Sexual and Asexual Processes in Reproductive Systems of Flowering Plants

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In understanding ontogenesis it is important to elaborate some aspects of the theory of flowering plant reproduction. As a result of critical analysis of the literature and original data, the unification of some concepts and terms is proposed. The terms "sexual" and "asexual" in reference to flowering plants should be used to characterize only the mode of formation of new individuals (with or without the participation of meiosis and gamete fusion). The concept "multiplication" is defined; it should denote an increase of the number of descendants, whereas the formation of a new individual, regardless of mode, is the meaning of the term "reproduction." The various modes of formation of the individual (sexual, asexual), morphogenetic pathways (embryogenesis, embryoidogenesis, gemmorhizogenesis), types of multiplication (seed, vegetative) and the correlations between them are described. Special attention is paid to the attributes of stem cells and their role in plant reproduction. Theoretical questions concerning such phenomena as polyembryony and genetic heterogeneity of seeds in plants are examined.

Key words: Sexual and asexual processes, morphogenesis, stem cells, seed and vegetative multiplication, vivipary, embryoidogeny, polyembryony, modes of reproduction.

A GENERAL LOOK AT REPRODUCTION AND MULTIPLICATION IN ANGIOSPERMS

An eminent biologist (Grant, 1981) emphasized the importance of studying the sexual process and reproduction for an understanding of the evolution of certain taxa. Considering reproduction in the broad sense, nevertheless he distinguished the concepts "reproduction *per se*" and "multiplication." According to him, reproduction *per se* "is the indispensable condition for perpetuation of the species through the succession of generations and hence over any prolonged period of time. And it is the only means of multiplication, increase in numbers, and colonization of new territories" (Grant, 1981). The peculiarities of reproduction inherent in plants are not so diverse as the ones inherent in animals, mainly because of their immobility and autotrophy. Thus, reproduction and multiplication are the main features of living beings.

The Italian scientist Battaglia (1947, 1963) examined the problems of amphimixis and apomixis in the general system of flowering plant reproduction. Organisms may give rise to the same phase (sporophyte from sporophyte) or the antithetical phase (sporophyte from gametophyte). From this point of view, he subdivided reproduction into homophasic (repetition of the same phase) and heterophasic (repetition of the antithetical phase). In this connection, Battaglia suggested using two different terms: "reproduction" (for a heterophasic increase in number) and "multiplication" (for a homophasic increase). In the concept "multiplication" (homophasic reproduction) he included not only sporophytic multiplication (adventive embryony) but also vegetative multiplication (by means of bulbs, bulbils, runners, etc.). In line with Battaglia (1947, 1963) and Grant (1981), regarding the concepts "reproduction" and "multiplication" I consider that "reproduction" should refer only to the mode of formation of a new individual (sexual and asexual). The concept "multiplication" (= propagation) is reasonably used when talking about the increase of progeny number, regardless of the mode of their formation (Batygina, 1992). In addition, I regard sporophyte multiplication (via adventive embryony) to be a variety of vegetative multiplication, as vivipary is.

There are contradictory points of view about the concepts of "sexual" and "asexual" reproduction in angiosperms (Batygina and Vasilyeva, 2002).

