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Offspring Development Conditioning (ODC): A Universal Trend in Evolution of Higher Organisms' Reproduction

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Abstract

Background All organisms evolve, according to Darwin. The question is how? Is there any general pattern or trend in the organisms' evolution? These are rarely asked – and almost never answered – questions. This situation makes the evolution frustrating and mysterious to many.

Results After surveying the reproductive modes in most animals and plants, we propose that all (at least most) of higher organisms demonstrate the similar trend underlying their reproductive evolution, namely, Offspring Development Conditioning (ODC). ODC benefit the organisms in two ways: one is enhanced physical protection, the other is secured nutrition supply.

Conclusions This pattern makes the origin and evolution of reproductive organs in both animals and plants rational and understandable. To the best of our knowledge, this pattern appears universal in higher organisms (including both plants and animals), although we encourage future colleagues to identify exceptions. We hope this will help frame the evolution of higher animals and plants, and make their evolution understandable to everyone.

Keywords: reproduction, evolution, oviparity, ovoviviparity, viviparity, animals, plants, angiosperms, Offspring Development Conditioning

Background

Sardines spawn in water body of temperatures of 14-15° off northern Spain in spring (Stratoudakis *et al.*, 2007).

Some fishes give birth to their live young (Blackburn D.G., 2005, Xu *et al.*, 2015, Helmstetter *et al.*, 2016).

Kunmingella douvillei (from the Early Cambrian) carries ovules on its biramous appendages (Duan Yanhong *et al.*, 2014).

Some baby spiders kill and consume their mother, who has been carrying and feeding them (Salomon *et al.*, 2015, Lubin, 2019).

A female praying mantis devours its partner during sex (Waleed, 2019).

Trichogramma lays its eggs inside the eggs of moths (Stouthamer, 1993).

Differentiation between megaspores and microspores started since the Devonian (Taylor *et al.*, 2009).

Ovules remain attached to their mother plants since the late Devonian (Taylor *et al.*, 2009).

Flowering plants have their ovules enclosed before pollination since the Mesozoic (Wang X., 2018).

Rhizophora apiculata give birth to their seedlings (Wilson and Saintilan, 2018).

Some parents pay for enrollment of their children in leading universities (Bacon, 2019).

Hundreds of penguins stand in freezing wind, warming their hatching eggs.

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The above amazingly different behaviors of animals and plants attract much attention from various biologists, but it is rarely asked “*Is there any common regularity underlying ALL these different behaviors?*” Evolution! Yes, it is right. Evolution is a concept widely-accepted since the Darwin, and human beings have spent billions of dollars on the evolution of organisms on the Earth. However, evolution appears emanating and elusive to many.

Results

Based on a survey of all reproductive processes and modes in higher organisms, we recognize a general trend in the origin and evolution of reproductive organs in animals AND plants, namely, **all higher organisms tend to increasingly condition the development of their offspring**. We termed it as “Offspring Development Conditioning” (ODC).

Discussion

If life is taken as an evolvable set of coordinated interactions among organic molecules, then evolution can be seen as a process maintaining and modifying such regulated interaction networks through times. Maintaining the lineage is the primary and also ultimate goal for all organisms, and also the premise for the on-going of evolution. A chain breaks at its weakest link. Since maintaining lineages through time is implemented through continued repetition of sexual reproduction cycles (SRC)(Bai, 2015), and early stage in each individual’s life cycle is the most vulnerable period in the SRC, therefore nurturing the babies and protecting them from harms are therefore the major challenges and tasks for all higher organisms. However, different higher organisms accomplish the same goal through different strategies (Angelini andGhiara, 1984, Wang X., 2018). We will go over the strategies of animals and plants, respectively.

Animals

All higher organisms are currently mainly categorized by, besides other characters, their reproductive modes in systematics. Among animals, several reproductive modes are recognized, namely, **ovulipary, ovipary, ovo-carrying, ovovivipary, histotrophic vivipary, and hemotrophic vivipary** (Table 1) (Angelini andGhiara, 1984). Considering these modes following the above order, which is also the order of their occurrence in their geological history, there is a common underlying trend, namely, that the developmental environment of the offspring becomes increasingly internalized and controlled (Table 1; Fig. 1). For example, the fertilization site is shifts from external (in water for fishes) (Fig. 2a) to internal (in the uterus for reptiles) (Fig. 2c). The hatching site of fertilized eggs shifts from *ex vivo* in fishes to the body surface of the mother in *Kunmingella* (Duan Yanhong *et al.*, 2014) and *Waptia* (Caron andVannier, 2016), until certain length of time retention within mother body before birth of babies in some amphibians, some reptiles, and mammals (Lodé, 2012).

As one of the ways to implement ODC, offspring environment internalization (**OEI**) is also the mechanism by which reproductive organs in higher animals originated and evolved. During the process of OEI nurturing babies is increasingly enhanced, secured and extended, and the nurture source changes from egg alone (in fishes), its peers (**oophagy**, intra-uterine cannibalism in salamanders (Lodé, 2012)), a secretion of the oviducts (in insects and reptiles (Lodé, 2012)), to placenta-like structure or a true placenta (in mammals (Lodé, 2012)). In the meantime, the nurture bond between babies and mothers

becomes increasingly physically reinforced and much extended in time. The net result of these coordinated changes is that mothers have gained increasingly tight control over the development of their babies, and babies become increasingly physically protected before birth and increasingly capable of surviving after birth. For example, baby rattlesnakes are born as live young fully loaded with fangs and venom at birth, and many mammals can stand and walk minutes after birth. Parent animals appear to play increasingly active roles in the life of their babies.

