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Insights & Perspectives

Skipping sex: A nonrecombinant genomic assemblage of complementary reproductive modules

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Abstract

The unusual occurrence and developmental diversity of asexual eukaryotes remain a puzzle. De novo formation of a functioning asexual genome requires a unique assembly of sets of genes or gene states to disrupt cellular mechanisms of meiosis and gametogenesis, and to affect discrete components of sexuality and produce clonal or hemiclonal offspring. We highlight two usually overlooked but essential conditions to understand the molecular nature of clonal organisms, that is, a nonrecombinant genomic assemblage retaining modifiers of the sexual program, and a complementation between altered reproductive components. These subtle conditions are the basis for physiologically viable and genetically balanced transitions between generations. Genomic and developmental evidence from asexual animals and plants indicates the lack of complementation of molecular changes in the sexual reproductive program is likely the main cause of asexuals' rarity, and can provide an explanatory frame for the developmental diversity and lability of developmental patterns in some asexuals as well as for the discordant time to extinction estimations.

KEYWORDS
amphimixis, apomixis, automixis, gynogenesis, hybridogenesis, parthenogenesis

INTRODUCTION

Sexuality is ubiquitous to most eukaryotes, but approximately one in 10,000 species is asexual. The phylogenetic distribution of asexuals is patchy.[1] The scarcity of obligate asexual lineages among multicellular taxa is at first sight counterintuitive if one considers their theorized two-fold reproductive advantage. Because they usually produce only one sex, every individual gives rise to offspring and with a lower investment in mating processes asexuality should be a much more successful and thus more widespread reproductive strategy. However, the absence of meiotic recombination is expected to hinder the creation of genotypic variation and/or adaptation to novel conditions (e.g., Red Queen, Tangled Bank, Lottery hypotheses), and is anticipated to accelerate the stochastic accumulation of slightly deleterious mutations and genetic degeneration (e.g., Muller's ratchet, Hill-Robertson effect) leading to genomic decay and extinction of asexual lineages after a brief existence. This has been observed indeed in a few examples (e.g., in *Daphnia*[2]), but it appears far from being the rule. Even with the prediction of an early demise, some well-known asexual lineages in invertebrates, vertebrates, and plants for which age estimates exist have persisted much longer than expected from mathematical models derived from such theoretical considerations.[3,4] Asexuals have developed various strategies to limit the negative consequences of ameiotic reproduction, for example, by sporadic recombination, "mutation based" diversity and clonal competition,[5–7] and thus neither reduced genetic variability nor evolutionary persistence of

lineages are critical constrains.[8] If rapid extinction is not a factor influencing asexual lineages lifespan, then why asexuals are not more frequent? Why are they a rare phenomenon? and why do they display a variety of developmental strategies, as has been particularly noted in many studies on asexual species?

Stanley[9] argued that asexual species are rare because speciation in asexuals (their origins) is exceedingly rare, and in the long-term species selection will eliminate most asexuals. However, as all asexuals arise from sexual forms, this does not explain why the frequency of de novo formation or of successful establishment of asexuals in nature is not higher. According to Maynard Smith,[10] meiosis and sexuality is so entrenched in life that any shift away from it creates "sexual hang-ups" difficult to be overcome by selection. Sexual-to-asexual transitions might follow Dollo's law of irreversibility,[11] which states that once a complex feature is lost in evolution it cannot be regained with the same original state. In this context, the difficulties imposed to new asexuals by developmental constraints derived from its sexual ancestry are responsible for their observed low occurrence, a view connected to the "balance" and the "duplicate-gene asynchrony" hypotheses, the two more widely accepted views about the origin of asexuality in otherwise sexual organisms. The "balance" hypothesis, proposed by Moritz et al.[12] to explain observations in animals, considered the divergence of parental genomes has to be the right one both to increase the rate of unreduced gametes and to maintain hybrid's viability and fecundity. The "duplicate-gene asynchrony" hypothesis, proposed by Carman[13] to explain observations in plants, considered that genes when originating from different genomes in polyploids respond differentially to temporal and spatial developmental signals causing the anomalies during meiosis and gametogenesis observed in apomicts (i.e., plants reproducing through asexual seeds) and polysporic species.

In a study of embryogenic developments in aphids, Le Trionnaire et al.[14] considered the switch between sexual and asexual developments to be a reproductive polyphenism, that is, a phenotypic dichotomy triggered by photoperiodic cues. Even when this fits observations in organisms that cycle between sex and asexual states, it does not explain why some organisms are facultative asexuals (i.e., produce both sexual and asexual progeny under the same environmental conditions). Likewise, from a slightly different perspective, Carman et al.[15] (see also Carman and Roche[16]) first suggested a similar concept for plants, recently reviewed by Albertini et al.[17] (see also Carman et al.[18]) emphasizing the role of epigenetic regulations on reproductive transitions and suggesting that sex and apomixis in plants (and expectedly in asexuals from other kingdoms) might respond to an ancient polyphenism channeled by metabolic signaling.

In former years, different experimental crossings and setups preceded and gave support to the above ideas[19–22] delineating most of relevant developmental constraints associated to asexual origins.[23,24]In recent years, testing at molecular level such theoretical hypotheses based on empirical observations started to be possible by using new omics approaches collecting massive sequence-level data and new tools of analysis that delivered new hints for testing and contrasting previous ideas. Thus, in a study on the Amazon molly, an obligate asexual fish, Warren et al.[6] concluded that its rarity is likely driven by the chance of occurrence of genomic combinations required to elude meiosis and create a functioning hybrid genome, and provided molecular evidence to the "rare formation" hypothesis (whose original idea can be tracked back to Stöck et al.[25]). In plants, agreeing with the "duplicate-gene asynchrony" hypothesis, studies on several apomictic systems have shown global heterochronic gene expression and developmental asynchronies in apomeiotic ovules compared to sexual ones.[15,26–34]

Even though these hypotheses have a clear theoretical frame and a conceivable causal basis, they lack a simple mechanistic explanation for the diversity and frequencies of intraspecific and interspecific developmental strategies observed in asexuals.[7,24]

Here, we integrate old ideas with recent molecular and genomic data to provide a single mechanistic model for asexuals' origins. In this model, the "rare formation" and older hypotheses can be linked to simple molecular conditions that apply to all asexual taxa. We highlight commonalities that benefit a causal explanation for both the developmental lability observed among and within asexuals, and the sporadic occurrence of asexual taxa. This new perspective offers a joining road for future research on phylogenetically divergent asexuals.