The sexual process in typical form is usually treated as the fusion of two generative cells (gametes) and the formation of a zygote (Fig. 1). The interpretation of the concept "sexual process" in angiosperms often does not consider one of the key periods (phases), that is, meiosis. However, some authors stress the importance of considering meiosis in studies of the sexual process.
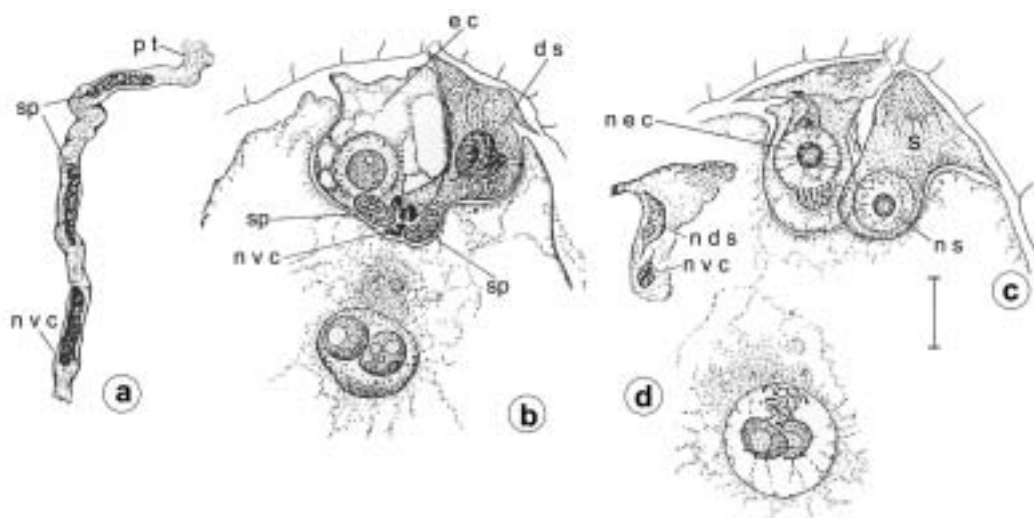
Fig. 1. Double fertilization in *Scilla sibirica*. (**a**) Pollen tube with sperms and nucleus of vegetative cell entering the ovary cavity, (**b**) Upper part of embryo sac after pollination: pollen tube has just discharged its content into the extracellular gap between the egg cell and central cell, with one of the synergids degenerated and with sperms and vegetative cell nucleus visible, (**c**) Male nuclei immersed in female nuclei, with intact synergid at right, (**d**) Degenerated synergid with its nucleus and vegetative cell nucleus. ds – degenerated synergid; ec – egg cell; nds – nucleus of degenerated synergid; nec – nucleus of egg cell; ns – nucleus of synergid; nvc – nucleus of vegetative cell; pt – pollen tube; s – synergid; sp – sperm. Bar = 20 μm (after Batygina and Vasilyeva, 2001).

Mogie (1986) discussed the biological and genetic sense of the sexual process in connection with the phenomenon of automixis. He suggested including in this concept all reproductive processes in which fusion of nuclei occurs, regardless of the origin of these nuclei (whether they originate as result of single or multiple meiosis).

Fincham (1983) excludes the fusion of the sperm cell with an unreduced egg cell from the sexual process. Harlan and de Wet (1975) supposed this phenomenon, occurring sporadically due to meiotic aberrations in the majority of organisms, to be very important for the phylogeny of plants. This is the usual way of polyploidization in plants, as most authors suggest.

Thus, not only gamete fusion but also meiosis in all its known forms must be included in considerations of the sexual process.

The sexual process does not cause an increase of the number of individuals; it should be defined as one of the modes of reproduction, but not of multiplication. The increase of sexual progeny is ensured by the large number of ovules, pollen grains, gametes and zygotes.

Asexual propagation can be realized through spores, vegetative parts, organs and separate cells of the plant (vegetative multiplication). Multiplication through spores is characteristic for the Algae, Bryophyta, Lycopodiophyta, Equisetophyta and Polypodiophyta. Asexual multiplication usually is not considered in flowering plants. Indeed, spores lost their main function related to multiplication and dispersal in the course of angiosperm evolution. Nevertheless, it is worth noting that such potencies (reserves) are still retained in natural as well as experimental conditions. Thus, in specific cases (some forms of apospory and diplospory in the case of apomixis; the homopolar tetrad of megaspores) an increase of the number of descendants is enabled by embryos arising in the embryo sacs, which form from additional megaspores (Noher de Halac and Harte, 1977; Czapik, 2000). The switching of the microspore developmental program to the sporophytic pathway of development, causing the formation of new individuals through somatic embryos, occurs under the influence of some factors in culture in vitro (Góralski et al., 1999, 2002a,b; Kruglova et al., 2005).