To cope with the various challenges of life and implement effective baby-protection, animals have developed various strategies and undergone several stages of adaptation, including **passive adaptation**, **active environment selection**, **active environment conditioning**. For example, fishes usually spawn in a water body. If the water body is congenial, their eggs can become fertilized and successfully develop into baby fishes. However, if the environment is not ideal, the eggs may not be fertilized or not develop at all. Under this scenario (passive adaptation), the eggs are passive and their fate is more due to chance. Avoiding such uncertainty, some fishes have developed a migratory habit as a strategy throughout the process of evolution. Migratory habits can guide fishes to water bodies of the right temperature for spawning at right time. Under this scenario (active environment selection), although the fate of eggs is still determined by water body, the fishes, relying on the habit carried on from their ancestors, are more active in choosing a suitable developmental environment for their babies.

A slightly more active selection for a suitable environment is **ovule-carrying** strategy adopted by some invertebrates (Fig. 3a), and this strategy can be dated at least back to the Early Cambrian (active environment conditioning) (Duan Yanhong *et al.*, 2014, Caron and Vannier, 2016). “Nothing is better than myself” may be the philosophy adopted by *Kunmingella* (Fig. 3b): by carrying their eggs on their bodies, these animals apparently had more liberty to choose a decent developmental environment congenial for their babies. Through ovo-vivipary (Fig. 3c) and histotrophic vivipary, such a trend culminates in hemotrophic vivipary, in which the fertilization takes place *in vivo*, the baby absorbs nutrients from the mother through a placenta and is not exposed to the external environment until birth. Compared to ovipary, vivipary with a higher degree of ODC brings many advantages including higher rates of speciation and greater species turnover through time, which triggered a burst of speciation and diversification (Fig. 1) (Pyron and Burbrink, 2014, Helmstetter *et al.*, 2016). It is not surprising that vivipary has evolved independently at least 29 times in fishes (Wourms, 1981, Blackburn D.G., 2005, Blackburn Daniel G. and Sidor, 2014), several times in anurans (Sandberger-Loua *et al.*, 2017), several times in salamanders (Buckley, 2012), and six times in squamates (Wang Y. and Evans, 2011).

Although famous for their ovipary, not all snakes are oviparous, for example, rattlesnakes are ovoviviparous (Ryan, 2019). In birds, there is no vivipary, but this is compensated for by brooding by hatching and baby-care. By brooding, birds warm and protect their eggs by sitting on their eggs fairly continuously for prolonged periods. As rare exceptions, birds in several families do not incubate their own eggs but lay eggs in the nests of other taxa (**brood parasitism**). The cuckoo (*Cuculus canoros*, Cuculiformes) of Europe and cowbird (*Molothrus ater*, Passeriformes) of North America are well known **obligatory parasites**. Although they do not brood themselves, they have developed strategies advanced enough to cheat others to brood on their behalf and ensure the safety of their own babies (Geltsch *et al.*, 2016). Needless to say, most mammals are viviparous. This at least partially contributes to the great diversity of mammals today (Fig. 1). As an exception among mammals, monotremes are the only living oviparous placentals (Eutheria) that, like marsupials, keep their larvae-like hatchings in a pouch and nurse them with milk.

Frequently, animals extend their prenatal offspring-caring beyond birth, sometimes by altruism.

Spiders and many mammals nurture their babies with milk (Chen *et al.*, 2018). Some spiders carry their babies and devote their bodies to nurture their babies (Salomon *et al.*, 2015, Lubin, 2019). Sexual cannibalism in the praying mantis similarly involves consumption of the male to nourish the babies (Brown and Barry, 2016). Humans extend their parental care beyond nutritional supply and physical protection in the juveniles (Fig. 2d), including intellectual training (e.g. college education) and wealth transfer as a legacy for future generations (Bacon, 2019).

It can be said that, unlike taught in textbooks, there is no strict one-to-one correspondence between taxa and reproductive modes in animals (Fig. 1). Instead, different lineages of animals have adopted different spectra and combinations of reproductive strategies, and within each lineage the strategies involving enhanced conditioning of the development for their offspring were derived later and have given the animals more advantages in competition for survival against peers. Lower animal groups tend to have wider spectra and more alternatives in reproductive mode, while higher animal groups tend to be more limited and are restricted to relatively more advanced modes.

Plants

Many assume that animals are more advanced than plants, which usually do not move. This thinking is apparently erroneous. Surveying reproduction in plants, you will be surprised that plants demonstrate exactly the same evolutionary reproductive trend as animals do above (Figs. 4a-i). According to their reproductive modes, these plants can be categorized as **spore plants** (early land plants and ferns *sensu lato*) and **seed plants** (including gymnosperms and angiosperms). Early land plants and ferns *sensu lato* are/were dispersed as **spores** (Fig. 4a). Each spore, when dispersed, carries very limited nutrient from the mother plant, and its survival is largely due to chance, depending on its reaching a suitable environment, which allows the development of gametophytes, ensuing fertilization, and germination of the sporophyte for the next generation. If a spore is unlucky, then the limited nutrient from the mother plant is soon exhausted and sets an upper limit of the vitality of the spore and its derivative. Initially, all spores were of the same morphology, namely, there is little differentiation in spore dimensions, morphology and nutrition allocation in early land plants. However, differences emerged soon (in the Devonian) in various aspects in more derived heterosporous plants.

Among heterospores, a **megaspore** receives more nutrients and this ensures that the female gametophytes have enough nutrient supply while the microspore is allocated only limited basic amount of nutrition (Wang Xin and Bai, 2019). Evolutionary history indicates that such differentiation apparently gives the plants more advantages, as the dominant plants seen in current ecosystems are heterosporous, and plants further extrapolate such a tendency to a later form, **seed** habit (Fig. 4b). Among fossils it is sometimes hard to distinguish seeds from megaspores morphologically. Yet it is easy to distinguish them in living plants; namely, a megaspore falls off from the mother plant when mature, while an ovule remains on its mother plant until it gives rise to a mature seed (Herr, 1995). The apparent advantage of a seed over a megaspore is that the seed maintains its nutrient bond with the mother plant until seed maturation. In addition, many gymnosperms can provide various additional protections for their seeds (Fig. 4c). Such enhanced nutritional bond and additional physical protection by mother plants is an evolutionary trend which has been followed since the origin of seeds (Figs. 4b-g).

