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Review

Asexual reproduction: Genetics and evolutionary aspects

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Abstract. Reproduction is essential to all organisms if they are to contribute to the next generation. There are various means and ways of achieving this goal. This review focuses on the role of asexual reproduction for eukaryotic organisms and how its integration in a life cycle can influence their population genetics and evolution. An important question for evolutionary biologists as to why some organisms reproduce sexually, as opposed to asexually, is addressed. We also discuss the economic and medical importance of asexual organisms.

Keywords. Asexual, vegetative, parthenogenesis, clonality, reproduction, population genetics, evolution.

Introduction

Asexual reproduction has been the subject of numerous studies and reviews from a diversity of biological disciplines. There is, for instance, an academic interest in: (i) what mechanisms allow a "normally" sexually reproducing organism to produce asexually? (ii) What are the consequences this can have in the short term (population dynamics, population genetics), or in the long term? (iii) How many species are clonal and how are they clonal?

Several reviews and books concerning asexuality are available in the literature (see [1–6] for a few examples from various perspectives). In this review, focusing mainly on eukaryotic organisms, we first deal with specific definitions as this subject area is littered with vocabulary that sometimes has ambiguous meanings. We then present the diversity of ways in which eukaryotes reproduce asexually. Following this, we describe the various ways that asexual reproduction is incorporated in eukaryotic life cycles. After a brief attempt to quantify the importance of asexuality in living organisms, the genetic consequences of asexuality are reviewed, followed by a section on the evolution and the paradox of sex. Finally, we conclude with economic and medical issues linked to asexual organisms.

Definition and limits for asexual reproduction

The literature on asexual reproduction is full of terms and definitions. Readers are often confused, even those familiar with asexual organisms. It thus may be worth beginning with reviewing the vocabulary associated with asexual reproduction and then focus only on what is relevant to this paper and leave the remaining aside, "Culture – an oriental moralist said – is what remains in mind when everything has been forgotten" (translated from [7]).

Asexual reproduction occurs when an individual produces new individuals that are genetically identical to the ancestor at all loci in the genome, except at

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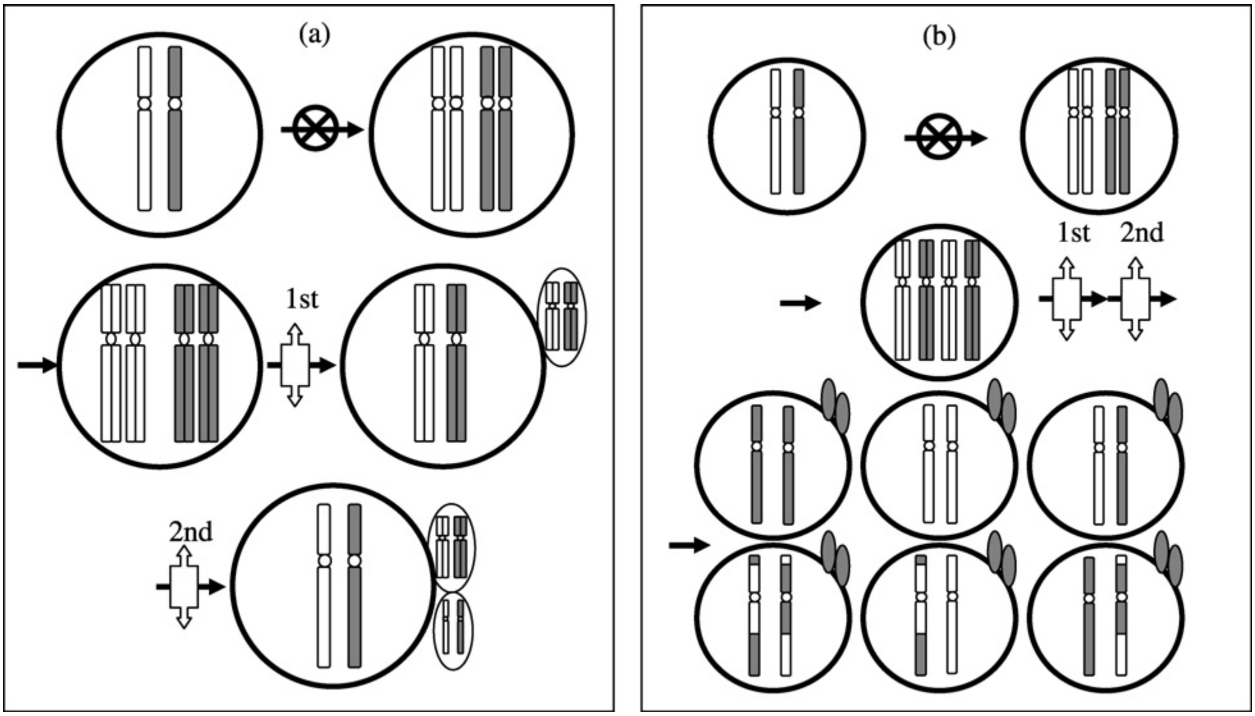

Figure 1. Endomitotic automixis. Here all chromosomes are doubled (symbolised by ⊗) prior a normal meiosis. With sister chromatid pairing (*a*) before the first meiotic division crossing-over is inefficient and the resulting egg is strictly identical to the mother and the process is equivalent to a clonal mode of reproduction. This kind of automixis is found in earthworms [21], planarians [56] and in *Allium tuberosum* [57]. With random pairing (*b*) then theoretically any kind of egg can be obtained and the process is equivalent to selfing. This mechanism is described in [1], but no natural example seems to be available. Double empty arrows symbolise the two (1st and 2nd) meiotic divisions and smaller ovals the resulting polar bodies.

those sites that have experienced somatic mutations. Asexual reproduction is synonymous to clonal reproduction. The word clone comes from the ancient Greek klonos (κλωνός), which means young shoot.

In the fields of animal and plant biology, several other terms are often synonymous with asexual (clonal) reproduction. Sometimes they refer to modes of reproduction that are really asexual reproduction (given the definition above), and some are not. This can lead to much confusion. We try to clarify these different aspects.

Agametic reproduction is a term generally used in animal science, while vegetative reproduction is generally used in plant science. Both terms have the same meaning and describe the production of new individuals from somatic cells or somatic structures (*i.e.*, not related to reproductive organs or gametes). They can take different forms in either plants or animals, but all lead to the production of individuals that are genetically identical to the parent. Consequently, agametic and vegetative reproduction both constitute true cases of asexual reproduction (clonality).

The term parthenogenesis in animal science is often synonymous with asexual reproduction. As shown below, this term regroups several types of reproduction that are not all cases of asexual reproduction given the definition above. As such, the use of this term should be avoided. Parthenogenesis derives from the ancient Greek παρθενος (partenos=virgin) and γένεσις (genesis) and was first described for aphids [8]. It concerns the production of individuals by descent without the need for male gametes. Strictly speaking the unfertilised female gamete develops into a new organism. Parthenogenesis can be divided into four classes: arrhenotoky, deuterotoky, pseudo-arrhenotoky and thelytoky. Table 1 describes the different modes of parthenogenetic reproduction found in animals. The etymology for "toky" is τόκος meaning childbirth in ancient Greek. The term "arrheno" comes from άρρενος (male). Arrhenotoky corresponds to the production of males from unfertilised eggs (in dioecious species). These males are necessarily haploid and therefore genetically different from their mother. As such, this reproductive mode cannot be considered as asexual reproduction *sensu stricto,* as define above. "Thely" stems from the Greek θήλυς (female). Thelytoky corresponds to the production of females from unfertilised eggs. Two forms are generally distinguished. (i) ameiotic thelytoky in which the (unfertilised) eggs are diploid and simply derive from unreduced oocytes (no meiosis during the production of the female gamete) and (ii) automictic thelytoky (also called

