

MULTIPLE ORIGINS AND LOSSES OF PLACENTAS IN VERTEBRATES: ECOLOGICAL AND EVOLUTIONARY SIGNIFICANCE

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Abstract: The vertebrate placenta represents a remarkable example of convergent evolution, having originated independently multiple times across diverse lineages, including fishes, amphibians, reptiles, and mammals. This review synthesizes current knowledge on the repeated origins, diversification, and secondary reductions of placental structures, emphasizing their ecological and evolutionary significance. Phylogenetic evidence indicates over 130 independent transitions to viviparity, frequently accompanied by the evolution of placental or placenta-like systems facilitating maternal–fetal exchange. These transitions are closely associated with ecological pressures such as temperature, predation, and habitat constraints, as well as life-history trade-offs involving reproductive allocation and offspring provisioning. Mechanistically, placental evolution is underpinned primarily by regulatory genomic changes, including shifts in gene expression and the co-option of pre-existing physiological pathways, rather than extensive structural genomic innovation. The review also highlights cases of placental reduction or loss, particularly in chondrichthyans and teleosts, where alternative provisioning strategies such as histotrophy or lecithotrophy have replaced placentotrophy. In mammals, diversification has occurred mainly through modifications in placental invasiveness and function rather than complete loss. Overall, the dynamic evolution of placentas illustrates the interplay between ecological context, developmental plasticity, and genomic flexibility, underscoring the placenta as both an adaptive innovation and an evolutionarily labile trait.

Keywords: placenta evolution, viviparity, matrotrophy, convergent evolution, reproductive strategies, squamate reptiles, chondrichthyans, teleost fishes, maternal–fetal interactions, ecological adaptation.

TERMINOLOGY

Understanding the evolution of reproductive modes in vertebrates requires a precise and consistent use of terminology, as many concepts describe overlapping or continuous biological phenomena rather than discrete categories. In particular, maternal–embryonic nutritional relationships form a continuum ranging from yolk-dependent provisioning to extensive maternal supply.

Viviparity refers to a reproductive mode in which embryos develop within the maternal reproductive tract and are retained until relatively advanced stages, often culminating in live birth. This condition has evolved multiple times independently across vertebrates.

Nutritional strategies during embryonic development are commonly described along a gradient between *lecithotrophy* and *matrotrophy*. *Lecithotrophy* denotes a condition in which the embryo relies primarily on yolk reserves deposited in the oocyte prior to fertilization. In contrast, *matrotrophy* involves substantial post-fertilization nutrient transfer from the mother to the developing embryo.

Within matrotrophy, several mechanisms have been described. *Placentotrophy* refers to nutrient transfer mediated by a placenta or placenta-like structure that facilitates physiological exchange between maternal and embryonic tissues. *Histotrophy* involves the absorption of nutrient-rich secretions (commonly termed “uterine milk”) produced by maternal tissues.

Oophagy is a specialized form of embryonic nutrition in which developing embryos consume unfertilized eggs produced by the mother, while related forms such as *adelphophagy* involve intrauterine cannibalism among siblings.

Importantly, the use of expressions such as “placental animals” requires careful qualification. The presence of placentation does not characterize entire taxonomic groups such as bony fishes, cartilaginous fishes, or squamates. Instead, placentation occurs in specific lineages within these groups and has evolved convergently multiple times. Therefore, in this study, references to “placental” conditions are restricted strictly to taxa or lineages in which placenta-like structures have been explicitly demonstrated, rather than implying that broader clades are uniformly placental.

THEORETICAL BACKGROUND

Placental animal groups—whether represented by bony fishes, cartilaginous fishes, squamates, or mammals—are generally recognized as highly diverse clades, each exhibiting substantial morphological, ecological, and genetic variation (Pires *et al.*, 2011). This diversity is not merely superficial but reflects deep evolutionary histories shaped by adaptive radiation (Păsărin & Petrescu-Mag, 2011), niche specialization, and complex environmental interactions (Petrescu-Mag, 2025).

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In ichthyological lineages, both osteichthyans (bony fishes - Oroian & Kovacs, 2022; Boaru & Petrescu-Mag, 2024; Gavriloaie *et al.*, 2025; Serihollo *et al.*, 2024; Garcia & Giraldo-Gongora 2023) and chondrichthyans (cartilaginous fishes – Sarmintohadi *et al.*, 2024; Arief *et al.*, 2025; Nafia *et al.*, 2023; Hartoko *et al.*, 2024) demonstrate remarkable variability in body plans, feeding strategies, and habitat preferences, ranging from deep-sea specialists to freshwater taxa.