This trend reached its greatest extent in **angiosperms**, which usually enclose their ovules before pollination (**angio-ovule**) (Figs. 3d,f). Such an enclosure ensures the nutrient supply to the ovules, protects the vulnerable ovules from various harsh biotic and abiotic harms, benefits the dispersal of seeds by an additional (usually fleshy) surrounding layer, gives many advantages to angiosperms, which are the most diverse plant group in the current world. Continuing this trend, angio-ovule is followed by

angio-carpy (Figs. 4e, g) and vivipary (Fig. 4h). In **angio-carpy**, fruits that enclose seeds are further surrounded or enclosed by an extra layer of tissues (Figs. 3e, g). Such a phenomenon has been observed at least in the living Monimiaceae (Lorence, 1985, Staedler *et al.*, 2007), Calycanthaceae (Staedler *et al.*, 2007), Moraceae (Kvitvik, 1997), Solanaceae (Wilf *et al.*, 2017), and also in some early fossil angiosperms (*Chaoyangia*, *Callianthus*) (Duan S., 1998, Wang X. and Zheng, 2009, Wang X., 2018). Many people assume that **vivipary** is a feature unique to mammals, and they rarely know that angiosperms also have this feature. To date, nearly one hundred species of angiosperms (in 40 genera and 23 families) have been described as viviparous (Elmqvist and Cox, 1996). *Rhizophora* is a typical mangrove tree. Unlike most plants, the seeds of *Rhizophora* germinate *in vivo*, namely, in fruits that are still attached to the mother plants (Fig. 4h). This means that the sporophytic seedlings rely on the mother plants (that usually nurture only their gametophytes) for their nutrient supply until the seedlings reach certain maturity.

Finally, the most animate strategy adopted by plants is **proactive self-fertilization (PSF)** in Orchidaceae. During PSF, the pollinarium is inserted into the receptive stigmatic cavity through the programmed movement of its stipe (Liu *et al.*, 2006) (Fig. 3i), thus culminating the ODC in plants. In this case, instead relying of external abiotic or biotic factors for pollination, the plant completes pollination through a series of self-driven movements of its own stamens. PSF makes the concerned orchids fully independent of otherwise indispensable pollinating agents during pollination and thus ensures the successful reproduction and continuation of lineage (Liu *et al.*, 2006). Apparently, PSF gives the plant more freedom and control over the whole process of its reproduction.

Conclusion

ODC is a general evolutionary trend underlying reproduction in most higher animals and plants. **First**, fertilizing site is shifted from *ex vivo* in less advanced higher organisms to a more controlled *in vivo* site in more advanced higher organisms. **Second**, the developmental site of the embryos becomes increasingly *in vivo* within each lineage. **Third**, the nutritional bond between mothers and their offsprings is increasingly reinforced throughout the evolution, not only in prenatal stage but also in postnatal stage. **Fourth**, the time during which the nutritional bond between mothers and their offspring becomes increasingly longer and stronger. **Fifth**, at least most lineages evolve comparable reproductive modes following the same trend in their own lineages, although each in a different way and in a different context, just like all rivers running from mountains into oceans in their own channels. So the evolution of most higher organisms (probably with exceptions of parasites) is destined to more enhanced Offspring Development Conditioning (ODC). One of the ways to implement ODC is internalizing the formerly external developmental site as a site within the organism's body, monitoring and controlling the developmental process of the offspring. This is how the reproductive organs (including flowers) originated.

Methods

No original or new data were generated during this research. We extracted and collected data about reproduction in all higher organisms from cited references. Partial data of some representative organisms (extant and fossil) shown in figures were collected by the authors during our research practice. All the information were mapped in phylogeny tree or tables. Analysis and generalization were performed based on these data.

Abbreviations and Terms

Angio-ovuly: Enclosure of ovules (precursors of seeds) before pollination.

Angio-carpary: Enclosure of fruits by additional tissues.

Angiosperm: A plant that, literally, has its seeds enclosed. Angio-ovuly ensures the affinity of a plant.

Brood parasitism: A type of parasitic organisms that rely on others to brood their young.

Endospory: Retaining spores within sporangia after their maturation.

Gymnosperm: A plant that, literally, has its seeds exposed to the exterior space.

Hemotrophic vivipary: Fertilization and embryogenesis occur in the female genital tract and find their nutriment from the maternal bloodstream through the placenta.

Heterospory: Occurrence of two different spores in a single individual.

Histotrophic vivipary: Giving birth to live offspring such that the zygotes develop in the female's oviducts, but receive their nutriment from the decomposition of maternal tissue and leakage of maternal blood.

Matriphagy: Babies are fed with the body of their own mother.

Megaspore: Relatively larger of two types of spores, usually develops into a female gametophyte.

Migratory habit: Regular seasonal movement of animals across regions to ensure the maintenance of the fauna.

Obligatory parasites: Organisms that are dependent upon a host for survival.

ODC: offspring development conditioning.

OEI: offspring environment internalization.

Oophagy (egg-eating): A means of nutrition in which some embryos in the mother's uterus develop at the expense of their 'potential siblings'.

Ovipary: A reproductive strategy with a lower number of larger eggs, generally with internal fertilization, direct development, and frequent parental care.

Ovovivipary: A method of reproduction in which young develop from eggs retained within the mother's body, but separated from it by the egg membranes.

Ovule-carrying: A breeding strategy in which ovules are carried on the body surface of animals during incubation.