ASEXUALITY CAN BE REACHED THROUGH ALTERNATIVE PATHWAYS

Sexuals share the genetic contribution to the formation of new offspring through the fusion of male and female gametes (amphimixis). Asexual reproduction implies the formation of a new organism with the genetic contribution of a single parent. Sometimes, asexuals do not require mating and in all cases, eggs develop either without fertilization or fusion of female and male nuclei.[24,35,36] Of note, the pathways of egg development vary among asexuals.

In automictic species, as opposed to apomixis, meiosis proceeds normally and an unreduced egg is formed either by endomitosis, fusion of two nuclei resulting from the same meiotic division, or fusion of cleavage division nuclei, which then develops parthenogenetically into a new individual. This exclude cases of nonparthenogenetic automixis in ferns and bryophytes.[37]Hence, automixis creates endogamous recombinant offspring without male contribution and leads to homozygosity.[35,36,38,39]

In gynogenetic and parthenogenetic species (including apomictic plants), meiosis is skipped and unreduced gametes carrying the maternal genetic information develop into new clonal individuals by parthenogenesis. While gynogenesis require mating and/or fertilization (without fusion of female and male nuclei) to trigger embryogenesis, parthenogens develop spontaneously.[36,39–41]

In hybridogenetic species, paternal chromosomes are eliminated during female meiosis and reduced gametes carry only maternal chromosomes. Such gametes require fertilization by a male gamete to develop a new individual. However, during the formation of the next generation, those individuals only transmit the maternal genetic information to the offspring.[36,41,42]

BOX 1

Glossary

Alloploidy: form of polyploidy where the multiple sets of homologous chromosomes are derived from the divergent genotypes or taxa.

Amphimixis: sexual reproduction where embryos develop from the fusion of male and female gametes.

Apomixis: form of asexuality, where gametes are produced without meiosis and develop a clonal embryo.

Asexuality: or asexual reproduction, where embryo formation involves only the contribution of gametes from one sex. Asexual reproduction can be obligate, when an asexual generation is always followed by another asexual generation, cyclic, when one or several asexual generations are followed by one or several sexual generations, or facultative, when asexual and sexual reproduction occurs irregularly and only under certain life history conditions.

Automixis: form of asexuality, where meiosis proceeds normally and an unreduced egg is formed either by endomitosis (e.g., Döpp-Manton or *Allium* schemes in plants), or fusion of two cell products of the same meiosis (e.g., by fusion of the polar body with the egg nucleus in animals), or fusion of cleavage division nuclei, followed by parthenogenetic development of a new individual.

Autonomous apomixis: form of asexuality, where pollination and fertilization of the female gametophyte are not required. The endosperm and the embryo develop spontaneously.

Autoploidy: form of polyploidy where the multiple sets of homologous chromosomes are derived from the same genotype or taxon.

Endogamy: the fusion of reproductive nuclei/cells from the same or closely related individuals.

Gynogenesis: form of parthenogenesis that requires the presence of sperm to activate the parthenogenetic development of the embryos as a physiological trigger, but without incorporation of genetic material from the sperm.

Hemigamy (or semigamy): type of fertilization in which a sperm nucleus penetrates the egg cell but does not fuse with the egg nucleus. Both nuclei divide independently but, in most cases, male nuclei do not contribute to the genetic make-up of the zygote.

Hybridogenesis: the consistent production of females from reduced eggs with sperm of host males. The female genome is clonally transmitted without recombination, while the paternal genome is excluded in female meiosis and thus exchanged in every generation.

Kleptogenesis: a genetic system involving hybridogenetic and gynogenetic elements.

Parthenogenesis: form of asexual reproduction where embryos develop from eggs without fertilization by sperm. In plants where endosperm development is required to form a functional seed, parthenogenesis is a component of apomixis (either autonomous or pseudogamous apomixis).

Polyphenism: the ability of a genotype to generate distinct phenotypes by changing the metabolic status in response to an environmental factor (e.g., nutrition, photoperiod, temperature, male deprivation).

Polyploidy: a genetic constitution where a cell, organ or organism has more than one pair of homologous chromosomes.

Pseudogamous apomixis: or pseudogamy, form of asexuality that requires pollination and fertilization of the central cell in the female gametophyte to complete the formation of the endosperm and trigger parthenogenetic development of the embryo.

Thelytoky: systems that consists exclusively of females. Thelytoky can be the result of parthenogenesis, gynogenesis or hybridogenesis.

Tychoparthenogenesis: the occasional occurrence of parthenogenesis.

A COMMON MOLECULAR CONTEXT AND INITIAL CONDITIONS TOWARD ASEXUALITY

In animals and plants, most asexual lineages for which the molecular genetics of developmental mechanisms are best characterized are known to be of hybrid and/or polyploid origin. Those few asexuals not having a hybrid or polyploid origin are mostly endogamic, displaying a wide developmental complexity, which, in different cases, blurs definitions of sex (e.g., in automictic parthenogenesis).