Similarly, squamates, encompassing lizards and snakes, represent one of the most evolutionarily successful reptilian groups, with extensive diversification in locomotion, sensory systems, and reproductive strategies (Tollis *et al.*, 2018; Title *et al.*, 2024; Watanabe *et al.*, 2019; Whiteside *et al.*, 2022; Ollonen *et al.*, 2024).

Mammals, as a placental lineage, further exemplify this pattern of diversification through their occupation of nearly all terrestrial and many aquatic ecosystems (Goswami *et al.*, 2022; Álvarez-Carretero *et al.*, 2022; Beccari *et al.*, 2024). Their adaptive success is reflected in the wide range of physiological, behavioral, and anatomical specializations, from volant bats to fully aquatic cetaceans (Goswami *et al.*, 2022; Title *et al.*, 2024; Amador *et al.*, 2018; Yuan *et al.*, 2021; Teeling *et al.*, 2018; Sadier *et al.*, 2023; Rossoni *et al.*, 2019; Amson, 2021).

Overall, the consistent diversity observed across these placental groups underscores the role of evolutionary processes such as natural selection, genetic drift, and ecological opportunity in generating and maintaining biological complexity.

The vertebrate placenta, broadly defined as an apposition or fusion of fetal tissues with parental tissues for physiological exchange, has evolved repeatedly and convergently across the vertebrate tree of life, and has also been secondarily reduced or replaced in several lineages (Roberts *et al.*, 2016; Blackburn, 2015; Whittington *et al.*, 2022). These transitions between egg laying and live bearing modes, and between placental and non-placental forms of gestation, are associated with ecological context, phylogenetic constraint and genomic re patterning of uterine and extraembryonic tissues (Blackburn, 2015; Blackburn, 1992; Gao *et al.*, 2019; Blackburn & Hughes, 2024; X, 2024; Warren & Grutzner, 2021; Carter, 2024).

The aim of this review is to provide a comprehensive synthesis of the multiple independent origins and secondary reductions of placental systems across vertebrates, with a particular focus on their ecological drivers, evolutionary trajectories, and underlying mechanistic bases. Specifically, the study seeks to (i) map the phylogenetic distribution of placental evolution and loss, (ii) examine the ecological and life-history correlates influencing these transitions, and (iii) evaluate the developmental and genomic mechanisms that facilitate both the emergence and reversibility of placentation. Through this integrative approach, the review aims to clarify the role of the placenta as a dynamic and context-dependent evolutionary innovation.

TAXONOMIC DISTRIBUTION AND REPETITION OF PLACENTAL EVOLUTION

Phylogenetic syntheses indicate at least ~132 independent origins of viviparity among vertebrates, with about 98 in squamate reptiles alone (Blackburn, 1992; Blackburn, 2015). Placenta-like structures for gas, nutrient or waste exchange evolved independently in chondrichthyans, bony fishes, amphibians, squamates and mammals, and are absent only in birds among major vertebrate classes (Blackburn, 2015; Blackburn & Hughes, 2024; Roberts *et al.*, 2016; Whittington *et al.*, 2022). In chondrichthyans, viviparity arose at least 12 times, with at least one origin of true placentotrophy and several origins of alternative matrotrophic systems such as histotrophy and oophagy (Blackburn & Hughes, 2024). Teleosts such as poeciliid fishes show multiple independent origins of complex placentas closely juxtaposing maternal and embryonic tissues (Blackburn, 2015; Furness *et al.*, 2021; Whittington *et al.*, 2022). Among amniotes, therian mammals and numerous squamate lineages possess chorioallantoic and/or yolk sac placentas, with some lizards (for example Mabuya and Chalcides) converging on eutherian like placental morphology and function (Blackburn, 1992; Blackburn, 2005; Van Dyke *et al.*, 2014; Hernández-Díaz *et al.*, 2021; Carter, 2024; Whittington *et al.*, 2022). Eutherian mammals subsequently diversified placental shapes and degrees of invasiveness, while marsupials typically deploy transient or less invasive placentas (Carter, 2018; Carter, 2024; Roberts *et al.*, 2016; Shiura *et al.*, 2026).