Ovulipary: A reproductive strategy with a great number of smaller eggs, with external fertilization and a larval stage.

Parasitic hatching: Some brood parasites rely on others to hatch their young.

Parental care: A parent invests time and/or energy in feeding and protecting its offspring.

Proactive Self-fertilization: Fertilization completed by self-driven movement of the stamen/pollinarium stipe, during which the pollinarium is inserted into the receptive stigmatic cavity.

Seed: A plant organ derived from an ovule, containing an embryo.

Sexual cannibalism: A female cannibalizing her mate during or after copulation.

Spore: A small single-celled propagule capable of giving rise to a gametophyte.

Vivipary: Giving birth to live offspring that develop within the mother's body, or producing seedlings.

Declarations

Availability of data and materials This paper covers all higher organisms, which include too many taxa or materials to fit in the space of this paper. Our information is extracted from cited references.

Competing interests We declare no competing interests.

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Authors' contributions XW initiated the project; XW, QF and JL collected data, performed analysis, wrote and finalized the manuscript.

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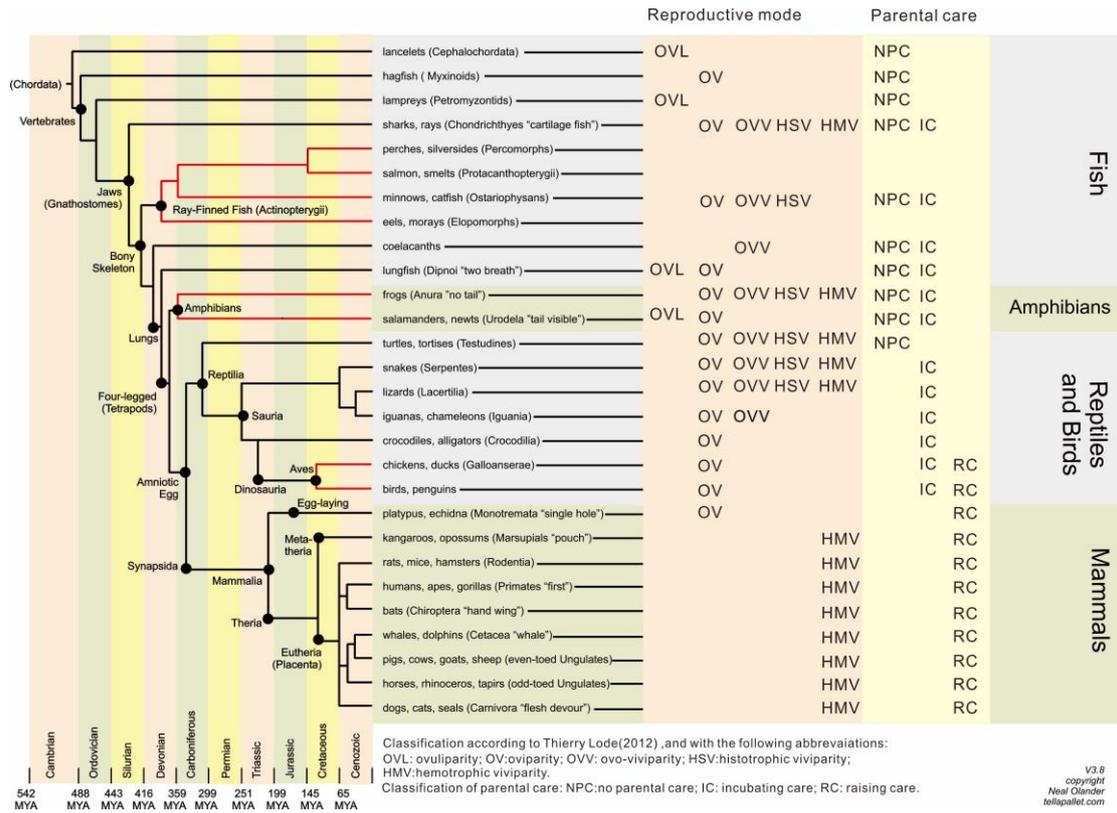