STEM CELLS AND POLYVARIANCE IN MORPHOGENETIC PATHWAYS

Plants are autotrophic organisms possessing a stationary mode of life. This determines their evolutionarily advanced and manifold propagation modes and pathways. The plasticity of plant development and reproduction is connected with the various activities of plant somatic cells, particularly stem cells (Batygina et al., 2004).

The concept "stem cell" is controversial in botanical as well as in zoological and medical literature. The problem of plant stem cells can be traced to research on the special meristem, designated by various terms: "dormant meristem" in the leaf (Yarbrough, 1932), "expectancy meristem" or "dormant meristem" in the

ovule (Batygina and Freiberg, 1979; Batygina, 1991, 2002), "quiescent center" in the root apex (Clowes, 1954) and "*méristème d'attente*" in the shoot apex (Buvat, 1955). For its clarification, ideas from investigations of human and animal stem cells are required (Thomson and Marshal, 1998).

Most investigators refer to plant stem cells as part of apical shoot and root meristems (Clark, 1997; Weigel and Jürgens, 2002; Groß-Hardt and Laux, 2003; Ivanov, 2003). Such a standpoint emerged obviously because the research did not include the first stages of ontogenesis, namely the specifics of the embryonal period. Analysis of embryogenesis in numerous flowering plants leads to the conclusion that the shoot and root apical meristems are derived from the zygote – the progenitor of stem cells (proximate stem cell; Barlow, 1997). Thus, stem cells represent not part of the apical meristem, but its source (Batygina et al., 2004).

Study of the reproductive biology and especially the comparative embryology of representatives of different flowering plant taxa shows that stem cells can arise not only in shoot and root apices (*méristème d'attente* and quiescent center). The formation of stem cells derived from the zygote appears to be characteristic for all organs (flower, stem, leaf, root) and for all stages of the life cycle (sporophyte, gametophyte). Moreover, it depends primarily on their localization and destination. It should be emphasized that not only the zygote but also the somatic cell are the initial cells of the plant rudiment.

The initial cells of somatic embryos (embryoids) of different origins in natural conditions and in culture in vitro should be regarded as stem cells. Therefore the study of a special category of vegetative propagation, embryoidogeny, acquires special significance (Batygina et al., 1978, 1996; Batygina, 1989, 1993, 2005). It is the initial cell (zygote or somatic cell) from which the process of embryogenesis and embryoidogenesis begins, involving essentially the organization of the shoot and root apical meristems of the future plant.

Such processes may occur at the various stages of ontogenesis and in all structures, for example the formation of somatic embryos from the epidermal cells of the sexual embryo (new sporophyte) in *Paeonia* (Batygina, 1997a). The phenomenon of gametophytic apomixis, widespread among the angiosperms, is the initiation of somatic embryo development without fertilization from the egg cell or synergid, that is, from female gametophyte cells. The multiplicity of these processes is due to the diversity of embryo sac structures and origins. The plasticity of the cells of maternal plant generative structures (*Poa*; Batygina, 1991) allows somatic embryos to be formed from the nucellus or integument. In these cases the cells of the somatic embryo can develop in the niche of the sexual embryo, that is, in the endosperm and gametophytic cells. The plasticity of the leaf tissues (*Bryophyllum*; Batygina et

al., 1996) enables somatic embryos to be formed from a single cell or group of cells (dormant meristem = stem cells); repetition of early ontogenesis stages takes place in tissues of the adult plant.

A survey of the literature (Clark, 1997; Barlow, 1997; Weigel and Jürgens, 2002; Byrne et al., 2003; Ivanov, 2003) and original data indicate the following features as the main characteristics of stem cells:
1. Totipotency, the capacity to form different tissue and organ types as well as new individuals through various morphogenetic pathways such as embryo-, embryoido- or gemmorhizogenesis;
2. Self-maintenance, resulting in the production of a pool of cells by symmetrical divisions and intracellular interactions;
3. The capacity to proliferate and produce cell precursors of different tissue types ("niches") owing to asymmetrical divisions under the influence of definite signals;
4. The rhythmic and multistage character of formation of tissues or organs, and the capacity to switch over the developmental program through different molecular/genetic mechanisms (Batygina et al., 2004).