ECOLOGICAL AND LIFE HISTORY CORRELATES OF PLACENTAL ORIGIN AND LOSS

The repeated appearance of placentas is intimately tied to ecological conditions and life history trade-offs. Across squamates, transitions from oviparity to viviparity correlate with colder climates and low body temperatures, consistent with advantages of maternal thermoregulation for developing embryos (Blackburn, 2015; Blackburn, 2005; Van Dyke *et al.*, 2014; Warren & Grutzner, 2021; Blackburn, 2000; Blackburn, 2015; X, 2024; Pyron & Burbrink, 2014). In poeciliid fishes, placental species display reduced instantaneous reproductive allotment and often superfetation, which together may streamline the body and enhance locomotor performance under high predation or fast flow environments (Furness *et al.*, 2021). Placental evolution in these fishes is associated with shifts in offspring size–number trade-offs that differ between small and large bodied species, suggesting alternative adaptive peaks (Furness *et al.*, 2021). In chondrichthyans, viviparity and matrotrophy evolved via multiple evolutionary sequences from an ancestral egg laying condition, with some lineages subsequently replacing placentotrophy by histotrophy, implying ecological or functional regimes in which a placenta became redundant or disadvantageous (Blackburn & Hughes, 2024). More broadly, placental elaboration tends to increase maternal–fetal resource exchange and conflict, potentially driving further adaptive

diversification or facilitating reversions toward less intimate, more redundant placentation when ecological or energetic contexts change (Blackburn, 1992; Blackburn & Hughes, 2024; Carter, 2024; Roberts *et al.*, 2016; Shiura *et al.*, 2026; Whittington *et al.*, 2022).

MECHANISTIC AND GENOMIC BASES OF REPEATED PLACENTAL EVOLUTION AND REDUNDANCY

Transition to viviparity demands coordinated changes in eggshell structure, uterine physiology, extraembryonic membranes, calcium transport and immune modulation, yet comparative genomics reveals that many changes are regulatory rather than structural at the coding sequence level (Blackburn, 1992; Van Dyke *et al.*, 2014; Gao *et al.*, 2019; X, 2024; Soncin, 2025; Whittington *et al.*, 2022). In squamate pairs differing in parity mode, extensive divergence in uterine gene expression underlies eggshell reduction, prolonged egg retention, placental development, improved gas exchange and immunological tolerance, with only limited convergence in amino acid replacements, implying that similar placental phenotypes can be generated by flexible gene expression programs (Van Dyke *et al.*, 2014; Gao *et al.*, 2019; X, 2024). This lability helps explain both the multiplicity of placental origins and the potential for reversals or reductions when selection relaxes (Gao *et al.*, 2019; X, 2024; Pyron & Burbrink, 2014). In viviparous Mabuya, calcium transport machinery in the placenta (for example TRPV channels and calcium binding proteins) was co-opted from pre-existing pathways elsewhere in the body, illustrating how ancestral functions in gas exchange, osmoregulation or mineral transport are repeatedly recruited into placentae with relatively small developmental changes (Blackburn, 2015; Blackburn, 1992; Hernández-Díaz *et al.*, 2021; Whittington *et al.*, 2022). In mammals, virus derived genes such as PEG10 and PEG11/RTL1, originally integrated into extraembryonic tissues, became essential for therian and then eutherian placentation, exemplifying how genomic innovations can both mediate the origin of the placenta and subsequently drive its diversification (Carter, 2018; Carter, 2024; Roberts *et al.*, 2016; Shiura *et al.*, 2026).

EXAMPLES OF SECONDARY REDUCTION AND DISAPPEARANCE OF PLACENTAS

Redundant or reduced placentas occur when alternative modes of embryonic provisioning replace placentotrophy. In chondrichthyans, placentation has been lost at least twice, with histotrophy evolving from placentotrophic ancestors, indicating true secondary disappearance of a placenta *sensu* Mossman (Blackburn & Hughes, 2024; Roberts *et al.*, 2016). Among sharks and rays, closely related species may differ in having yolk sac placentas, uterine milk provision, or oophagy, implying ecological and energetic trade-offs that allow placentas to be abandoned without loss of viviparity (Blackburn, 2015; Blackburn & Hughes, 2024; Whittington *et al.*, 2022). In teleosts, even within Poeciliidae, non-placental and placental species are interdigitated phylogenetically, requiring multiple gains and likely multiple reductions of placental complexity, although viviparity is retained throughout (Blackburn, 2015; Furness *et al.*, 2021; Whittington *et al.*, 2022). In mammals, phylogenetic reconstructions show that some lineages evolved less invasive placentation (for example epitheliochorial) from ancestors with more invasive, haemochorial placentas; these cases represent functional attenuation or partial loss of invasive placental traits rather than loss of placentas themselves (Carter, 2018; Carter, 2024; Roberts *et al.*, 2016). Squamate evolution illustrates an intense debate about reversals from viviparity to oviparity: some large-scale reconstructions suggest an early origin of viviparity followed by multiple reversions to egg laying, whereas others, incorporating anatomical and developmental evidence, argue that oviparity is ancestral and that viviparity generally evolves unidirectionally (Blackburn, 1995; Warren & Grutzner, 2021; Blackburn, 2015; X, 2024; Pyron & Burbrink, 2014) (Figure 1). Notably, even in putative reversals to oviparity, embryonic retention, uterine histology and extraembryonic membranes are often modified, so any placenta that once existed may have left vestigial or transient structures rather than disappearing entirely (Blackburn, 1995; Van Dyke *et al.*, 2014; Gao *et al.*, 2019; Warren & Grutzner, 2021; Blackburn, 2000; Blackburn, 2015; X, 2024; Whittington *et al.*, 2022) (Table 1).