Fig. 1 Reproductive modes and phylogenetic dendrogram in Vertebrates

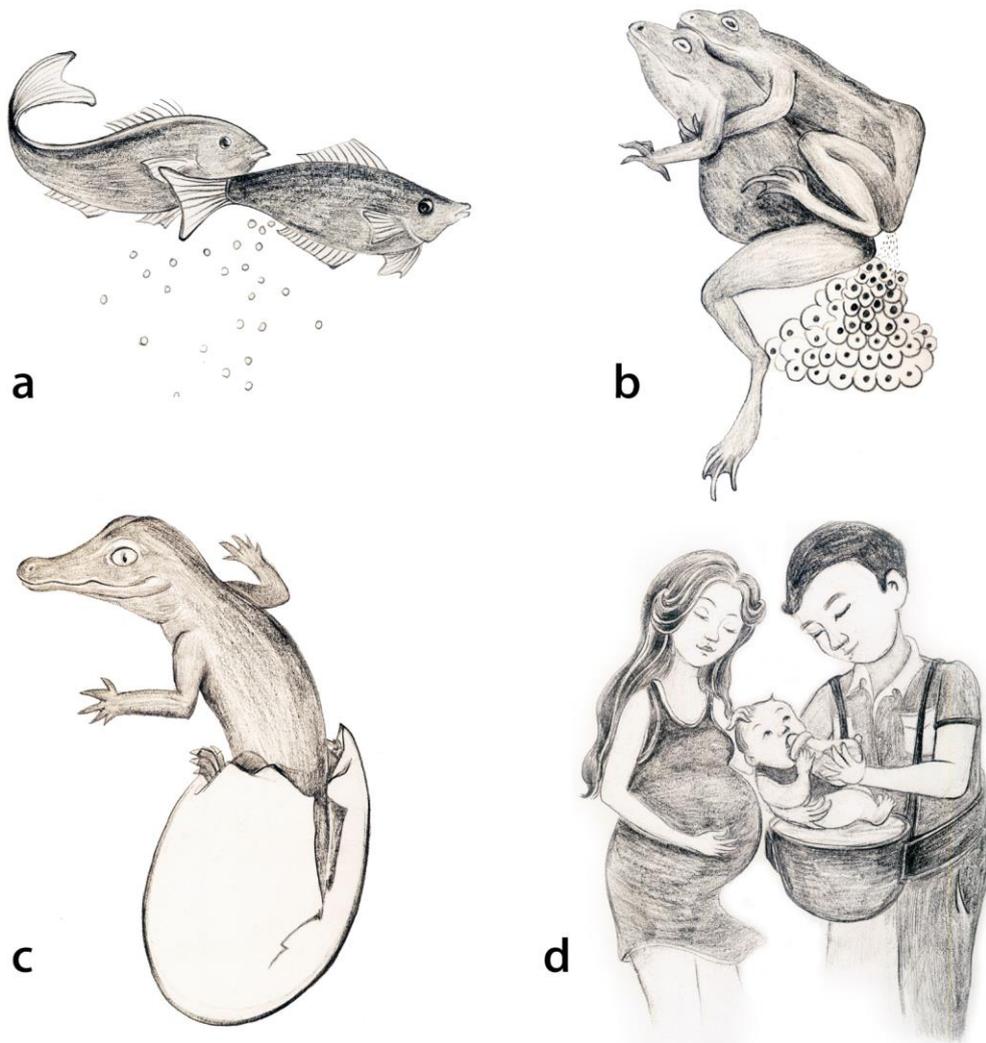


Fig. 2 Diversified reproductive modes in vertebrates. **a.** Ovulipary in fishes. **b.** Ovipary in frogs. **c.** Ovipary in reptiles. **d.** Vivipary in mammals (human beings).

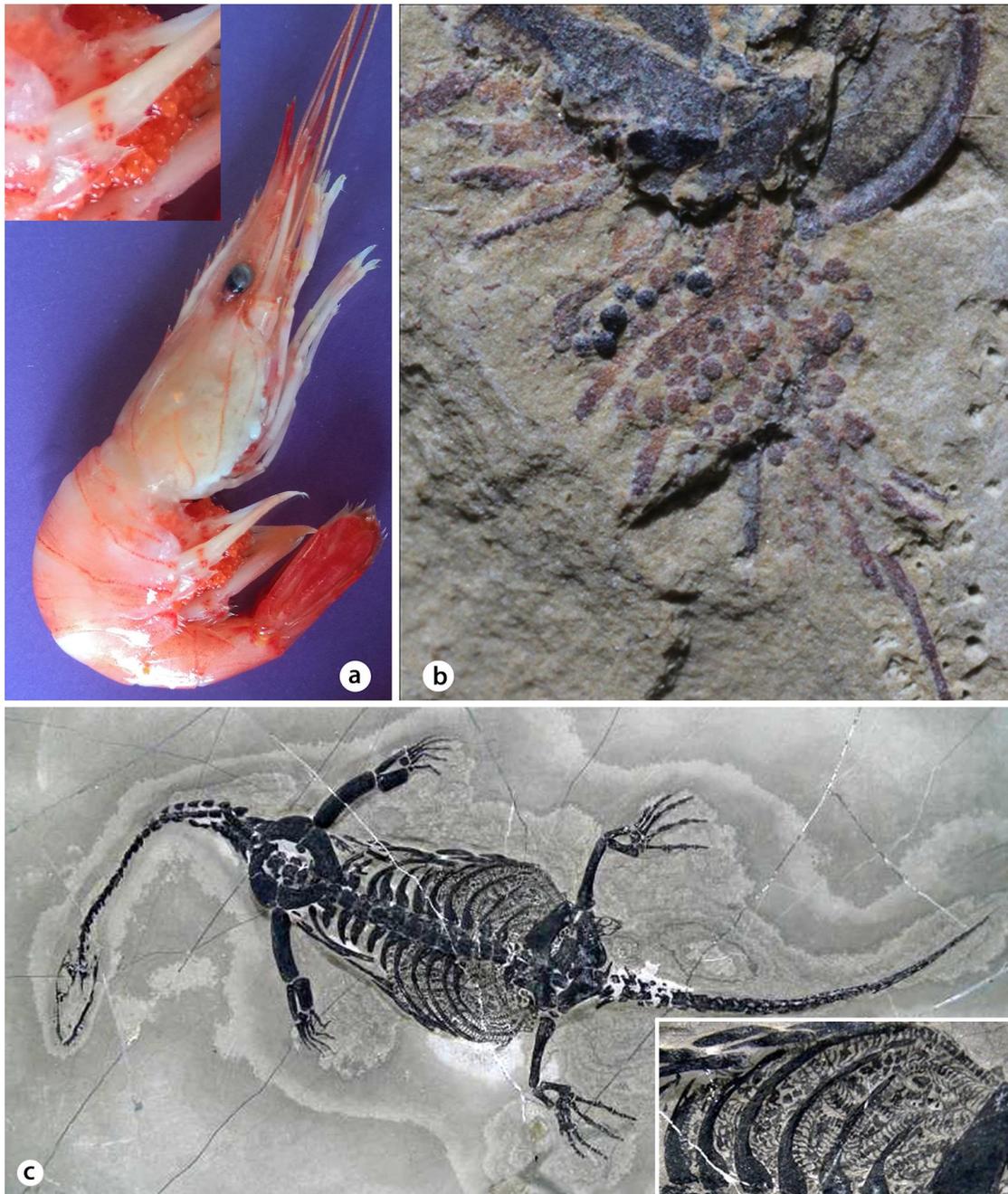


Fig. 3 Ovule-carrying and ovovivipary. **a.** Extant shrimp carrying ovules on its body surface. The inset shows the ovules on the appendages. **b.** *Kunmingella* (the Early Cambrian) carrying ovules on its appendages. **c.** Ovoviviparous marine reptile *Keichousaurus* with multiple young in its abdominal cavity. Inset shows detailed view of young inside mother's body (Reproduced from *The Triassic Park* with courtesy and permission from Pang Guangfan, Jin Renyi and Fu Xiaoping).