Hybridization, that is, the process of breeding individuals from the same or different populations or species, is a significant evolutionary force during speciation acting as an isolating reproductive barrier. Hybrid individuals combine alleles from different genomes having variable degrees of divergence, holding short- or long-term separate evolutionary histories and likely having deviating regulatory controls and spatiotemporal patterns of development. Therefore, hybridization results in intergenomic conflicts (genomic shock) where alleles at different loci do not interact well and exhibit altered expression patterns (transcriptomic shock) and a variety of abnormal developments leading to hybrid incompatibility.[43] Similarly, polyploidy, that is, the concurrence of more than two genome sets in a cell, can display the same irregularities owing not only to the interaction of divergent genomes (e.g., in alloploidy, when polyploid formation involved hybridization of species) but also due to dosage effects and changes in the molecular stoichiometry of molecules and macromolecular complexes (e.g., in autoploidy, when polyploid formation involved individuals from the same or different populations with similar or slightly similar genomes).[44] Another condition that may drive to comparable modifications at molecular level is in breeding. Selfing and sib mating increases homozygosity and accumulate mildly deleterious alleles, and

components of reproduction	Sexuals biparental	Automicts uniparental	Hybridogens hemiclonal	Gynogens clonal	Parthenogens clonal
meiotic recombination	+	+	-	-	-
chromosomal reduction*	+	+	+	-	-
fertilization	+	-	+	+	-
ploidy restoration	needed	needed	needed	not needed	not needed
embryogenesis progression	sperm-dependent	sperm-in(dependent)	sperm-dependent	sperm-dependent	sperm-independent
non-recombinant genomes†	0 (zero)	0 (zero)	1 (one)	2 (two)	2 (two)
		Automicts uniparental	Uniparental genome loss	Pseudogamous apomicts	Autogamous apomicts

FIGURE 1 Recurrent modification of components of sexual reproduction observed in asexual organisms. The graph shows the increase in the number and complexity of developmental changes required in each reproductive category (occasional occurrence of deviations on reproductive components in each category is expected but not included here; e.g., kleptogenesis). In automictic species, meiotic recombination and chromosomal reduction are not affected, but fertilization is skipped by different mechanisms that restore the ploidy. In hybridogenetic species, the paternal chromosomes are eliminated during the formation of gametes, and the offspring inherit only the maternal chromosomes. Fertilization by a male donor restores ploidy and enables embryo development. Gynogenetic and pseudogamous apomict species are also sperm-dependent because they still require fertilization to trigger the parthenogenetic development of the diploid egg physiologically but need to skip meiosis to retain the ploidy of the genome. Sperm-independent embryogenesis of unreduced eggs occurs in apomictic invertebrates, parthenogenetic vertebrates and autogamous apomict species. *it refers to the formation of gametes carrying half the number of chromosomes of the mother. †Based on a potential parental contribution of up to two genome sets ($2n;n = 1x, 2x…ix$) to the offspring. In the case of automicts, both genomes behave like nonrecombinant once fully homozygosity has been reached.

might well cause aberrant sexual developments (e.g., different forms of automixis), an important factor in invertebrates with low vagility (e.g., cladocerans, acari, insects), wherein low level of genetic variation in local populations and several asexual lineages are known.

Hence, individuals under the above genetically diverging conditions (hybridization, polyploidy, or endogamy) often display highly reduced fertility or sterility owing to malfunction of cellular and molecular components of sexual reproduction, for example, meiotic recombination and fertilization.

Whenever reproduction can proceed in those conditions, the resulting lineages will gradually ameliorate gene expression and developmental patterns to recover sexual functions and fertility.[45] Alternatively, a new hybrid, polyploid, or endogamous organism might produce offspring under a paucity or lack of sexual recombination. However, in such a case, since sexual reproduction is a complex, highly regulated mechanism involving multiple developmental steps and cell types, these organisms require a unique combination of changes in particular sets of genes able to disrupt the cellular mechanisms of meiosis and gametogenesis, and affect discrete

components that loose sexual restrictions and simplify the formation of clonal or hemiclonal offspring (Figure 1). Mating independence may well be an example of loose sexual restrictions in animals and plants.

The genetic and epigenetic composition of such new asexual offspring will depend upon the components of sexual reproduction modified. Hence, we rationalize that in order to maintain an asexual condition a new lineage must meet two conditions, *id est* the particular set of gene states for asexuality have to remain unchanged at least in one genome and affect complementary reproductive modules (Figure 1). Having a nonrecombinant genomic assemblage is a *condicio sine qua non* to retain that particular gene combination and epigenetic states needed to modify the sexual program and to transmit it unaltered to the offspring. Hence, in this frame the "sexual hang-ups" of Maynard-Smith can be pictured not as difficult to overcome by selection but rather as a consequence of recombination most likely segregating such particular genetic setting and disassembling the molecular basis for asexuality. The second condition linked to the emergence of an asexual lineage, the one of "complementation" between altered components of the sexual reproductive program, is needed to maintain physiologically and

genetically balanced intergenerational transitions. As an example, in a new asexual in which meiosis is skipped, the unreduced egg shall also avoid incorporating an extra set of paternal chromosomes during fertilization to assure the proper development of offspring.

Consequently, and opposed to sexual organisms, asexuals shall momentarily avoid genetic shuffling and character segregation of reproductive modules, weakening amelioration and purging mechanisms by natural selection. As a result, some asexuals are expected to retain post-hybridization genomic and transcriptomic shock states for more extended periods than under sexual reproduction,[46] likely a reason why asexuals often exhibit lower fitness compared to sexual relatives[47,48] even when they can display superior abilities populating diverse habitats.[49–51] The fact that reproductive tissues of long-existing clonal animals and plants display divergent patterns of gene expression and massive gene dysregulation compared to sexual ancestors (e.g.,[27,52]) support this interpretation.

AN INTEGRATED VIEW FOR ASEXUALS ORIGINS AND MODEL TEST

Under this model, genes related to the development of asexuality and the formation of asexual offspring are expected to segregate together as a unit (either in a chromosome or a genome set). Even when such genetic assemblage can be uniform due to the lack of recombination, initial allelic variations in genes affecting reproduction may occur mainly because of the phase of establishment and developmental stabilization of the asexual lineage.