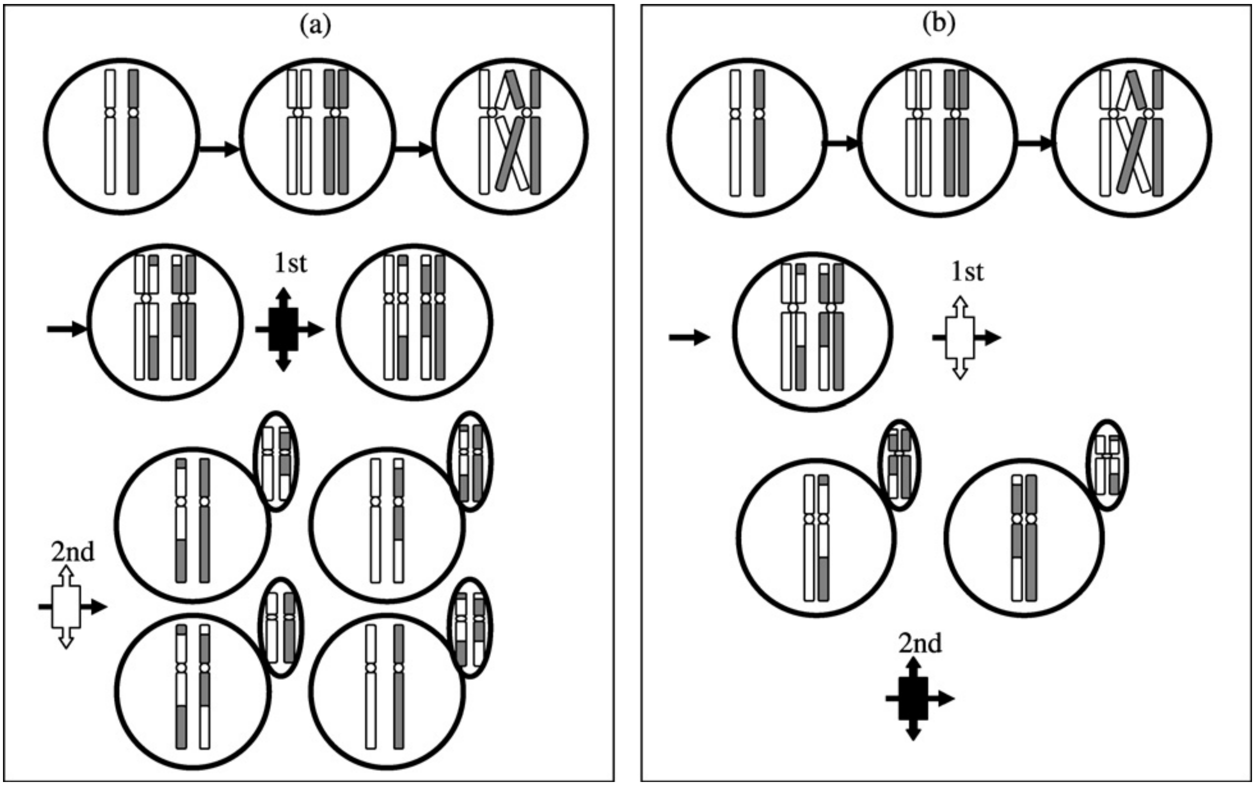

Figure 2. Automixis with suppression of the first (*a*) or second (*b*) meiotic division. Even if not fully equivalent to selfing, some segregation and recombination occur and heterozygosity is progressively lost in both cases. The case described in (*a*) has been found for a few psychid moths [40]. Case (*b*) seems more frequent and is the only parthenogenetic mode of reproduction for oribatid mites [58]. It is also found in some species of coccid, thrips, dipterans and hymenopteran insects [40]. A few tardigrades (mostly ameiotic [22]) are involved ([1] page 236) as are some Gastrotricha ([1] pages 200–201), even if in apparent contradiction with Table 1.1 of [1] (page 36). Diploid parthenogenetic Artemia species also use this reproductive mode [59, 60]. The suppressed division is symbolised by a black double arrow. Other legends are as in Figure 1. Notice that in case (*a*) (suppression of first meiotic division) heterozygosity is lost distal to chiasmata, whereas in (*b*) (suppression of second meiotic division), heterozygosity is lost between the centromere and the chiasmata.

automixis) in which the (unfertilised) eggs are diploid, although meiosis occurs during oocyte formation. The diploidy of the egg is either restored *a posteriori* or due to a genome duplication of the female gamete mother cell just before meiosis. Figures 1–3 summarise the major forms of automixis. In Figure 1 we see two forms of endomitotic automixis: (a) where sister chromatids pair before the first meiotic division, and (b) where chromatids pair randomly. Figure 2 shows automixis where (a) the first, or (b) the second meiotic division is suppressed. Two additional forms of automixis are found in Figure 3, where diploidy is restored after meiosis: (a) by a doubling of the gametic nucleus or (b) by fusion of two haploid polar bodies. As shown, the different forms of automictic thelythoky may have very different genetic consequences (see Figs 1–3) and only the processes in Fig. 1a and 3b are in fact equivalent to clonal reproduction because only in those cases are the offspring genetically identical to the mother. Ameiotic thelytoky is also a true form of asexual reproduction. Note, a single case of automixis is known for plants and involves *Rubus caesius.* This example does not involve asexual reproduction, as the unreduced egg is formed from the fusion of two reduced nuclei coming from the division of the haploid egg nucleus [4]. It is equivalent to the type of automixis described in Figure 3a, which is not a case of asexual reproduction. “Deutero” comes from δεύτερος (second), and deuterotoky is similar to the previous example, except that some males are produced, but these males apparently serve no role in reproduction. Finally, “pseudo” comes from ψευδής, which means false. Pseudo-arrhenotokous species produce both male and female individuals from fertilised eggs, but males secondarily become haploid. As fertilisation occurs, this cannot be considered as asexual reproduction. In summary, the use of parthenogenis as a synonym of asexual reproduction in animal biology is problematic, as only ameiotic thelytoky with some forms of automictic thelytoky and deuterothoky can be considered as true asexual reproduction. This is because they lead to the production of progeny that are genetically identical with their mother.

In plant science, the term parthenogenesis is generally used in a narrower sense as it only refers to a particular