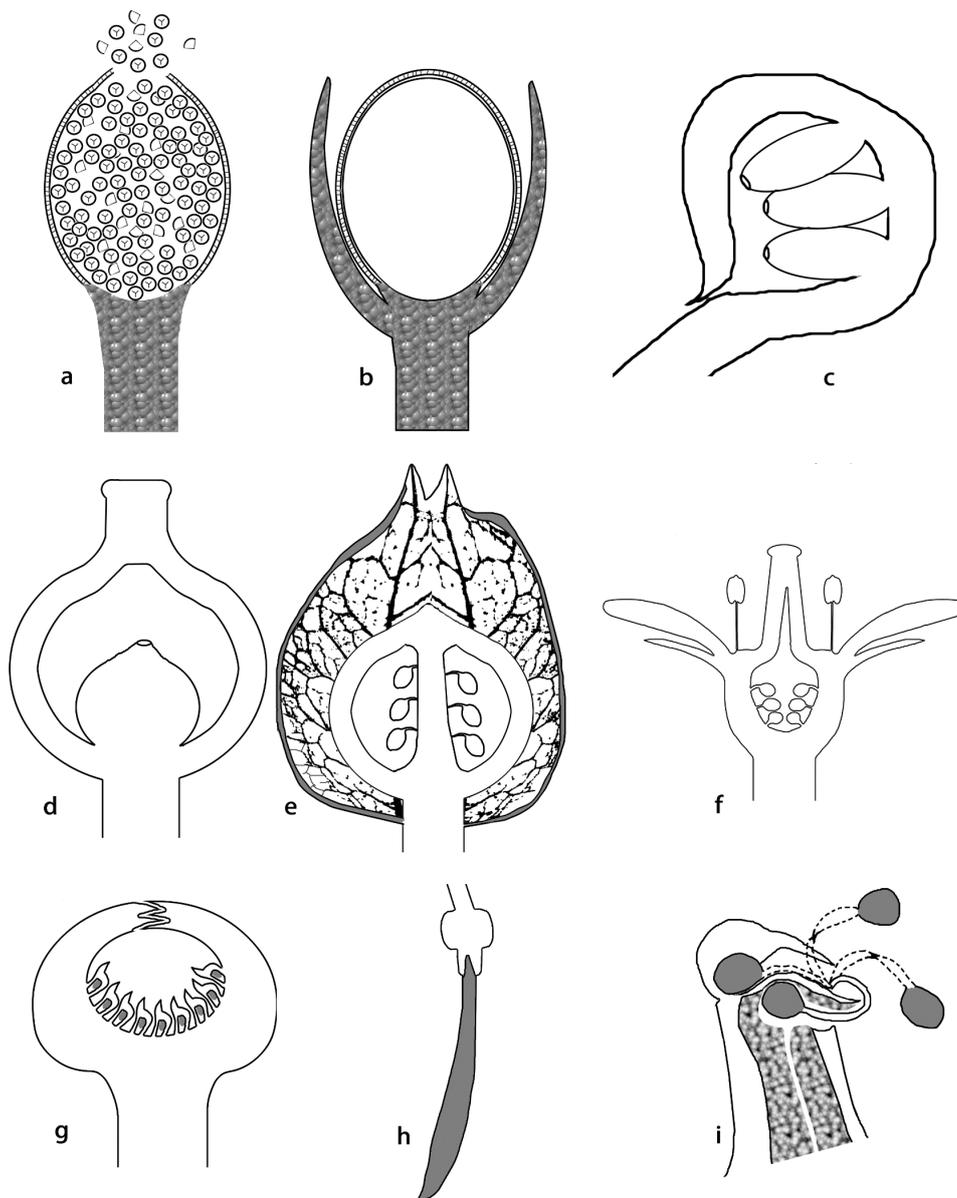


Fig. 4 Diverse reproductive modes in vascular plants. **a.** Spores dispersed from a sporangium in a spore plant. **b.** Ovule with protection from the integument. **c.** Ovules/seeds protected by cupule in *Caytonia*. **d.** A basal ovule protected by ovary in an angiosperm. **e.** A *Physalis* fruit with seeds inside and a protective layer around. **f.** Ovules protected by an inferior ovary in an angiosperm. **g.** Fruits inside and protected by hypanthodium. **h.** Sprout of *Rhizophora* on its mother plant. **i.** Proactive self-fertilization in *Holcoglossum* (Orchidaceae).