Getting the right combination of genes and genetic modifiers altering reproductive steps (without affecting other developmental programs) into a nonrecombinant genomic assemblage able to complement reproductive changes and produce physiologically balanced asexual offspring may require more than a single attempt. Whenever a new asexual individual fulfilling the two above conditions arises, it may carry the genomic combinations required for one or more than one gametogenetic mechanism and show a variable incidence of different reproductive modes, including sexuality (i.e., facultative parthenogenesis). During the first generations after the initial asexual event, the new lineage will suffer from cytogenetic and molecular stabilization of reproductive pathways.[7,22,46] The new lineage (either hybrid and/or polyploid or endogamic) will likely exhibit low coordination of gene expression and altered reproductive developments causing low reproductive efficiency (fitness). Such patterns have been observed in different recently established organisms exhibiting asexual reproduction or tendencies to asexuality.[32,53] Later, occasional recombination and sex in these individuals may play a pivotal role for fine-tuning the efficiency of any reproductive mode and contributing to alleviate a reversal to the sexual program or to establish a persistent asexual lineage.[46] In nature, different animal and plant groups display a variable incidence of alternative reproductive modes and patterns of clonal diversity.[24,41,42] This may well represent a consequence of different developmental outcomes derived from merging particular genomes combining specific gene variants and genetic backgrounds

and denote distinct stages in the evolution of such asexual lineages. This implies that, once the parental species with the right genomic combinations met the appropriate ecological setups in nature, the chances for the emergence of lineages with tendencies toward asexuality will be high. Thus, on a short-time scale, asexual lineages might arise multiple times and show developmental variations of reproductive modes (as observed in many asexuals, see below). Sooner or later, and mainly driven by fertility, surviving aptitudes and – in specific cases – occasional gene flow (introgression), selection will sift the more reproductively effective lineages and those carrying complemented mechanisms for asexuality will likely become established and persist.

Thus, this model introduces a genetic and developmental frame for the emergence of alternative types of asexuality and predicts parallelisms among groups (Figure 1, see discussion below).

From a cytological viewpoint, the puzzling complexity of sexual-asexual transitions in different groups and the occurrence of multiple types of asexual developments sporadically observed in single lineages of animals and plants can be explained as a consequence of genomic and developmental constraints during the first generations to the establishment of an asexual lineage. Depending upon the modified genes and stabilized reproductive modules, incomplete loss of sex and alternative forms of asexuality are possible in the same species or genus. The model also predicts the emergence of automictic forms whereby meiosis but not fertilization is kept functional in the new asexual lineage. Unlike highly heterozygous clonal organisms bypassing meiosis, automicts with functional meiosis would maintain the nonrecombinant assemblage through homozygosity and genetic co-segregation. Moreover, since automixis may not retain heterozygous gene copies likely needed for a shift to sexuality, automictic lineages evolving into cyclic parthenogenesis systems should be rare.

From an evolutionary viewpoint, chances for single (monophyletic) or multiple (polyphyletic) origins are not neglected, despite a likely higher probability of recurrent origins in parental species with the right genomic setting. In either case, the model predicts possible genetic and developmental variability, including the appearance of polyploids during the stabilization of the new asexual lineage. Post-establishment recombination events among genes of the asexual assemblage would lead to loss of reproductive complementation and asexual instability, including bias from (homozygous or heterozygous) clonal developments, low fertility, and extra ploidy shifts. However, recombination among genes not involved in the control of reproductive modules leading to parthenogenesis shall not be impeded, and even in low frequencies, could help clonal lineages to purge some of the mutational load and adapt to the environment.

Overall, the present model can (1) explain the occurrence of alternative asexual developments and lineages exhibiting single or multiple stabilized modes of parthenogenesis, (2) provide a logical frame for the origin and evolution of asexuals' complexity from sexual parents, including automixis and polyploid forms, and (3) remove the focus of asexuals' rarity as a consequence of genetic degradation and place no limit to the age of asexual lineages.

NOT ALL ROADS LEAD TO ASEXUALITY: THE NATURAL EVIDENCE

Invertebrates show the widest diversity of asexual types

Invertebrates present the most diverse collection of genetic systems, in particular insects being known for their remarkable variation.[42] Here, we will focus on a few well-documented examples of relevance to the case being made.

Despite automictic species not producing clonal offspring and showing different genetics, the evidence also points to a modular flexibility and a developmental connection to apomixis. For instance, in the automictic bagworm moth *Dahlica triquetrella*, meiosis can proceed without recombination, and different populations show variable levels of development and fertilization of parthenogenetic eggs.[35] The data suggest a transition from bisexual diploids to variable automixis in diploids, and stabilized automixis in tetraploid populations. In insects, the gradual (or direct) evolution from systems wholly or partial amphimictic to obligate all-female systems, including transitions likely to be reversible,[42,54,55] support the present hypothesis of increase in complexity of asexuals.

In all-female (thelytokous) systems, clonal parthenogenetic females are produced through apomixis, but also by sperm-dependent thelytoky through gynogenesis and hybridogenesis.[42]*Otiorhynchus* spp. is a genus of curculionid beetles showing diploid sexuals and diploids, triploids, and tetraploids with apomictic parthenogenesis. Transition from obligate sexuals to obligate asexuals are likely irreversible.[42] The distinct evolutionary histories observed in different clonal populations, including diploids and polyploids of hybrid origin in *O. scaber* and clonal autopolyploid *O. sulcatus*,[56] show that different genomic combinations and associated ploidy transitions play an important role in stabilizing asexual lineages with alternative developments.