Models of stem cell functioning are seen not only in proliferation but also in different modes of individual formation (sexual, asexual), morphogenetic pathways (embryogenesis, embryoidogenesis and gemmorhizogenesis) and multiplication types (seed, vegetative). These peculiarities of reproduction appear to be connected with the stationary mode of life of plants.

The totality of such stem cell properties as totipotency, self-maintenance, the rhythmic and multistage mode of formation, and especially the capacity to switch over developmental programs, ensures reliable maintenance of plants at the various stages of ontogenesis.

The active use of in vitro culture methods has renewed interest in a number of unsolved problems in morphogenesis, reproduction and multiplication, already much examined in classical morphology. For example, does parallelism always characterize the development of sexual and somatic embryos developing in natural conditions and in culture in vitro (Batygina, 1998, 2004)? What is the mechanism of the sporophyte → gametophyte transition?

As is well known, the formation of a new individual in flowering plants occurs either by the sexual mode (the sexual process precedes embryogenesis; heterophasic reproduction) or by an asexual one (the formation of buds and roots, i.e., regeneration; homophasic reproduction). However, it appears that in homophasic reproduction a new individual may be formed not only through regeneration but also by the formation of somatic embryos (bipolar structures) – somatic embryogenesis (= embryoidogenesis).

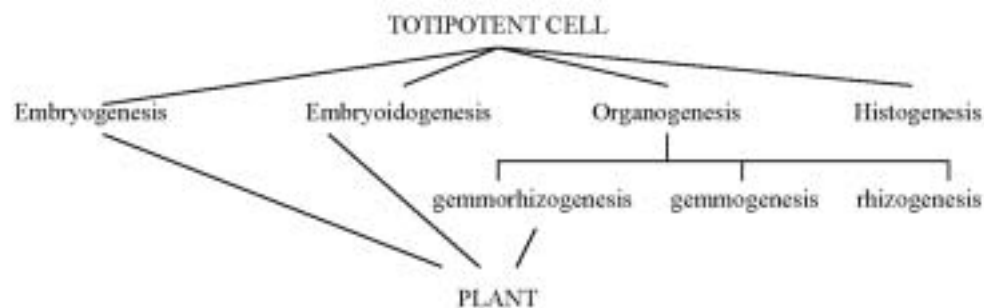Thus it has become possible to distinguish a new category of vegetative multiplication, embryoidogeny,

Fig. 2. Scheme of morphogenesis pathways leading to the formation of a new organism (after Batygina, 1987).

and to identify three pathways of morphogenesis leading to the formation of a new individual – embryogenesis, embryoidogenesis and organogenesis, not two as thought earlier (Fig. 2). These ways and modes of new sporophyte formation are universal in natural and experimental conditions, particularly in culture in vitro (Batygina, 1987, 1997b, 1998, 2004, 2005; Batygina et al., 1978; Batygina and Butenko, 1981; Brukhin and Batygina, 1994).

VEGETATIVE MULTIPLICATION

If the maternal plant produces many daughter individuals asexually, such a process is referred to as vegetative multiplication, caused by the separation of viable parts of the plant vegetative body (buds, brood buds, shoots, roots, etc.). It is a nontraditional idea that vegetative multiplication can be realized by two morphogenic pathways – not only gemmorhizogenesis but also embryoidogenesis (Batygina and Vasilyeva, 2002). The progeny arisen as a result of vegetative multiplication forms clones that are genetically uniform individuals ("genets") genotypically identical to the maternal organism. This is widely represented in nature by plants multiplying mainly by vegetative means.

Gemmorhizogeny, a type of vegetative multiplication, can be either non-specialized or specialized (Shorina, 2000). Non-specialized vegetative multiplication occurs as result of decay of creeping shoots (*Trifolium repens*, *Lysimachia nummularia*), lodging shoots (*Veronica hamaedris*) and epigeous rhizomes (*Asarum*, *Geum*, *Alchemilla*). Specialized vegetative propagation occurs with the participation of specialized and often modified shoots, which are either above-ground (*Fragaria*) or underground (*Trientalis europaea*) quickly decaying stolons, hypogeal rhizomes (*Pyrola*, *Convallaria*), tubers (*Solanum tuberosum*), bulbotubers (*Gladiolus, Crocus*), bulbs (*Tulipa, Allium*) and brood buds (*Ficaria verna*).