	Fertilization site	Eggs hatching site	Nutritional supply	Fecundity	Larvae survival rates	Parental care	Examples
Oviparity	External	External	Yolk (Lecithotrophy)	Very high	Very low	No	Teleostei: most of marine forms with pelagic floating eggs Amphibia: many Anura Cyclostomata: Petromyzontoidea
Oviparity with aquatic egg	External, internal	External	Yolk (Lecithotrophy)	Moderate	Moderate	Frequent	Chondrichthyes: many Elasmobranchii Teleostei: most fresh-water forms with demersal eggs Cyclostomata: Myxinoidei Amphibia: many Urodela and Apoda
Oviparity with terrestrial amniotic egg	Internal	External	Yolk (Lecithotrophy)	Low	High	Frequent, sometimes intensive	Reptilia Aves
Aplacental viviparity (ovoviviparity)	Internal	Internal	Yolk (Lecithotrophy) or reproductive tract (uterine or ovarian secretions and sibling yolks)	Moderate	Moderate	Frequent (lactation in Prototheria)	Chondrichthyes: many Elasmobranchii Amphibia: several Apoda; one Anuran Reptilia: some Squamata Mammalia: Prototheria
Placental viviparity (histotrophic)	Internal	Internal	Mother (Matrotrophy)	Low	High	Frequent	Chondrichthyes: Elasmobranchii, including <i>Rhizoprionodon terraenovae</i> and <i>Carcharhinus plumbeus</i> Reptilia: (several Squamata, e.g. <i>Mabuya heathi</i>)
Placental viviparity (histotrophic versus hemotrophic)	Internal	Internal	Mother (Matrotrophy)	Very low (with exceptions)	High	Parental care, with lactation	Mammalia: Metatheria and Eutheria

Table 1. Main characteristics of various reproductive modes in Vertebrates. Data derived mainly from Angelini and Ghiara (1984).