Likewise, in root-knot nematodes, the observation of a hybridization event predating the origin of multiple asexual *Meloidogyne* species fits this view. Post-hybridization, *M. floridensis* retained diploidy and the ability to carry out meiosis in a form of automixis, while all other four species including *M. incognita* shifted to triploidy and acquired an apomictic strategy.[57] Since then, homeologs in the genomes of these apomicts have diverged, but in the automict most homeologs have been lost.

Similar evidence comes from stick insects. In *Bacillus* spp., two obligate sexual diploid species (*B. rossius* and *B. grandii*) have hybridized and produced allodiploid *B. whitei* and allotriploid *B. lynceorum*, both the lytokous parthenogens, and the hybridogenic *B. rossius-grandii benazzii*.[58]Attempts to resynthesize the hybridogenetic species in laboratory conditions had failed, but crosses between hybridogens and different males show the sporadic formation of all-paternal and gynogenetic offspring, and some crossing combinations display a progressive disruption of the hybridogenetic system toward thelytoky. The thelytokous species *B. whitei* had apparently derived from an hybridogenetic *B. rossius-grandii benazzii* ancestor.[58]

The frequent observation of introgression from sexual lineages[59,60] and the rare occurrence of cyclic thelytoky (i.e., species that can alternate between sexual and all-female asexual systems) observed in animals (only eight origins[42,61]) can be a response to environmental variations (e.g., by temperature-sensitive gene expression changes) restabilizing temporally or shortly functional meiosis (and formation of males). Since only clonal (nonrecombinant) organisms (all above cases but automixis) may keep genomic copies to functional meiosis and fertilization, the fact that all systems with cyclic parthenogenesis involve clonal developments[42] further supports the present hypothesis. Reproductive polyphenisms and environmental modulation of meiosis are known in asexual animals and plants.[14,48] Sporadic occurrence of meiosis would only require avoiding genetic segregation (or assuring cosegregation) of the asexual genetic assemblage in the new offspring.

Vertebrates require the right genomic combinations for stable asexuality

Among vertebrates, a good example of such variation is the Iberian fish *Squalius alburnoides*. In this species, a wide range of parallel reproductive strategies from syngamy to gynogenesis and altered patterns of hybridogenesis – including paternal leakage – are combined to create a complex of diploid, triploid, and tetraploid populations interacting with closely related sexual species. The production of gametes with or without meiosis is strictly depending on the combination of haplomes[62] – showing the importance of the right genomic conditions to warrant an asexual mode of reproduction – and pinpoint the potential to switch between reproductive modes if the genomic background and ecological conditions are met.

In the fish genus *Poeciliopsis*, diploid hybridogens of different genomic combinations exist. Hybridogens can accommodate various sexual haplomes transiently, but it is only the *P. monacha* haplome, common to all asexual lineages that can dominantly impose the reproduction mechanism of hemiclonality.[63]Occasional failure of the meiotic mechanism responsible for the elimination of paternal chromosomes in diploid hybridogenetic biotypes had given rise to triploid gynogenetic biotypes where the sperm is only needed to induce embryogenesis.[64]

In salamanders, gynogenesis is not complete, and the female genome routinely incorporates genetic information from sympatric sexual male donor DNA into their diploid or polyploid genomes,[41,65] a mechanism named kleptogenesis.[66]This might benefit the lineage with an exceptional longevity[67] because it can counteract the genomic decay and low genetic diversity by bringing in new genetic information. Like kleptogenesis, tychoparthenogenesis – the occurrence of sporadic parthenogenesis in sexual species – is unusual among asexual lineages,[7] and both represent weird cases in which selection driven "complementation" is achieved through incomplete or temporal functional alteration of components of the sexual reproductive program. So-called "facultative parthenogenesis" – well known from enigmatic cases where single females of sharks, snakes and Komodo

dragons sired offspring after being deprived from males for extended periods – may represent SOS mechanisms rather than natural reproductive strategies. Producing diploid eggs, for example, through automixis,[68] orapomixis in those cases could be due to stochastic gene expression variation or epigenetic changes. Whether there is an adaptive mechanism behind these accidental cases, and if those lineages would be more prone to provide the genomic pre-condition for asexuality are interesting questions.

The importance of the right genomic combinations is supported by crossing experiments between the parental species that once gave rise to the gynogenetic *Poecilia formosa*. In the interspecific hybrid females, the majority of the oocytes have meiosis problems and are diploid.[69] While in the experimental situation these oocytes are fertilized to give rise to triploid offspring, the missing step to fully established gynogenesis is then just the suppression of karyogamy. Similarly, while finding the right genome combination to synthesize hybridogenetic fish of *Poeciliopsis* and *Pelophylax* frogs in the laboratory was after many attempts finally successful, in almost all other cases the many efforts to produce unisexual lineages from crossing the known parental species failed (see Choleva et al.[70]). In nature, however, long-term attempts obviously have recurrently delivered in some species the right genome combinations transitioning to asexuality, as diverse assemblages of asexual lineages have arisen on multiple separate occasions.[39,71–76]

Plants fine-tune asexuality through polyploidy and supergenes

In plants, support to the current hypothesis comes from embryological, molecular, and genetic evidence indicating that apomixis is induced in diploids by genomic and transcriptomic shocks initiated after inter- or intra-specific hybridization and is stabilized by a rise of ploidy, thus creating allo- and auto-polyploids (for a detailed discussion see Carman,[22] Hojsgaard,[46] and Hojsgaard and Hoerandl[77]). The observed hemizygosity of the genomic region for apomixis in autopolyploids[78] implies that a single haplome might be sufficient to cope with the mentioned conditions to establish an asexual lineage. However, modifier factors and gene dosage compensation are likely needed to stabilize apomixis functionally as most apomicts are polyploids, and so far the only documented diploid apomict belongs to the *Boechera holboellii* complex, a relative of *Arabidopsis thaliana* showing diploid sexuals, and diploid and triploid apomictic populations.[27] Nonrecombinant genomes in apomicts must combine a particular genomic setting and gene states to restrain the sexual pathway bypassing meiosis (i.e., apomeiosis) and initiating embryogenesis (parthenogenesis), and at the same time developing the seed nourishing tissue (the endosperm).

