aquatic animals such as sponges or corals.
Indirect parent-parent interaction	Sperm is released over previously deposited eggs. In many fishes and aquatic invertebrates. Also in the rare cases where the spermatophore is uptaken from the environment by the female, and retained for subsequent releasing upon deposited eggs (in some myriapods).	Sperm is contained in a structure named a spermatophore which is transferred to the female or deposited in the substratum and later uptaken by the female. In some cases, the male interacts chemically or physically with the female before or after depositing the spermatophore. In some urodeles and many invertebrates such as crustaceans, insects, and arachnids.
Direct parent-parent interaction	Male and female actively interact to facilitate the release of sperm directly onto the eggs. Anurans' amplexus is paradigmatic of this kind of reproduction, where the male grasps the female and releases sperm directly upon the eggs as they are deposited into the water. There~~'s~~ is also direct contact between parents for external fertilization in some marine worms, which are surrounded by a mucus sleeve for reproducing (i.e., pseudocopulation).	There is active internal insemination (i.e. copulation), in many cases facilitated by specific organs for sperm transfer, such as intromittent or copulatory organs. In most vertebrates and many invertebrates, with a high diversity of methods for direct sperm transfer, including the juxtaposition of the genital openings (e.g., some birds and snakes), dermal impregnation (e.g., marine worms), hypodermic injection through the body wall (e.g., many insects), male appendage amputation (e.g., some spiders) and, in the most extreme cases of parent-parent contact, it is the whole male that enters the female's body (e.g. some marine worms and abyssal fishes).

Table 3: A taxonomy of reproductive modes in sexually reproducing animals attending to the conditions under which syngamy is realized, according to site of fertilization and the kind of parent-parent interaction.

	Limited or no post-fertilization nourishment	**Increased post-fertilization nourishment**
Absence of incubation	**Ovuliparity**. Eggs are released prior to fertilization. Fertilized eggs with little yolk are incubated in the environment. No direct contact between parents and offspring. In anurans, some fish, amphibians, and reptiles, and some aquatic invertebrates, such as annelids, and mollusks.	
Limited pre-partition incubation	**Oviparity**. Short period of internal incubation of fertilized eggs. Sometimes, post-natal incubation in nests~~ (e.g., birds)~~. ~~Some amphibians, most invertebrates and reptiles, and all birds.~~ In all birds, turtles, crocodiles, butterflies, bees, ants, and octopuses, most fishes, lizards, beetles, crustaceans, mollusks and other invertebrates.	**Monotreme oviparity**. A particular reproductive mode only found in monotremes, in which eggs absorb oviductal secretions during development and before oviposition.
Increased pre-partition incubation	**Lecithotrophic viviparity**. Embryos are retained within the female body so that parent-offspring interaction is extended in time, which confers protection during embryonic development. Eggs either hatch within the female cavities or organs or do not develop any form of external coating. There is little to no provisioning of nutrients, although varying degrees of water and ion transport can be found. In some lizards, snakes, amphibians, fishes, and invertebrates (brachiopods and chaetognaths).	**True viviparity**. The extended period of internal incubation (usually within the female tract) is accompanied by a closer interaction between the parent and offspring in the form of more efficient transfer of substances which includes extended provision of nutrients through two different means: • *Phagic nurturing*. Ingestion of tissues (histophagy), eggs (oophagy) or siblings (adelphophagy or embryophagy) provided by the parent. • *Trophic nurturing*. Nutrients are absorbed directly (histotrophy) or with the mediation of specialized structures such as placentas or pseudo-placentas (placentotrophy).
Post-partition incubation or secondary incubation	**Brooding**. After partition (either oviposition or parturition), eggs and/or embryos are incubated on the surface (e.g. spider back brooding), in cavities (e.g., frog gastric intubation, and seahorse pseudo-pregnancy), or in the organs ~~of the parents~~ (e.g., ovarian incubation in guppy fish) of the parents.	**Matrotrophic brooding**. Secondary mechanisms can evolve that extend nurturing in brooding species, such as lactation in marsupials or other forms of milk-like provision in some insects.

Table 4. A taxonomy of reproductive modes with respect to the conditions under which embryos are developed, according to the form of incubation and the form of nourishment provision.