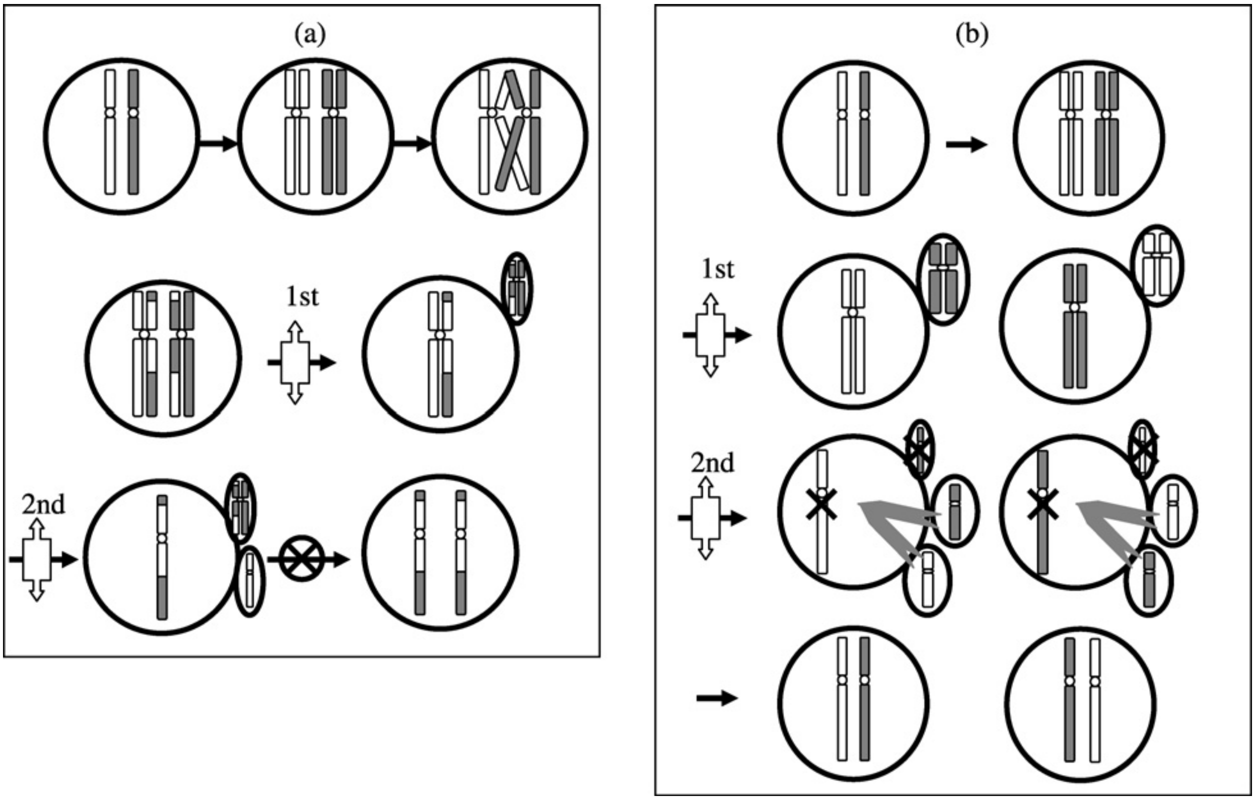

Figure 3. Complete meiotic automixis. In the first case (gametic genome doubling) (*a*) diploidy is retrieved through doubling of gametic nuclei leading to instantaneous homozygosity across the whole genome. This particular automixis, genetically equivalent to clonal haploidy, is frequently found in insects (parthenogenetic grasshoppers, two species of stick insects, four genera of coccids, one whitefly and one ichneumonid wasp) [1] and known for one plant species, *Rubus caesius* [4]. In the case of fusion of achiasmatic polar bodies (*b*), found in psychid moths [61], the fusion (symbolised by grey converging arrows) of the reduced first polar body with the second polar body results in the full restoration of the maternal genome and is thus fully equivalent to clonality. Black X symbolises chromosome sets that do not participate in the egg's genetic material. Other legends are as in Figure 1.

form of gamethophytic apomixis (see paragraph below) where the sporophyte (the seed) is produced from the unreduced egg cell and not from another cell of the embryo sac (the gametophyte). Parthenogenis therefore describes only part of the mechanism by which asexual reproduction occurs. The term is not therefore directly synonymous with asexual reproduction. To avoid confusion, we think that its use should also be avoided in plant science.

In animals, some other modes of reproduction are sometimes referred to as cases of clonal reproduction. This is so for androgenesis, gynogenesis and hybridogenesis. In androgenesis, the hybrid egg nucleus degenerates and is replaced by paternal nuclear genes through the fusion of two sperm nuclei. Few species display this mode of reproduction, *e.g.*, stick insects [62]. It is not a true case of clonal reproduction. With gynogenesis (also called pseudogamy), offspring are produced from diploid oocytes that do not undergo meiosis, but the production of an unfertilised egg needs stimulation by the sperm of a male [3]. Individuals produced in this way are all females identical to their mother and gynogenesis is therefore a true case of asexual reproduction. Finally, in some species, only one half of the genome (maternal or paternal) is retained in the germline without recombination. This phenomenon is called hybridogenesis [63] and has been well documented for the hemiclonal waterfrogs *Rana esculenta*, in which either the maternal or paternal genome may be retained [64]. In maternal hybridogenesis, male sperm of one parental species is still needed. As only half of the genome is transmitted to the offspring, this is not a case of clonal reproduction, *sensu stricto.*

Apomixis (άπο-μί́ξις=without mixing), is synonymous with agamospermy (α-γάμος σπέρμα=seed without marriage), and involves the production of seeds without fertilisation [5]. Several kinds of apomixis exist. As Bicknell and Koltunow [65] state, there are certainly, "as many mechanisms of apomixis as there are plant taxa that express the trait". However, some clear common properties have been identified [65]: (i) the generation of a cell capable of forming an embryo without prior meiosis; (ii) the

Table 1. Parthenogenetic modes of reproduction in animals.

Type	R	F	C	Clade	Sub-clade	Frequency	Ref.
Arrhenotoky	Yes	Yes	No	Nematoda	Oxyurid	Universal	[9]
				Acarina	Mesostigmata	Common, predominant in several families	[10]
					Prostigmata	Very common, predominant in several families	[10]
					Astigmata	Dominant in Anoetidae	[10]
				Hexapoda	Hymenoptera	Universal	[9]
					Thysanoptera	Universal	[9, 11]
					Hemiptera	Several Margarodidae and Coccidae, common in Aleyrodidae	[9]
					Coleoptera	Several Scolytidae and Micromalthidaes	[9]
Pseudo-Arrhenotoky	Yes	Yes	No	Acarina	Mesostigmata	Common in Phytoseiidae and Dermanyssidae	[10]
				Hexapoda	Thysanoptera	Common	[9]
					Hemiptera	Found in several Coccoidea	[9]
					Diptera	Found in several Cecidomyidae and Sciaridae	[9]
					Coleoptera	Found in several Scolytidae	[9]
Thelytoky and Deuterotoky	No*	No	Yes*	Cnidaria	Anthozoa	Very rare	[12]
				Turbellaria		Rare	[3]
				Monogenea	Gyrodactylidae	All	[13]
				Cestoda		Rare	[14]
				Trematoda		Rare	[14]
				Gastrotricha	Chaetonotida	All	[15, 16]
				Rotifera	Monogononta and Bdelloida	Universal	[17]
				Nematoda	Aquatic and animal parasitic	Rare	[18, 19]
					Soil and plant parasitic	Common	[19, 20]
				Annelida	Polychaeta and Oligochaeta	Common in Lumbricidae, rare elsewhere	[3, 21]
				Mollusca	Gastropoda	Rare	[3]
				Onycophora		Exceptional	[3]
				Tardigrada		All	[22, 23]
				Opiliones		Rare	[24]
				Araneae		Rare	[24]
				Scorpiones		Rare	[24]
Thelytoky and Deuterotoky				Acarina	Mesostigmata	Common	[10]
					Metatstigmata	Rare	[10]
					Prostigmata	Common	[10]
					Astigmata	Rare	[10, 25]
					Cryptostigmata	10 %	[25, 26]
				Myriapoda	Diplopoda	Several dozen	[27]
					Chilopoda	Rare	[3, 28]
					Pauropoda	Rare or absent	[29]
					Symphyla	Common	[3]
				Branchiopoda		Very common	[3]
				Maxillipoda	Ostracoda	Common in freshwater, rare in marine	[3]
					Tantulocarida	Universal	[30]
				Malacostraca	Isopoda	Exceptional	[31]
					Decapoda	One case	[32]

Table 1 *(Continued)*

Type	R	F	C	Clade	Sub-clade	Frequency	Ref.
				Hexapoda	Collembola	Common	[33]
Thelytoky				Hexapoda	Odonata	Exceptional	[34]
and					Ephemeroptera	Very common	[35]
Deuterotoky					Blattoptera	Very common	[11, 36]
					Mantoptera	Very common	[11]
					Isoptera	Very common	[11]
					Plecoptera	Rare	[37]
					Orthoptera	Very common	[11]
					Embioptera	Occurs in Oligotomidae	[11]
					Phasmida	Very common	[11]
					Psocoptera	Less than 4 %	[38]
					Phthiraptera	*Bovicola* sp (Mallophaga)	[39]
					Hemiptera	Common, universal in aphids	[11, 40]
					Thysanoptera	Some species	[41]
					Strepsiptera	One possible example	[42]
Thelytoky and				Hexapoda	Coleoptera (beetles)	54 Curculionidae, 11 Chrysomelidae, rare in other families	[11, 40, 43]
Deuterotoky					Hymenoptera	Very common	[11]
					Diptera	Found in several families	[11]
					Lepidoptera	Several Psychidae exceptional elsewhere	[40]
				Echinodermata	Asteroidea and Stelleroidea	Rare or absent	[44]
				Vertebrata	Pisces	About eight species (Poeciliidae, Cyprinidae, Atherinidae and Cobitidae)	[45]
					Amphibia	About three Ambystoma	[45]
					Reptilia	About 36 lizards and two snakes	[46–55]

R: Reduced eggs; F: fertilisation of eggs; C: equivalent to clonality. * Except for certain automicts (see Figures 1–3).

spontaneous, development of the embryo independently of fertilisation; and (iii) the capacity to either produce an endosperm autonomously or to use an endosperm derived from fertilisation. In sporophytic apomixis (also called adventitious embryony) (see Fig. 4), a sporophytic cell from the mother plant develops into an embryo (without the need for fertilisation by male gametes). This embryo develops using nutrients provided by the sexually produced endosperm. In the case of adventitious embryony, sexually produced embryos may abort or not, hence the term "adventitious" is used. Sporophytic apomixis is equivalent to vegetative reproduction, as the formation of new embryos does not involve production of the gametophyte stage (the embryo sac). This is a true case of clonal reproduction. In gametophytic apomixis, the embryo develops from an unreduced embryo sac (the gametophyte). The four major forms of gametophytic apomixis are illustrated in Figure 4. "True parthenogensis" is only achieved when the embryo is derived from an unreduced egg cell. In other cases, the embryo is provided by another cell of the sac and is known as apogamy, whose existence is controversial [66]. Endosperm development in these plants can be either spontaneous or fertilisation induced. More detailed reviews of apomixis in plants can be found elsewhere [5, 67–70]. Gametophytic apomixis, whatever its form (true parthenogenesis or apogamy), is a true form of asexual reproduction. Paternal apomixis, involving the production of embryos from the unreduced diploid material of the male, has also been recently demonstrated for a species of *Cupressus dupreziana* [71]. As in Cupressaceae, both mitochondrial and chloroplast genomes are paternally inherited [72], this example is also a true case of clonality.