As in animals, plants exhibit variations in the incidence of developmental pathways. Some asexual species show sporadically more than one type of apomixis (i.e., diplospory, apospory, adventitious embryony)[30,79,80] and/oroccasional noncomplementarity between reproductive components causing, for example, a decrease or an increase of ploidy in the progeny of apomicts after developing seeds

from haploid gametes (i.e., haploid parthenogenesis) or from fertilized unreduced gametes (i.e., B_{III} hybrids).[24,78] All natural apomicts studied so far show major shifts in gene expression, the extent and patterning of which require further investigation. Such regulatory changes in gene expression – many related to germ cell specification, meiotic progression and gametogenesis[81] – are associated to temporal and spatial developmental asynchronies, and are subjected to environmental modulation (e.g., in *Boechera* spp.,[27,28,33]; in *Brachiaria* spp.,[82]; in *Eragrostis* spp.,[83,84]; in *Hieracium* spp.,[29,85]; in *Hypericum* spp.,[86,87]; in *Panicum* spp.,[88]; in *Paspalum* spp.,[34,48,89–91] in *Pennisetum* spp.,[31,92]; in *Poa* spp.,[93]; in *Tripsacum* spp.,[26]; in *Ranunculus* spp.,[3,32,94–97]).

Asexual plant lineages had also been resynthesized experimentally in rare cases[98] and multiple independent origins had been identified in natural populations (e.g.,[99–101]). Occasionally, these apomictic polyploids retain a low level of functional sexuality (i.e., facultative apomixis), which might depend upon the genetic background and the ecological environment[89,95,102,103] as well as the evolutionary age of the asexual lineage. Recently formed asexuals exhibit more dramatic changes in gene expression, developmental alterations, and reduced fertility, including noncomplementarity in the alteration of sexual components and comparatively lower levels of apomixis than older natural lineages.[3,32,96] The older the asexual lineage, the higher the efficiency of apomixis and the harsher the depletion of sex. Except for those regions within the genome associated to apomixis that do not recombine and provide stability for the asexual state, the haplomes of old apomicts are expected to display signatures of sporadic sex and chromosome repatterning. Therefore, functional shifts in components of sexual reproduction can be linked to genomic regions behaving as supergenes (in which even individual genes can be identified) rather than to complete haplomes.[78,104–109]

The above-stated conditions and the developmental and molecular evidence present in asexuals do not neglect the different hypotheses on asexual origins. In fact, they all agreed with the different standpoints and theoretical frames of each hypothesis and suggest a common molecular basis for asexuality. The "sexual hang-ups" from Maynard-Smith emphasize the consequences of shifting out of sex and indirectly, point to the implications of having recombination between genetic sequences responsible for altering reproductive components. The "balance" hypothesis from Moritz and co-workers points indirectly toward the need of complementation of reproductive components to have a functional asexual organism, while the "rare formation" hypothesis from Warren and co-workers, the "duplicate-gene asynchrony" and the "polyphenism" hypotheses from Carman and co-workers put more weight on a probable molecular basis, giving different relevance to genetic and epigenetic contributions.