Table 1.

Contrasting origins and reductions of placentas across major vertebrate clades

Vertebrate group	Number and nature of placental origins / losses	Typical embryonic tissues involved	Ecological or functional correlates	References
Chondrichthyes (sharks, rays, chimaeras)	≥12 origins of viviparity, ≥6 matrotrophic clades; at least one origin of placentotrophy and two independent replacements of placentas by histotrophy, representing true secondary losses of placentation	Yolk-sac or uterine villi forming placentoid structures	Transitions among egg-laying, placental and histotrophic modes linked to long evolutionary history and diverse habitats	(Blackburn, 2015; Blackburn & Hughes, 2024; Roberts <i>et al.</i> , 2016; Whittington <i>et al.</i> , 2022)
Teleost fishes (e.g. Poeciliidae)	Multiple, phylogenetically independent origins of complex placentas; repeated shifts between non-placental and placental viviparity; likely multiple reductions of placental complexity	Modified ovarian or follicular tissues forming maternal–fetal exchange surfaces	Placentation associated with superfetation, reduced reproductive allotment, altered offspring size–number trade-offs, enhancing locomotion under predation or flow	(Blackburn, 2015; Furness <i>et al.</i> , 2021; Roberts <i>et al.</i> , 2016; Whittington <i>et al.</i> , 2022)
Amphibians	Several independent origins of viviparity and substantial matrotrophy, including placentotrophy, histotrophy and embryophagy in some lineages, often using hypertrophied embryonic tissues	Hypertrophied gills, skin, fins or gut acting as fetal exchange organs	Frequently associated with specialized reproductive modes such as brooding and extreme parental care in constrained or predator-rich environments	(Blackburn, 2015; Blackburn, 1992; Whittington <i>et al.</i> , 2022)
Squamate reptiles (lizards and snakes)	>100 independent origins of viviparity with concomitant placentation; multiple matrotrophic clades; controversial evidence for reversals to oviparity; no clear documented complete loss of placenta without loss of viviparity	Chorioallantoic and yolk-sac placentae; in some scincids, highly eutherian-like chorioallantoic placentae	Viviparity and placentation correlate with cold climates, altered thermoregulatory regimes, and diverse life-history strategies; possible relaxed selection for placentation in warmer or stable environments	(Blackburn, 2005; Blackburn, 1995; Blackburn, 1992; Van Dyke <i>et al.</i> , 2014; Gao <i>et al.</i> , 2019; Warren & Grutzner, 2021; Blackburn, 2000; Blackburn, 2015; X, 2024; Pyron & Burbrink, 2014; Whittington <i>et al.</i> , 2022)
Mammals (marsupials and eutherians)	Single origin of therian viviparity with subsequent divergence of marsupial and eutherian placentas; extensive secondary modifications of placental invasiveness and structure; no complete loss of placenta in viviparous taxa	Chorioallantoic (dominant) and yolk-sac placentae; invasive haemochorial to non-invasive epitheliochorial forms	Shifts in placental invasiveness and endocrine function associated with maternal–fetal conflict, body size, gestation length and ecological niche specialization	(Blackburn, 2005; Warren & Grutzner, 2021; Carter, 2018; Carter, 2024; Roberts <i>et al.</i> , 2016; Shiura <i>et al.</i> , 2026; Whittington <i>et al.</i> , 2022).