Note that the term parthenogenesis (in its animal sense) is sometimes used as a surrogate of apomixis [5, 67, 73], but certain authors disagree with that use [73]. Equally, the term apomixis (apomictic thelytoky) is sometimes used when referring to animals [74].

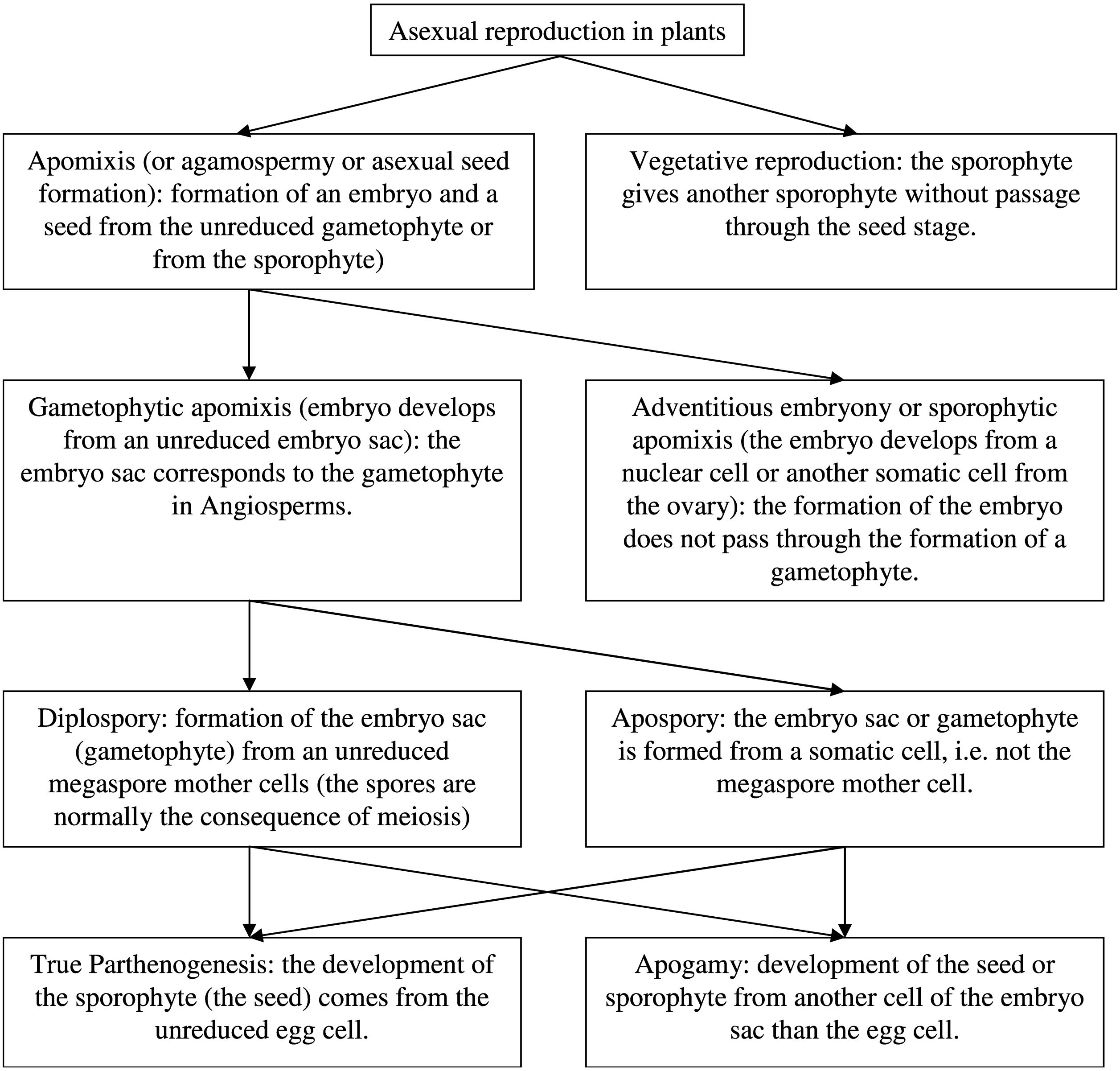

Figure 4. The different forms of asexual reproduction in plants (modified from [4]).

Table 2 recapitulates the different forms of reproduction that correspond to true clonality in animals and plants. It is worth noting from Figure 4 and Table 2, that apomixis is more easily applied to plants. In fact, only ameiotic thelytoky is a particular kind of gametophytic apomixis. Indeed, apomixis covers a much wider range of reproductive mechanisms than are seen in animals. This is probably due to the complexity of sexual reproduction in higher plants. Sporophytic apomixis would even be termed vegetative by a zoologist.

Description of different forms of clonal reproduction and life cycles

The most classical form of asexual reproduction involves cell division (mitosis) in unicellular organisms (prokaryotes and protists). For multicellular organisms, asexual reproduction can be achieved in many different ways.

In plants, rhizomes (underground, horizontal stems giving birth to new plants), layers (branches that root and grow as new individuals), bulbs or corms and tubers (storage organs that can produce new individuals), can be considered as clonal propagators. There is, however, an ambiguity because the individuals

Table 2. Modes of reproduction corresponding to asexual reproduction.

Type	Sub-type
Vegetative multiplication (animals and plants)	*e.g.*, gemulation, budding, fragmentation, fission, bulbs, stolons, polyembryony[1]
Parthenogenesis (animals)	Ameiotic thelytoky and deuterotoky Sister chromatid endomitotic automixis (Fig. 1a) Post-meiotic fusion of achiasmatic reduced polar bodies automixis (Fig. 3b)
Gynogeneis or pseudogamy	No sub-type
Apomixis (plants)	Gametophytic and sporophytic apomixis (adventitious embryony)

[1] Notice that in plants, polyembryony is not necessarily clonal. There can be mixtures of clonal and sexual embryos in seeds (*e.g.*, citrus).

produced can stay attached to the mother plant, in which case they can be considered as branches of the same individual. This is different from the production of independent individuals. However, plants do not move and the term colony would perhaps best describe individuals produced by such means. In liverworts, the gametophyte (haploid stage) propagates itself vegetatively and produces the gametes, which give rise by fertilisation to the sporophyte (diploid stage). In the gametophyte, vegetative reproduction may occur as a result of fragmentation of the main plant body (thallus) or by gemma cup production. With fragmentation, new plants are formed when older plant parts die at the fork of a branch of a thallus. The two branches then become independent individuals. Gametophytes produce propagative structures called gemma cups. Each gemma gives rise to numerous gemmae, which are released when cups fill with water and disperse to favourable sites where they form young plants.