A MODULAR DEVELOPMENTAL FRAME AND ITS EVOLUTIONARY PERSPECTIVE

In all cases of asexuality, the asexual state creates a self-propagating condition that is central for their establishment and maintenance (Figure 2).
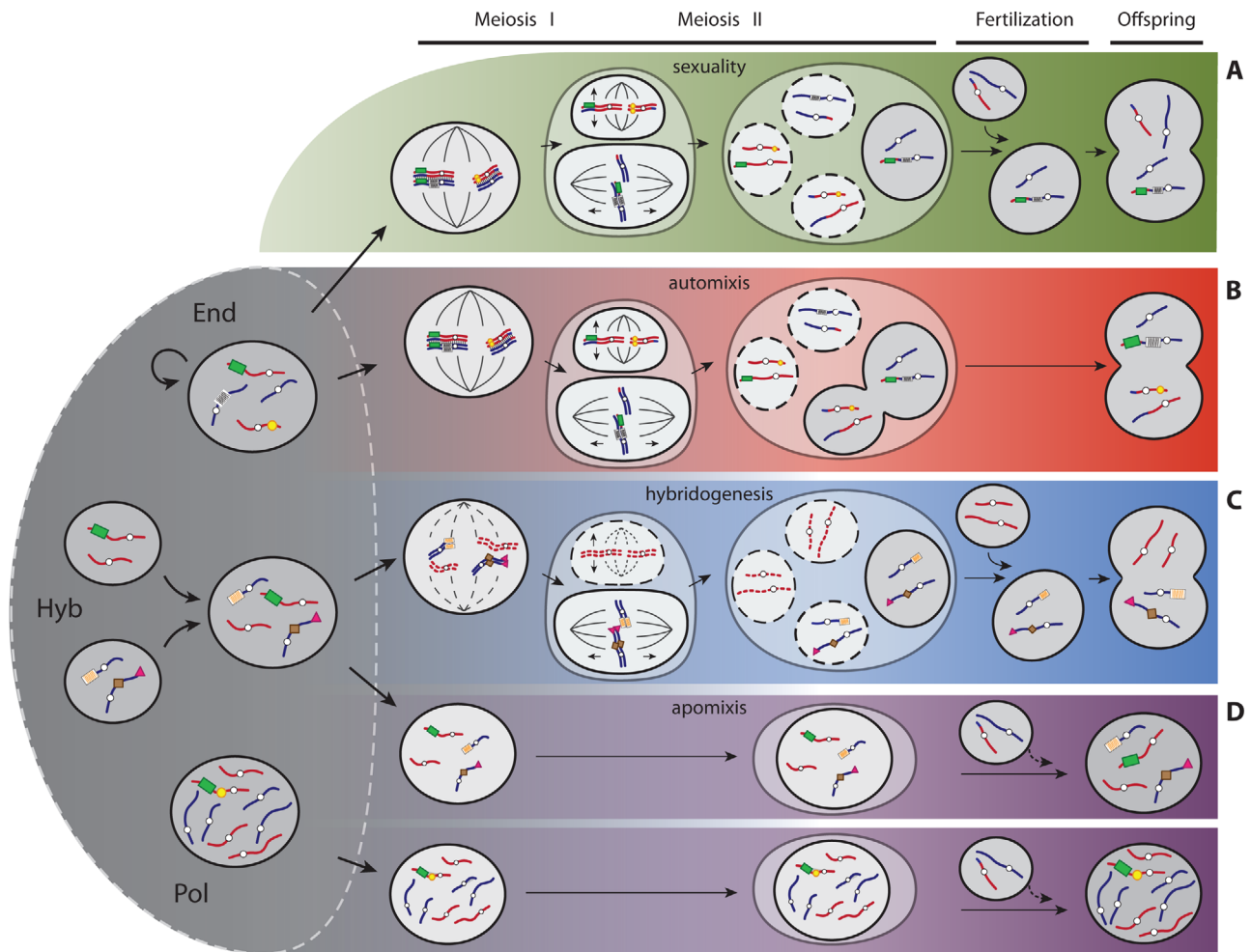
FIGURE 2 Representation of reproductive changes that lead to asexual states based on three main life history conditions (End = endogamy; Hyb = hybridization; Pol = polyploidy). Only specific genomic settings that lack recombination (either the mechanism or its functional consequences) are able to self-replicate themselves and persist along evolutionary times. In the case of a sexual event occurring in an asexual lineage (**A**, green pathway), asexuality might be destabilized (the genomic state required for asexuality is not recovered, as in the example here) or fine-tuned (the genomic state is recovered plus other recombined genomic regions) depending upon the combined gametes. Main changes in asexual pathways relate to alterations in meiosis and fertilization, the two steps involved in the exploitation of variability. Coloured geometric figures on chromosomes represent genetic changes modifying reproductive modules and their complemented states observed in each asexual type: (**B**, red pathway) normal meiosis but modified fertilization in automictic individuals, whereby two gametes from the same meiosis fuse and develop into an organism that acquires full homozygosity in one or few generations; (**C**, blue pathway) modified meiosis during hybridogenesis, whereby the paternal chromosomes are eliminated before, during or after meiosis, and the gamete carrying nonrecombinant female chromosomes is fertilized every generation (the graphic is only illustrative and does not imply a mechanistic representation; see text for more details); (**D**, purple pathway) modified meiosis during apomixis (gynogenesis and parthenogenesis), whereby meiotic recombination and chromosomal reduction is omitted or altered and the unreduced gametes develop into a clonal organism with or without fertilization triggering the development. Broken line nuclei are non-functional or non-viable.

In automictic species undergoing meiosis but skipping fertilization, the alternative mechanisms to form a diploid egg would lead to homozygosity in one or few generations, and with it, to the transmission of those gene states responsible for automixis in a nonrecombinant-like way. In either case, the stabilization of such development may come after fixing homozygosity at genome level, but it will depend upon the consequences of inbreeding. Variable levels of heterozygosity are expected in automicts depending upon the number of crossovers *per* chromosome arm and generation, the genome size, and the type of gamete fusion.[35,36] Jumping from an automictic (likely highly homozygous) development to a sexual one or one of the clonal alternatives might be triggered by a hybridization event, perhaps reinforced by a ploidy shift. This would explain cases of gain of sexuality in some automictic species[110,111] and provide a reason for most automicts being diploids and the clonal asexual alternatives being of hybrid or polyploid origin.

In the case of apomictic species skipping meiosis, the emergence of an asexual lineage requires nonrecombination on specific genetic

and genomic attributes that usually leads to fixed heterozygosity, and a rarely met complementation on altered reproductive components to stabilize the lineage.

On the one hand, this explains why – once established – asexuality in clonal organisms behaves as a dominant trait, be it in genetic inheritance studies (mainly in plants;[78]), or because asexuals do not give birth to sexuals (mainly in animals;[7]). This is not necessarily due to any individual component of the asexual machinery being dominant over the sexual counterpart but rather because meeting the conditions for asexuality implies unchanged transgenerational transmission of genetic factors, and any recombination event between reproductive factors might modify regulatory mechanisms (e.g., epigenetic signals, cis- or trans- molecular interactions) and disassemble the molecular basis for asexuality. Such transgenerational transmission of factors through males would also explain observed cases of "contagious" acquisition of obligate asexuality.[112,113]

On the other hand, in practical terms, this means that we should observe parallelisms in functional reproductive changes among asexuals from taxonomically and phylogenetically diverse groups. Even though establishing an asexual lineage in plants may require different molecular and cellular interactions compared to animals as well as overcoming diverse ecological constraints (e.g., crowding, starvation, day length), the known asexual animals and plants show in fact intriguing parallelisms in functional aspects and modified components of sexual reproduction (Figure 1), unlikely to be a consequence of chance.