Figures

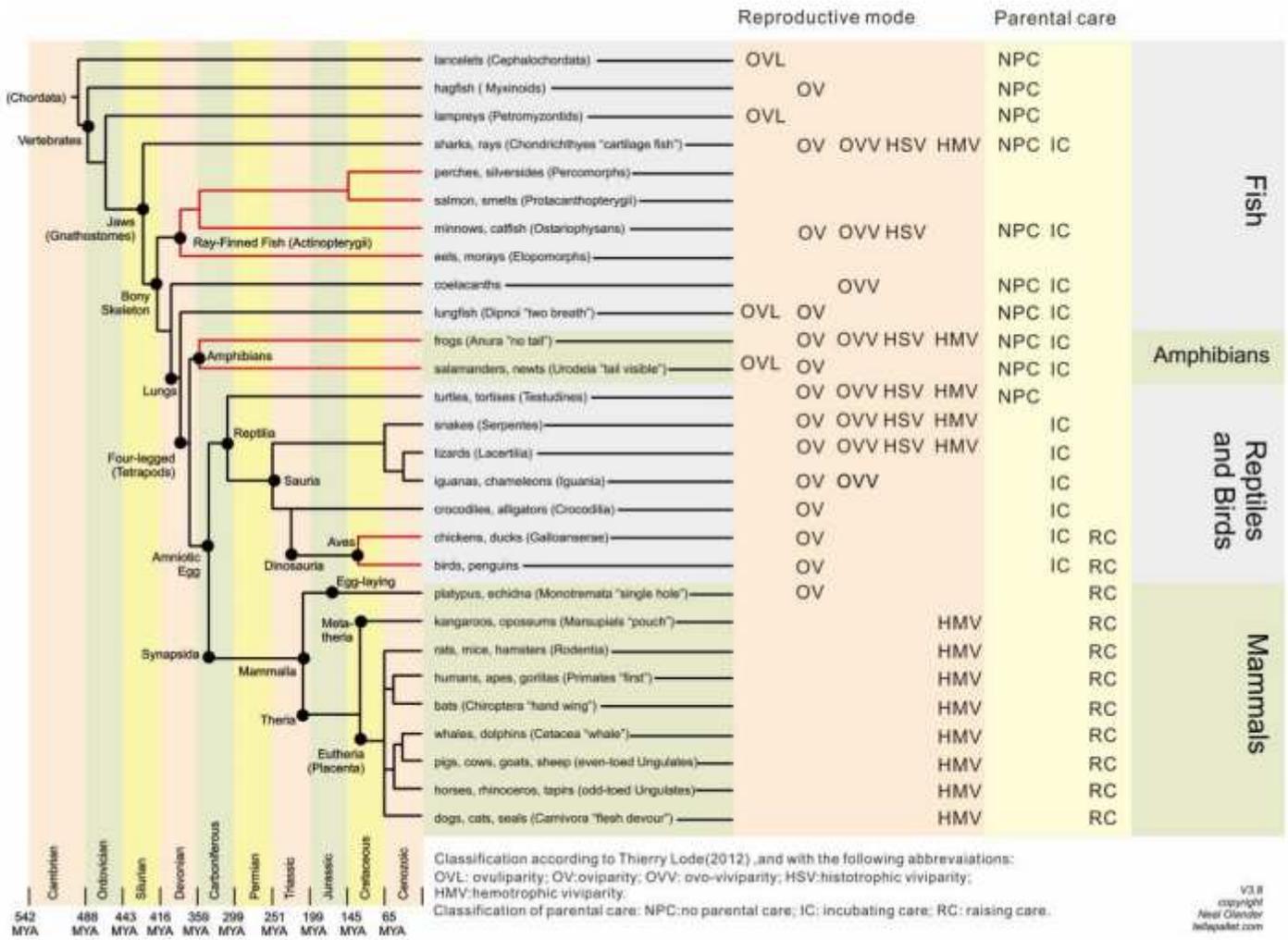


Figure 1

Reproductive modes and phylogenetic dendrogram in Vertebrates

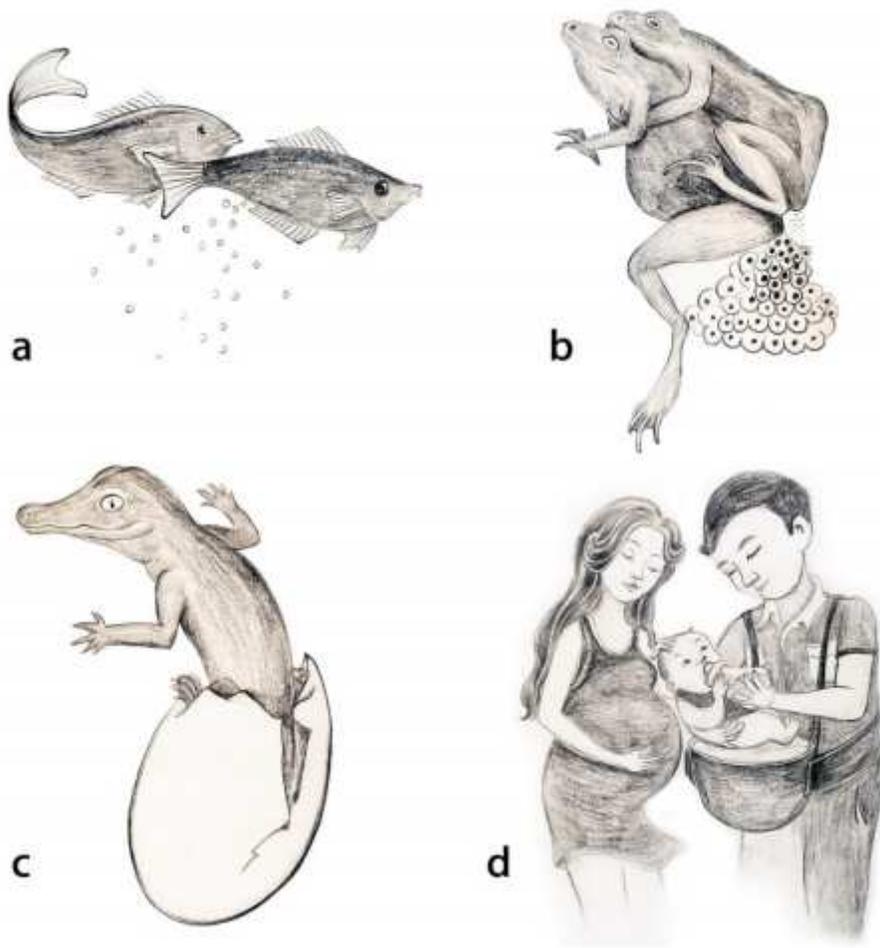


Figure 2

Diversified reproductive modes in vertebrates. a. Ovulipary in fishes. b. Ovipary in frogs. c. Ovipary in reptiles. d. Vivipary in mammals (human beings).



Figure 3

Ovule-carrying and ovovivipary. a. Extant shrimp carrying ovules on its body surface. The inset shows the ovules on the appendages. b. *Kunmingella* (the Early Cambrian) carrying ovules on its appendages. c. Ovoviviparous marine reptile *Keichousaurus* with multiple young in its abdominal cavity. Inset shows detailed view of young inside mother's body (Reproduced from *The Triassic Park* with courtesy and permission from Pang Guangfan, Jin Renyi and Fu Xiaoping).

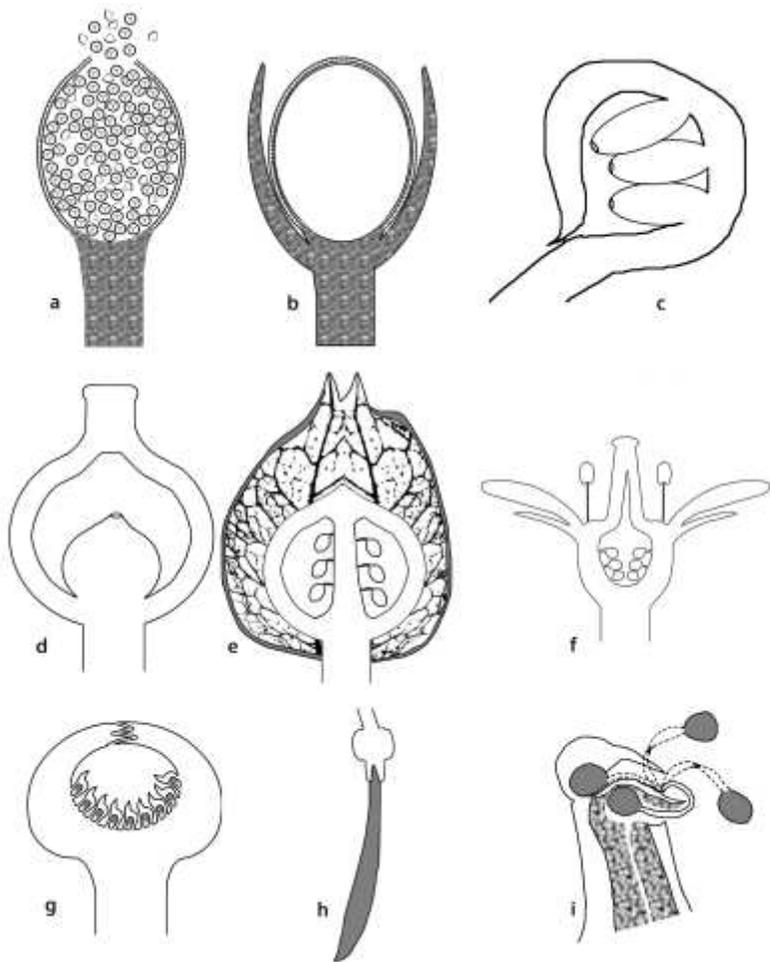


Figure 4

Diverse reproductive modes in vascular plants. a. Spores dispersed from a sporangium in a spore plant. b. Ovule with protection from the integument. c. Ovules/seeds protected by cupule in Caytonia. d. A basal ovule protected by ovary in an angiosperm. e. A *Physalis* fruit with seeds inside and a protective layer around. f. Ovules protected by an inferior ovary in an angiosperm. g. Fruits inside and protected by hypanthodium. h. Sprout of *Rhizophora* on its mother plant. i. Proactive self-fertilization in *Holcoglossum* (Orchidaceae).