As previously underlined, apomixis corresponds with, "asexual reproduction through seeds" [5]. Apomixis *sensu stricto* applies only to spermaphytes, as by definition it requires the production of seeds through asexual reproduction. This applies mainly to angiosperms, as gymnosperms have rarely, if ever, been found to perform apomixis. Plants with sporophytic apomixis are generally diploid and frequently found in tropical and sub-tropical fruit trees (lemon tree, mango). In contrast, gametophytic apomicts are polyploid most of the time [70]. Apospory is found in tropical and sub-tropical grasses, including *Cynodon* (couch grass), *Panicum* (millet), *Brachiaria*, *Pennisetum*, *Poa pratensis* (Kentucky bluegrass), *Harpochloa falx* (caterpillar grass) and in some Asteraceae (Compositae), such as, *Hieracium.* The most typical cases of diplospory are known from allium (Liliaceae), Asteraceae , *e.g.*, *Taraxacum* (dandelion), *Antennaria*, Brassicae (*Boechera holboellii*), and also weed and forage grasses (*Eragrostis*, *Tripsacum*). A complete description of the angiosperm families displaying different kinds of reproduction and their commonness are described in Table 3. Some forms of reproduction occurring in bryophytes or pteridophytes, as well as in algae, may be considered as sporophytic or gametophytic apomixis (see [4] for a discussion about this issue), even if these plants do not produce any seeds.

As for plants, multicellular animals can reproduce asexually in two main ways: agametic reproduction and parthenogenesis (thelytokous, deuterotokous). Agametic reproduction can occur by many means. This can be passive (fragmentation), as is often found for major reef-building corals and sponges [3]. Active clonality by laceration is reported from sea anemones, benthic ctenophores, and for some turbellarians; fission is found in starfishes, sea cucumbers, echinoderms, turbellarian flatworms, some polychaete and oligochaete annelid worms, encrusting sponges, alcyonian corals and sea squirts [3]. Budding is the production of new individuals from small parts of the parent without the division of the parent individual. While rare in sponges and cestode flatworms (*Echinococcus* sp), budding is common or universal in cnidarian (jellyfishes, hydras, corals, sea anemones), phoronids (horseshoe worms), entoprocts (goblet worms), urochordates (sea squirts) and trematodes (flukes). Polyembryony involves the development of identical twins from the same embryo. It is universal in the Mesosoa (parasites of invertebrates), rare in olygochaete worms and parasitic hymenoptera, and exceptional in mammals (armadillos). A more or less similar mechanism is found in Gyrodactylid Monogenea (flatworms that parasitise fish), where polyembryony is combined with automictic parthenogenesis, as described in detail in [13]. In animals, thelytokous ameiotic parthenogenesis involves the production of individuals from diploid oocytes that do not undergo meiosis, or for which meiosis does not lead to segregation or recombination (Figs 1a and 3b). Thus, individuals produced in this way are all females identical to their mother. Some authors state that vertebrate gynogens are only found in anamniotes (fish, amphibians), while true parthenogenesis is only encountered in amniotes (*i.e.*, reptiles) ([76] cited in

Table 3. Apomixis commonness in angiosperms. Data on presence of different kinds of apomixis in Angiosperm families are summarised from [75].

Type	Sub-type	MMC	G	E	Rd	F.EbF	F.EnF	Order	Commonness
Gametophytic apoximixis	*Diplospory*	Yes	Yes	Yes[1] or No[2]	No	No	Yes[3] or No[4]	Poales	1 family (Poaceae); 9 genera
								Asparagales	2 families: 1) Alliaceae, 1 genus; 2) Amaryllidaceae, 2 genera
								Burmanniales	1 family (Burmanniaceae), 1 genus
								Cucurbitales	1 family (Cucurbitaceae); 3 genera
								Rosales	1 family (Rosaceae); 5 genera
								Balanophorales	1 family (Balanophora), 1 genus
								Caryophyllales	2 families: 1) Amaranthaceae, 1 genus; 2) Chenopodiaceae, 1 genus
								Asterales	1 family (Asteraceae), 15 genera
								Nymphaeales	1 family (Saururaceae), 1 genus
								Piperales	1 family (Saururaceae), 1 genus
								Rhamnales	1 family (Rhamnaceae), 1 genus
Gametophytic apomixis	*Diplospory*							Thymelaeales	1 family (Thymelaeaceae), 1 genus
								Urticales	1 family (Urticaceae), 3 genus
								Plumbaginales	1 family (Limoniaceae), 1 genus
								Fagales	1 family (Betulaceae), 1 genus
								Casuarinales	1 family (Casuarinaceae), 1 genus
								Brassicales	1 family (Brassicaceae), 1 genus.
	Apospory	No	Yes	Yes[1] or No[2]	No	No	Yes[3] or No[4]	Arales	1 family (Aracae); 1 genus (Aglaonema)
								Poales	1 family (Poaceae), 31 genus
								Asparagales	1 family (Hyacinthaceae), 1 genus
								Dioscoreales	1 family (Taccaceae), 1 genus
								Orchidales	1 family (Orchidaceae), 2 genus
								Asterales	1 family (Asteraceae), 27 genus
								Caryophyllales	1 family (Chenopodiaceae), 1 genus
Gametophytic apomixis	*Apospory*							Cornales	1 family (Adoxaceae), 1 genus
								Ericales	1 family (Cyrillaceae), 1 genus
								Lamiales	1 family (Globulariaceae), 1 genus
								Myrtales	1 family (Myrtaceae), 1 genus
								Polygonales	1 family (Polygonaceae), 1 genus
								Urticales	1 family (Urticaceae), 1 genus
								Rosales	1 family (Rosaceae), 12 genus
								Polygalales	1 family (Malpighiaceae), 1 genus
								Rutales	1 family (Rutaceae), 4 genus
								Boraginales	1 family (Boraginaceae), 2 genus
								Theales	2 families: 1) Hypericaceae, 1 genus; 2) Ochnaceae, 1 genus
								Brassicales	1 family (Brassicaceae), 1 genus.
								Cucurbitales	1 family (Cucurbitaceae); 2 genus
Sporophytic apomixis[5]		No	No	No	No	No	Yes	Poales	1 family (Poaceae), 1 genus
								Asparagales	1 family (Amaryllidaceae), 1 genus
								Dioscoreales	1 family (Trilliaceae), 1 genus

Table 3 *(Continued)*

Type	Sub-type	MMC	G	E	Rd	F.EbF	F.EnF	Order	Commonness
								Asterales	1 family (Asteraceae), 1 genus
								Caryophyllales	1 family (Cactaceae), 1 genus
								Thymelaeales	1 family (Thymelaeceae), 1 genus
								Urticales	1 family (Urticaeae), 1 genus
								Orchidales	1 family (Orchidaceae), 4 genus
								Myrtales	2 families: 1) Melastomataceae, 1 genus; 2) Onagraceae, 1 genus
								Rosales	1 family (Rosaceae), 1 genus
								Boraginales	1 family (Boraginaceae), 1 genus
								Solanales	1 family (Solanaceae), 1 genus
								Curcubitales	1 family (Cucurbitaceae), 1 genus

MMC : Megaspore mother cell; G: gametophyte (embryo sac); E: egg cell; R: reduced; F.EbF: fertilisation required for embryo formation; F.EnF: fertilisation required for endosperm formation.

[1] Parthenogenesis [4].

[2] Apogamy: the embryo develops from another cell of the embryo sac.

[3] Pseudogamy.

[4] Autogamy.

[5] Sporophytic apomixis is also called adventitious embryony.

[3]). In some cases, a parthenogenetic species is only composed of females that still need elaborate courtship behaviour, where a female acts in the male role to stimulate ovulation [77]. In vertebrates, true parthenogenesis and gynogenesis appears to be restricted to taxa of a hybrid origin, as all known cases are hybrid. Thelytokous parthenogenesis is unequally distributed in animals (see Table 1). In Rotifera, it is universal in the Monogononta and is the unique reproductive mode known for the Bdelloida [17]. In Echinodermata, it is rare or absent and totally unknown for birds and mammals. More details can be found in Table 1.

Finally, it can be instructive to subdivide organisms using asexual reproduction into different categories based on the complexity of their life cycle. By a complex life cycle, we mean organisms that alternate between sexual and asexual phases of reproduction. Different life cycles have different consequences for the genetics of the populations concerned. In Figure 5a, we describe a life cycle with only one (I) round of clonality (LC-I). Here an individual produces new individuals in a single round of asexual reproduction and these individuals must then reproduce sexually. Figure 5b describes a life cycle with several rounds of asexuality (LC-S). Here the life cycle is also necessarily completed by sexual reproduction; however, asexual reproduction is maintained for several generations before this occurs. The life cycle illustrated in Figure 5c is what we call an acyclic life cycle (A-LC). In this case, the life cycle is not defined by a regular pattern of sexual or asexual reproduction. Individuals in a population may be issued from either mode of reproduction in the previous generation. The frequency of sexually or asexually derived individuals can vary widely and be dominated by either mode of reproduction.