ALTERED SEXUAL MODULES SHOW PARALLELISMS AMONG ANIMALS AND PLANTS

In our analysis, the simplest transition from sexuality to asexuality is represented by automictic organisms, in which fertilization is blocked or skipped (e.g., *Extatosoma* spp., *Dahlica* spp. in insects; *Aspidium* spp. in pteridophytes; *Allium* sp., *Rubus* sp., *Brassica* sp. in angiosperms).[37,38,41,42,114] In all groups, genomic imprinting mechanisms like molecular modifications of centromere proteins (H3 and H4) can induce paternal chromosomal elimination.[115,116] In insects, the elimination of a sex chromosome or the full set of paternal chromosomes is linked to the formation of haploid males in cyclic parthenogens (e.g., scale insects, mites;[42]). In plants, centromere-mediated genome elimination is used to produce maternal haploids,[117,118] and case studies of rapid preferential uniparental chromosome elimination in wide-cross hybrids (e.g., *Avena sativa* × *Zea mays*) show changes on reproductive components alike those in hybridogenic animals (Figure 1). However, this mechanism is neither recurrent nor stable in nature and so far, a system fully equivalent to that of hybridogenetic animals has not yet been discovered in plants. In hybridogenic insects and vertebrates the paternal genome is active in the soma of the offspring and only eliminated during gametogenesis.[119] In hemigamous plants, the sperm enters the egg cell but karyogamy (the fusion of sperm and egg nuclei) does not happen, and the male nucleus and its derivatives are often excluded during embryo patterning and hence paternal chromosomes do not participate in the genetic make-up

of the offspring.[120,121] The majority of polyploid apomictic plants are pseudogamous (e.g., *Hypericum* spp.; *Paspalum* spp.; *Ranunculus* spp.), often tetraploids, and display functional changes in the sexual reproductive program equivalent to those of gynogenetic animals (e.g., *Ips* spp.; *Poecilia* spp.) (Figure 1). The combination of specific genomic modifications in pseudogamous apomicts allows them to annul the consequences of meiotic recombination and chromosomal reduction, while sperms are used to initiate the endosperm and thus stimulate embryogenesis and completion of the development of a functional seed. Finally, autogamous apomictic plants (e.g., *Antennaria* spp.; *Hieracium* spp.; *Erigeron* spp.) alike parthenogenetic animals (e.g., *Daphnia* spp.; *Otiorhynchus* spp.; *Timema* spp.; *Darevskia* spp.; *Aspidoscelis* spp.) became free of the requirement for sperm fertilization, and the offspring is produced without male contribution (Figure 1). These asexuals are tightly associated with polyploidy (mainly triploids but also tetraploids) and represent the most extreme cases of asexuality. Particularly in animals, polyploids are likely by-products of the process of stabilization of reproductive modes and the transition between sexual and asexual strategies in newly formed hybrid lineages. In plants, however, polyploidy is frequent and most polyploids are sexual though a potential role of transient activation of apomixis in the establishment of sexual polyploids shall not be discarded.[46]

This model of nonrecombinant genomic assemblages and complemented reproductive components can also help us explain the occurrence of asexuals of very dissimilar ages. As the initial stage of establishment of a new asexual is the most critical one, the model anticipates that many asexual lineages will have an ephemeral lifespan and be short-lived. However, the likelihood of asexuals being much older than expected is also anticipated and hinges critically on the quality of the reproductive complementation and developmental lability (or its flexibility to incorporate variability and fine-tune reproductive fitness) of the asexual lineage.

We reason that the number of reproductive components and complexity of their molecular interactions needed during formation of an asexual organism increase from automictic invertebrates/plants and hybridogenetic vertebrates to gynogens/pseudogamous apomicts, and to apomictic invertebrates/parthenogenetic vertebrates/autogamous apomicts (from left to right in Figure 1). This increasing complexity also reflects a conceivable evolutionary direction for asexuals and thus places the possibility of transient reproductive states displaying more than one reproductive mode (as discussed above). The increase in complexity implies a rise in the rarity of complementation between reproductive components, and thus, a progressive decrease in the proportions of asexuals observed for each category is expected. In nature, such a rare complementation might have the additional challenge of meeting the right ecological setup, a concurrence not easy to replicate instantaneously under experimental conditions. This may explain why obtaining a first-generation clonal hybrid is much harsher than crossing extant clonal hybrids.[23,122] Anyhow, as anticipated, hybridogens are more frequent in nature and "easier" to replicate under experimental conditions than gynogens or parthenogens.[7,70] Similarly, in plants, pseudogamous apomicts are much more frequent than autogamous apomicts. In nature, a reproductive system

analogous to that of hybridogensis unmet in plants. Plausible reasons are likely connected to differences in their reproductive biology (e.g., frequent hermaphroditism, development of a gametophyte, double fertilization and parallel development of embryo and endosperm tissues), timing of germline specification, and epigenetic resetting of maternal and paternal chromosomes (genomes) compared to animals.[123,124]

CONCLUSIONS AND OUTLOOK

Genomic and developmental restrictions imposed both by gene inter-actions, physiological responses, and ontogeny of sexual processes hamper the evolution of asexuality in all living groups. In both plants and animals, the first generations after the initial asexual event have drastic consequences on retaining specific genomic combina-tions needed to stabilize reproductive modes and assure the lineage's subsistence. Stabilized asexual reproduction requires a cytological complementation of the altered modules and its specific genomic assemblage to be transmitted unchanged. The observed variability in asexual patterns suggests that in many cases asexuality is not yet evolutionarily stabilized. The higher the complexity of cytologi-cal mechanisms inducing asexuality, the lower the chances of putting together in a new individual the required genomic combinations. While genomic decay is a long-term force acting upon asexuals, their rare occurrence may well be determined by the stochastic chance of con-verging and maintaining the appropriate genomic combinations and reproductive complementation rather than by a short-lived fate. As implicitly exposed in many previous works, discussions of asexual lin-eages in the future should emphasize the likelihood of their formation based on biochemical and molecular mechanisms rather than on specu-lative discussions concerning shorter lifespans or degenerating fitness benefits.

DATA AVAILABILITY STATEMENT
Data sharing is not applicable to this article as no new data were cre-ated or analyzed in this study.

CONFLICT OF INTEREST
The authors declare there are no competing interests concerning this study.

AUTHOR CONTRIBUTIONS
DH conceptualized and designed the study, collected data, drafted the manuscript, and prepared the figures; MS collected data and helped draft the manuscript. Both authors gave final approval for publication and agree to be held accountable for the work performed therein.

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