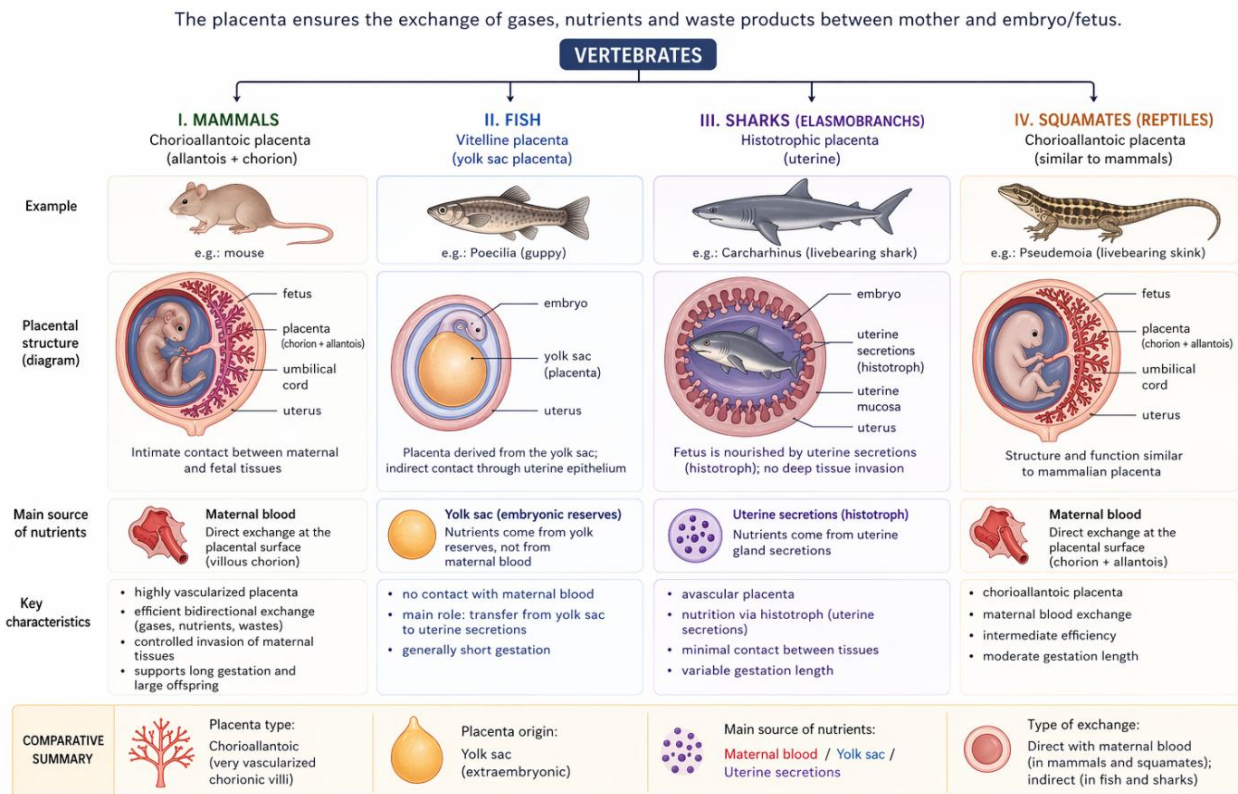


Fig. 1. Placenta in vertebrates: classification and differences. The diagram presents four discrete categories; however, vertebrate reproductive strategies are more accurately understood as a continuum, encompassing transitional forms between lecithotrophy (yolk-based provisioning) and matrotrophy (maternal provisioning) (original plate, designed by the author, edited using OpenAI, 2026).

CONCLUSIONS

The evolution of the vertebrate placenta is characterized by exceptional plasticity, repeated convergence, and context-dependent diversification. Multiple independent origins of placentation across phylogenetically distant lineages demonstrate that similar selective pressures—such as environmental temperature, predation risk, and reproductive efficiency—can repeatedly drive the emergence of maternal–fetal nutrient exchange systems. At the same time, the occurrence of secondary reductions or losses of placental complexity highlights that placentation is not an irreversible evolutionary endpoint but a flexible trait subject to ecological and energetic constraints.

Comparative evidence indicates that placental evolution is primarily mediated by regulatory changes in gene expression, allowing rapid phenotypic innovation without extensive modification of coding sequences. The co-option of ancestral physiological pathways and, in some cases, the integration of novel genomic elements (e.g., viral-derived genes in mammals) further underscores the mechanistic versatility underlying this trait.

Importantly, transitions between placental and non-placental reproductive modes are embedded within broader life-history trade-offs, including offspring size–number dynamics, maternal investment, and developmental timing. These trade-offs generate multiple adaptive peaks, enabling both the elaboration and reduction of placental structures under shifting environmental conditions.

As a final remark, the vertebrate placenta should be viewed not as a singular evolutionary innovation but as a continuum of functionally analogous systems that arise, diversify, and sometimes regress in response to ecological opportunity and constraint. Its study provides critical insights into the interplay between development, genomics, and evolutionary ecology.

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AUTHORS CONTRIBUTIONS

Ioan Valentin Petrescu-Mag contributed to all aspects of the work.

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

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