LC-I applies to all species with polyembryony and many budding species. For example, this cycle is typical of trematodes (flukes). LC-S is typical of aphids, monogonont rotifers, cladocerans, of many fungi, and most Sporozoa (parasitic unicellular organisms, including the malaria agents *Plasmodium* spp.). A-LC is common in plants and unicellular organisms. In particular, it is found for strictly clonal organisms, or at least those organisms for which sex is unknown, such as, Bdelloid rotifers, imperfect fungi (*e.g.*, *Candida albicans*), Parabasalia (*Trichomonas vaginalis*), Metamonadina (*Giardia lamblia*), parasitic amoebas and kinetoplastid parasites (*Leishmania*, *Trypanozoma*).

Quantitative importance of asexual reproduction

Is asexual reproduction widespread or not? How rare is it? These questions are more difficult to answer than it would appear. Many papers dealing with this issue offer very low estimates for the frequency of asexual species on earth (from 0.1% [78] to 1% [74]). However, such papers only refer to higher eukaryotes and to species that are strictly clonal (*i.e.*, A-LC organisms with 0% sexual reproduction). Furthermore, the definition used to define a species also determines the number of species likely to fit this classification. As species description is less ambiguous for sexual, as opposed to asexual, species the literature may be strongly over-represented by sexual species

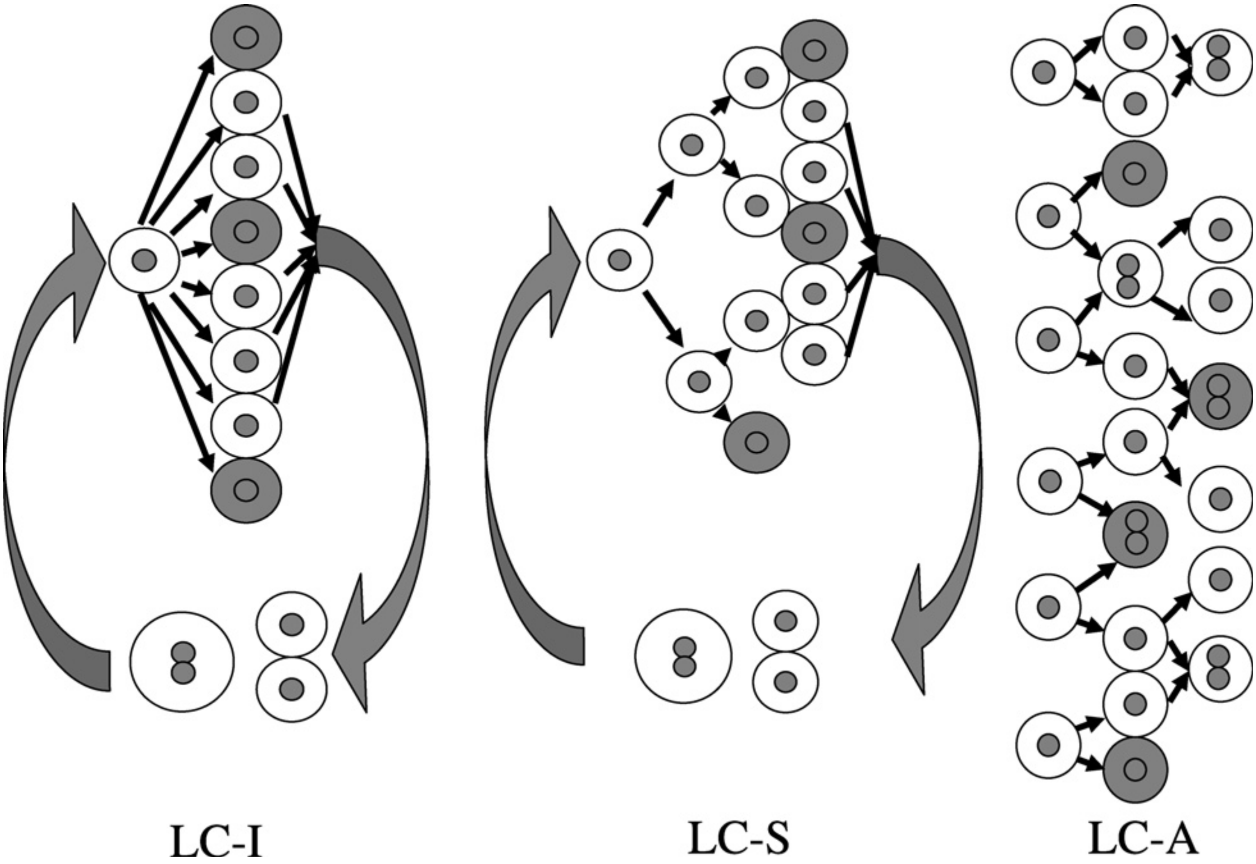

Figure 5. The three categories of reproductive life cycles considered in this review. (*a*) Life cycles with only one (I) round of clonal reproduction per cycle (LC-I). (*b*) Life cycles with several rounds of asexuality (LC-S), where the clonal phase involves more than one clonal generation. In both cases sexual reproduction (segregation and recombination) must intervene at one point of the cycle to form zygotes. (*c*) Acyclic life cycles (A-LC), where sexual reproduction may be more or less frequent (or even absent). In this case, the life cycle is not defined by a regular pattern of sexual or asexual reproduction. Diverging arrows symbolise asexual reproduction and converging arrows symbolise sexual reproduction. Individuals in grey represent individuals that will not participate in the next generation (death) and grey cycling arrows symbolise the alternation between asexual and sexual phases. Zygotes are represented as cells with two nuclei.

[79]. Many more species might be asexual if one includes prokaryotes and unicellular eukaryotes, not forgetting the undiscovered diversity they may contain [79, 80]. Alternatively, we may want to calculate how frequent asexual reproduction is in the living world, whatever the life cycle in which it occurs (LC-I, LC-S, A-LC). For instance, while apomixis is present in only 400 angiosperms [65], some biomes are predominantly occupied by plant species that are facultative apomictics [73]. The same trend is found for most animals, except in the most complex ones (insects, birds and mammals) [3]. By this definition, it is probable that clonality is by far the most frequently used mode of reproduction by eukaryotes.

Genetic consequences of asexual reproduction

From a genetic point of view, the consequences of asexual reproduction are multiple and may vary depending on whether clonality is the only mode of reproduction (or not) occurring in the species considered, and whether it concerns polyploid or haploid stages of the organism. In the following we discuss only some of these consequences.

One interesting consequence of strict asexual reproduction is called the Meselson effect [81] and was first (and uniquely to our knowledge) described for Bdelloid rotifers [82]. If a lineage of diploid organisms evolves for a sufficient number of generations without any sexual reproduction (no segregation or recombination), it is expected that each allele at any locus or gene will accumulate genetic differences due to mutation from the point when the lineage became asexual. Consequently, genetic divergence between alleles will be the maximum possible (Fig. 6). This