The formation of offshoots from apical, lateral or adventive buds on stolons, rhizomes and roots, which

separate from the maternal individual after rooting, is referred to as sarmentation (Barykina, 2000a). Another method for vegetative multiplication is particulation (Barykina, 2000b), that is, longitudinal splitting of the plant, usually its underground organs (caudex, vertical rhizome, main root, caulorrhizous tubers) into separate living parts (particules) capable of independent existence and development after separation.

There is a distinction between "vegetative multiplication," "vegetative renewal" and "vegetative spreading." Vegetative renewal is the development of new parts of plants to replace dead or damaged ones. It is manifested sharply as the seasonal rhythm in plants. Vegetative spreading is enlargement of the body size of individuals. It is accompanied by an increase in the number of structural modules that compose the plant and are relatively autonomous, that is, potentially they can live independently. Examples of such modules are rosette shoots (*Aegopodium podagraria*), tufts (*Vaccinium myrtillus*) and bunches (*Carex pilosa*).

Embryoidogeny is one of two types of homophasic reproduction in angiosperms. The main structural unit of embryoidogeny is the embryoid. We used two criteria to single it out as a particular type of reproduction and multiplication: ontogenetic (homophasic reproduction, uniparental inheritance) and morphological (bipolar organization of the structure, with root and shoot apices and a new polar axis).

The embryoid is the germ of an individual, formed asexually in situ, in vivo and in vitro. At all stages of its formation, typically the embryoid is bipolar in organization, just like the sexual embryo. Synonyms are somatic embryo, embryo-like structure, and adventive embryo (see Batygina, 1989).

The embryoid can be formed exogenously or endogenously, usually from one somatic cell, rarely from an embryonic cellular complex, in homophasic reproduction (i.e., in the absence of meiosis and fertilization).

It is typical of the embryoid to form a new axis, which joins the shoot and root apices. As a rule, it has no common vascular system with the maternal organ-
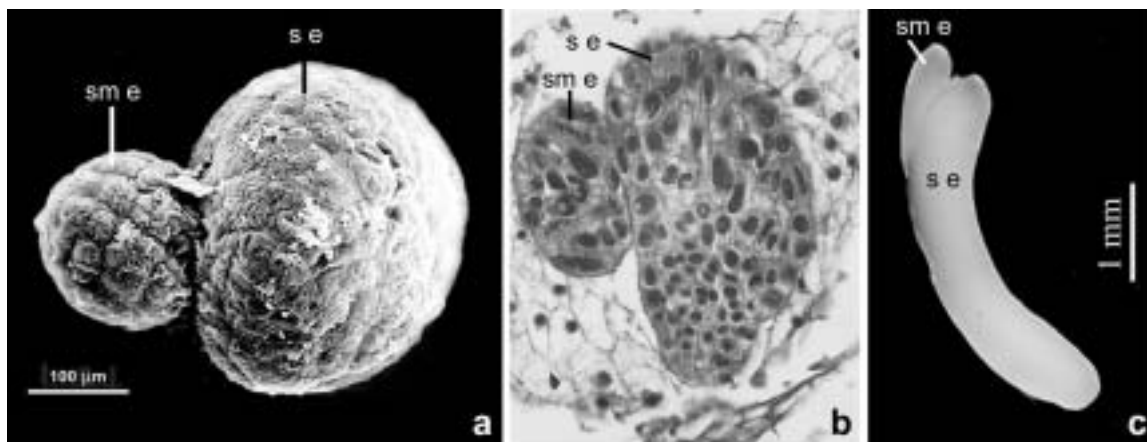
Fig. 3. Polyembryony in *Agapanthus praecox*. (**a,b**) Two embryos from one seed (a – SEM, b – LM), (**c**) Two mature embryos. (b) × 400. se – sexual embryo; sme – somatic embryo (courtesy of G.E. Titova).