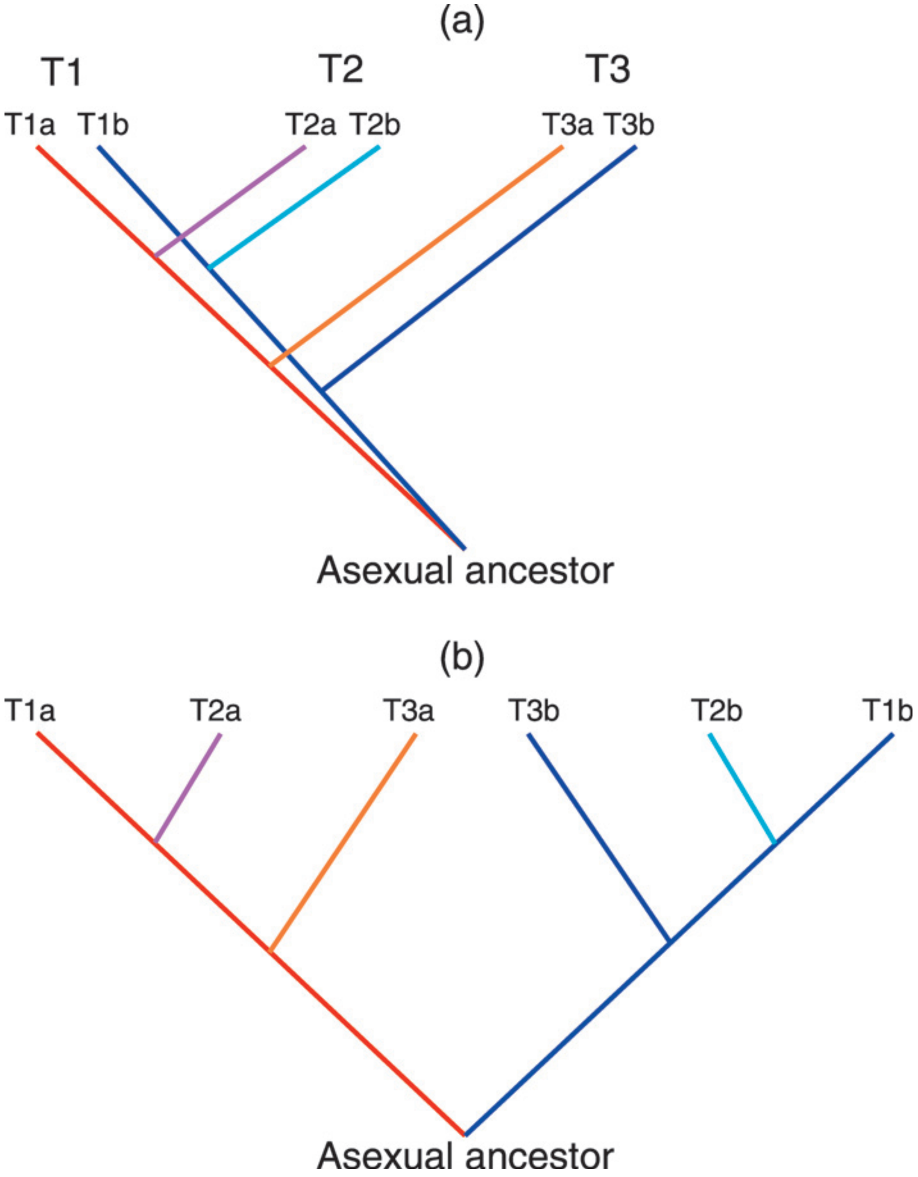

Figure 6. Illustration of the Meselson effect. In (*a*) the evolutionary relationships among three asexual diploid taxa are represented (T1, T2 and T3). The genetic divergence is also represented with varying colours providing the two alleles present in each taxon (alleles a and b). If we develop the tree corresponding to all DNA sequences (all alleles) as in (*b*) it is easily seen that the maximum divergence is obtained between the two alleles of the same taxon. This is what is expected in ancient clones and can be used as a criterion for detecting a long absence of sex in a group of taxa (Meselson method).

particularity can be used to detect ancient clonality in a group of clonal lineages [82]. To date, this phenomenon has only been found for bdelloids. Its absence in other organisms may reflect the rarity of ancient asexuals or the existence of homogenising factors, such as gene conversion, that can strongly modify the expected pattern of genetic differentiation [74].

Short-term consequences of asexual reproduction, perceptible in single species (populations), also exist. Since the pioneering works in 1908 of Hardy [83] and Weinberg [84], it is known that, in a sexually reproducing population of diploid individuals, when gametes meet randomly (panmixia) to form zygotes, the expected genotypic distribution of two alleles (A and a) of frequency p and $q = (1\text{-}p)$ in the population has the form p^2, $2pq$ and q^2. Where p^2 and q^2 represent the expected frequency of homozygous individuals (AA and aa) in the population, while $2pq$ is the expected frequency of individuals that are heterozygous (Aa). This result is known as the Hardy-Weinberg equilibrium (HW). Clonality tends to modify this expected distribution of genotypes. Associated with random genetic drift and mutation, it tends to produce an excess of heterozygotes as compared to HW expectations at all polymorphic loci [85–87] (for A-LC organisms). This tendency stays true even for selfing hermaphrodites [88] (for LC-S organisms). In particular, in full clones (no sex), all individuals are expected to be heterozygous at all loci. This leads to the (more or less) counterintuitive notion that more polymorphism can be maintained at individual loci in asexual populations than sexual populations.

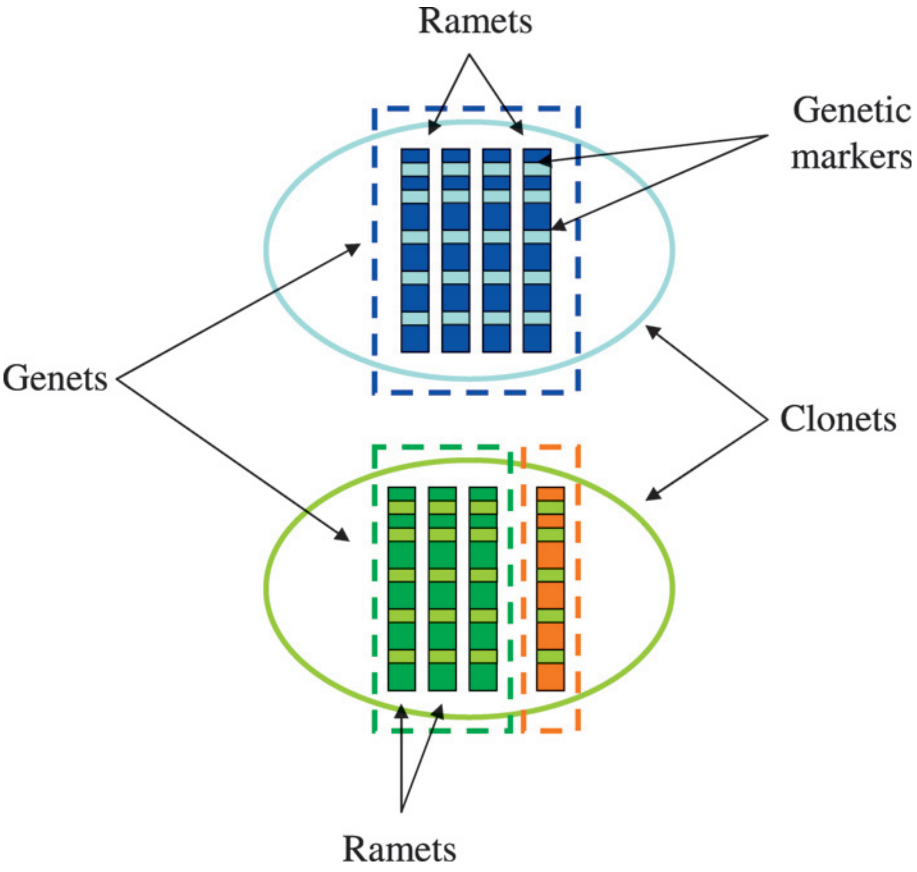

Figure 7. Schematic definition of genets, clonets and ramets. The vertical bars represent the individuals and ramets. Individuals belonging to the same genet are surrounded by dashed squares. Individuals belonging to the same clonets are surrounded by circles. For clonets, only the genetic markers used (small squares) need to be identical, while genets are identical over the entire genome.

Another characteristic of asexual reproduction is the absence of recombination among loci. The consequence is that the less recombination there is, the more statistical linkage disequilibrium will be produced and maintained in natural populations. In totally asexual populations all loci of the whole genome are linked and thus should share the same destiny. In particular, selection at one locus will drive the whole genome with it, a phenomenon known as "hitch-hiking". In the case where several linked loci are submitted to selection, the effect of selection at one locus will interfere with the selection at the other locus, which can reduce its efficiency in certain cases. This is known as interference selection.

The existence of repeated identical multilocus genotypes in a population is one recognisable sign of clonal organisms. This is what justified the distinction between genets [89] or clonets [90], *i.e.*, collections of individuals produced clonally and thus sharing the same multilocus genotype at all loci (genet) or at all investigated markers (clonet), from ramets, which are individuals belonging to one genet [89]. Figure 7 illustrates the differences among these three often unclear notions. Note, a clonet is often the empirical approximation of a genet. With the high resolution of current markers like microsatellites, this approximation can be so good as to make these terms interchangeable.

In each respect, the different kind of life cycles described above will display very different patterns of genetic structure at individual and population levels. This is not purely academic as the use of variable molecular markers can provide very useful information on the population biology of the organism under scrutiny, in particular pathogenic organisms (molecular epidemiology) [90]. For LC-I, it has been shown that it can be wiser to study the polymorphism of local populations with a single representative of each clonet (by withdrawing repeated genotypes) [91]. On the contrary, for A-LC organisms, it has been suggested that all individuals are informative and should be kept for the analysis and to infer their epidemiology [86, 87, 92]. In LC-S species, depending on the number of generations during the clonal phase, the expected pattern may look more like LC-I or A-LC. Most of the time authors prefer using the "single individual per clonet" option (see [93] for review), even if the comparison between the results obtained with or without repeated genotypes may be worth trying [87].

Asexual reproduction and the evolution of sex

In higher organisms, asexuality is rare compared to sexual reproduction. Why is this so? This question has been and is still at the heart of a major debate in evolutionary biology. This debate is based on a very simple problem: if in a population, females can either reproduce by sexual reproduction or asexually with the same fertility (same number of eggs laid) then clonal females should transmit their genes twice as efficiently as sexual females. This is because sexual females have to produce half of their progeny as males, which has been called the twofold cost of sex [94]. Asexual females should therefore invade the population and completely replace any sexual individuals. The problem worsens if one takes into account the cost of meiosis and reproductive structures (*e.g.*, flowers) [6]. However, obligate asexuals are rare in higher organisms. So far, no general agreement exists to resolve this apparent paradox. Sex is ancient in eukaryotes, as suggested by the huge number of genes involved in sexual processes [6]. The DNA repair function of sex does not provide a satisfactory explanation to this problem and the selective constrains that appear to limit the number and distribution of chiasmata (during meiosis) across numerous taxa does not argue for a strong direct benefit of recombination [6]. One obvious advantage of sex is to increase the creation of new combinations of genes able to compete in an ever-changing world, and in particular, to fight against parasites (Red Queen hypothesis) [81]. On the other hand, sex is incapable of keeping the best combinations together as they are dismantled in the next generation [3]. Furthermore, theoretical models show that sex does not necessarily generate genetic variation very well and may even be unfavourable for this cause [6]. Sexual reproduction can recreate good associations that were lost due to Muller's ratchet, a phenomenon where asexuals accumulate deleterious mutations [95]. In contrast, some advocate that sex is a homogenising process [74] that helps reduce intra-genomic conflict. Nevertheless, no single explanation can account for the predominance of sex because none of the existing arguments compensates the twofold advantage that asexuals instantaneously experience when in competition with their sexual counterparts. For more discussion on this topic, readers are encouraged to consult the excellent review from Otto and Lenormand [6] and references therein.

Asexual reproduction: medical and economic importance

Beyond their quantitative importance in terms of biodiversity, asexual organisms, even eukaryotic ones, are often of medical and economical importance [93, 96]. Important human diseases, such as malaria and schistosomiasis, involve organisms that use asexual reproduction in at least one stage of their life cycle. In certain cases, medically important parasites are suspected to be mainly or even totally clonal; *Leishmania*, *Trypanosoma*, *Giardia*, *Trichomonas* or *Candida.* For instance, at the CDC (Center for Disease Control, USA; Division of Parasitic Diseases) web site (http://www.cdc.gov/ncidod/dpd/) it can be read (in the corresponding fact sheets), "During the past two decades, *Giardia* infection has become recognized as one of the most common causes of waterborne disease (found in both drinking and recreational water) in humans in the United States. *Giardia* are found worldwide and within every region of the United States"; "Trichomoniasis is one of the most common sexually transmitted diseases, mainly affecting sexually active women. In North America, it is estimated that more than 8 million new cases are reported yearly"; "Worldwide, approximately 25 000 new cases of both East and West African trypanosomiasis are reported to the World Health Organisation each year"; "Although schistosomiasis is not found in the United States, 200 million people are infected worldwide"; " The number of new cases of cutaneous leishmaniasis each year in the world is thought to be about 1.5 million. The number of new cases of visceral leishmaniasis is thought to be about 500 000"; "Each year 350–500 million cases of malaria occur worldwide, and over 1 million people die, most of them young children in sub-Saharan Africa"; " One form of invasive candidiasis, candidemia, is the fourth most common bloodstream infection among hospitalised patients in the United States". All these diseases are caused by agents that are exclusively (or almost exclusively) clonal at one stage or another in their life cycle.

Important crop pests, such as aphids, and important tropical grass species used as forage are clonal and of considerable economic importance, as are several invasive taxa [5, 93, 97].

The study and understanding of the biology and mechanisms involved in the reproduction of such organisms is not only an academic matter as advocated by the considerable literature available, a small part of which was touched upon in this review. Understanding how and how much these organisms reproduce asexually is of practical importance for several reasons. Concerning pathogens or pests, this information may help explain the dynamics of drug (pesticide) resistance and pathogenicity or their evolution when facing new environments (artificial or not). As clonality affects the population genetic structure of the organisms (as described above), this automatically affects their evolutionary potential and so their ability to respond to environmental change. For example, pathogens with mixed reproductive systems including both sexual and asexual reproduction may have a considerable potential to evolve because they receive benefits from both mechanisms of reproduction. Sexual recombination allows many new combinations of alleles to come together and to be tested in a new local environment. Asexual reproduction allows the fittest genotype to reproduce as a clone, keeping together a fit combination of genes, and making it possible for this combination to spread over the entire population. It is worth noting many epidemics are caused by the emergence and spread of a particular genotype. For example, mutation in otherwise commensal populations of *Escherichia coli* bacteria can lead to the emergence and spread of virulent asexually reproducing strains that cause epidemics of severe dysentery [98]. While the epidemic outbreak of particular clones or strains is best documented for microbes and fungi [99], it is not limited to them; the most prevalent and virulent strains of the protozoan *Toxoplasma gondii*, causing toxoplasmosis, are associated with the asexual propagation of particular genotypes following a recombination event [100]. It is also worth noting the French wine industry was nearly destroyed in the 19th century following the introduction of an aphid, the grape phylloxera. This invasive species is completely parthenogenetic across its introduced range but cyclically parthenogenetic in its home range [101].

Determining the extent or rates of genetic rearrangements that occurs through recombination (and so sex) in natural populations of pathogens is also crucial if we are to use genetic mapping information to locate genes that underlie important phenotypes (*e.g.*, genes associated with virulence, drug resistance, transmission, immune evasion for pathogens) [102]. Genetic association studies are of little use for studying organisms that do not (or very rarely) recombine.

For agriculture, the potential benefits of clonality are extensive and have been previously extolled (*e.g.*, [5]). The main agronomic benefit that clonality could deliver is the immediate fixation of any desired genotype and its indefinite propagation. Man-made methods of vegetative reproduction are usually enhancements of natural processes, but range from simple cloning, such as, rooting of cuttings to grafting and artificial propagation by tissue cloning in the laboratory. It is common practice to propagate cultivars with desirable characteristics. Fruit tree propagation is frequently performed by budding or grafting desirable cultivars (clones) onto rootstocks that are also clones, propagated by layering. A number of commonly cultivated plants are propagated by vegetative means (*e.g.*, potato, cassava, banana, avocado). A better understanding of clonal reproduction in plants from either a genetic, physiological or cellular point of view is therefore of fundamental interest for engineering new technologies of propagation.

Concluding remarks

Asexual reproduction is a widely used means of reproduction, for both eukaryotes and prokaryotes. Our understanding of how asexual reproduction affects the biology and population genetics of prokaryotes is more advanced than it currently is for eukaryotes. Let us hope this gap in our knowledge will soon be filled, not only for our own understanding of how and as to why many organisms reproduce asexually, but also because asexuality has an important role in the life of many eukaryotes economically and is medically important to ourselves.

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