ism (closed radicular pole). The genesis of the embryoid, its shape and size are taxon-specific. The basic features that have been established for sexual embryos (polarity, cellular and histogenic differentiation, autonomy, etc.) are typical of the embryoid as well. In embryoid germination, a new individual is born (Batygina, 1987, 1989, 1993), and a short-term connection with the maternal organism has been made. The duration of the contact and the stage of embryoid development at which this contact occurs differ between species. The bud, with which the somatic embryo is often connected, is a structure with monopolar development, and only during further regeneration does it transform into a bipolar structure making a new individual.

In the light of new concepts concerning the modes and types of reproduction and propagation of flowering plants (Batygina et al., 1978; Batygina, 1987, 1992, 1993), the embryoid is regarded as an elementary structural unit of the embryoidogenic type of vegetative propagation. At all stages of ontogenesis, starting from the zygote, a tendency towards an asexual mode of reproduction exists in somatic embryos.

Historically, the term "embryo" is used to designate the germ of a new organism, resulting in fertilization. In this connection the word combination "somatic embryo," used mostly in papers on tissue culture, appears contradictory because it expresses opposite concepts: sexual (embryo) and asexual (somatic) processes. From the point of view of modern embryological science, this contradiction is ameliorated because the embryoid is the germ of a new individual, which differs from the sexual embryo mostly by its origin (from the somatic cell or cells) (Batygina, 1997b). Present-day comparative analysis of the genesis of the sexual and somatic embryos indicates parallelism in their development (Batygina, 1997b, 2004, 2005).

The term "adventive embryo" is hardly worth using for embryoids formed in callus and suspension cultures, because we do not know which is the main one and which is additional. This also applies to embryoids formed on vegetative organs.

SEED MULTIPLICATION

The seed is one of the structural units of reproduction, propagation and dissemination, containing the embryo (or embryos with different genotypes) and usually specialized reserve tissue (endosperm, perisperm, etc.), which are enclosed in protective envelopes (seed coat). Embryos can be sexual, or zygotic (gamospermy) or nonsexual, originating without fertilization (agamospermy). There are several agamospermy types. The embryo may be formed on the basis of a gametophyte (from the egg cell in the case of parthenogenesis, from the synergid in the case of apogamety, etc.), or on the basis of the maternal sporophyte (i.e., from nucellar or integumentary cells in the case of ovular embryoidogeny), or on the basis of the daughter sporophyte (in the case of embryonic, i.e., cleavage embryoidogeny – the formation of monozygotic twins, triplets, etc.). The formation of several embryos in a single seed is traditionally referred to as polyembryony (Fig. 3). Unlike "normal" seeds that contain only zygotic embryos, heterogenous polyembryonic seeds are characterized by various sexual and asexual processes occurring together, leading toward the formation of a new individual. Often these reproductive processes are not expressed in pure form. For example, the formation of monozygotic twins and triplets is preceded by the sexual process, which later changes to an asexual one, that is, the developmental program is switched.

All these complex multistage processes cause genetic heterogeneity in seeds, enabling reproduction and multiplication of new generations with different genotypes. Either biparental or uniparental inherit-
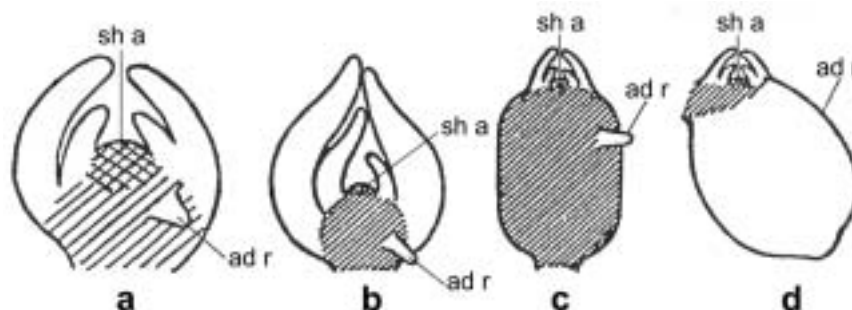
Fig. 4. Types of brood buds. (**a**) Unmetamorphosed axile or adventitious bud with adventive root, (**b**) Bulblet, (**c**) Tubercle originated from stem, (**d**) Tubercle originated from root. adr – adventive root; sha – shoot apex; shoot axis shaded (after Serebrykova, 1978).

ance may occur. Multiplication through somatic embryogenesis occurring in the seed significantly increases the genetic diversity of seeds. This suggests that not only must morphological and anatomical features of seeds (e.g., the surface sculpture) be taken into account, but also embryogenic features defining the heterogeneity of the population.

Consolidation of the functions of multiplication and spreading in the seed occurred as a result of the presence of both the gametophyte and sporophyte in it. Multiplication of plants is greatly enhanced by the formation of seeds in large numbers, with one or several embryos.

Maintenance of optimal population density through seed multiplication (seed renewal) is the final stage of the reproductive biology of species. The success of this stage defines the biological efficiency of all reproductive processes preceding it. The course of seed renewal is conditioned by seed yield: the bank of seeds in the soil and the number of surviving seedlings. As Levina (1981) stated, the seed bank in the soil actually is the "embryonic population" of the species and its long-term reserve.

There is still no complete answer to the important question of the ratio of seed to vegetative multiplication in various taxa. Moreover, discussion of the different types, forms and means of reproduction and multiplication raises the issue of the interrelations between seed multiplication and seed renewal, and also between vegetative multiplication and vegetative renewal.

The terms "multiplication" and "renewal" mean different things: the first refers to the individual, and the second to the population. Although multiplication of individuals is the basis of renewal of species (or populations) in general, the term "multiplication" is not applicable to systems above the level of the organism. With the concepts thus delimited, it makes sense to use the term "vegetative renewal" for renewal of the population by vegetative multiplication. The process of restoration of above-ground parts is referred to as regrowth. Four types of regrowth can be distinguished.

Vivipary is a special type of multiplication that occurs when a generative diaspore containing the embryo or a vegetative diaspore forms a seedling (propagule) on the maternal organism without a period of dormancy. Viviparity in plants (*Festuca ovina*) was first described by Linné (1737). At present, vivipary is known in 281 species of flowering plants belonging to families situated both at the base (Nymphaeaceae, Ranunculaceae) and the apex of the phylogenetic system (Orchidaceae, Poaceae). Besides flowering plants, 197 species of viviparous ferns belonging to eight families are known (see Batygina and Bragina, 2000). The localization of seedling formation on specific generative and vegetative organs is taxon-specific.

In considering the various cases of vivipary, we note that plant reproduction can be heterophasic (with meiosis and fertilization) or homophasic (without meiosis and fertilization). Our classification of vivipary (Batygina and Bragina, 2000b) incorporates the morphogenic pathway leading to new plant formation (embryogenesis, embryoidogenesis, gemmorhizogenesis) and the site of propagule formation on the maternal organism (seed, fruit, inflorescence, leaf, stem, root).

An example of generative vivipary is seedling development in mangrove plants (*Rhizophora, Bruguiera, Ceriops* – Rhizophoraceae).

Vegetative vivipary proceeds on the basis of the vegetative diaspore, arising without the sexual process. Vegetative diaspore development can follow two morphogenic pathways, gemmorhizogenic and embryoidogenic. We therefore divide vegetative vivipary into gemmorhizogenic and embryoidogenic vivipary. In systematizing the phenomena of vivipary, we took into account the site of vegetative diaspore formation on the plant: the inflorescence in floral vivipary (*Polygonum viviparum, Allium oleraceum, Poa bulbosa*); the leaf in foliar vivipary (*Cardamine, Nymphaea, Bryophyllum, Hammarbya paludosa*); the stem in cauligenic vivipary (*Lilium tigrinum, Gagea bulbifera*); and the root in rhizogenic vivipary (this form of vivipary is possible theoretically). Generative
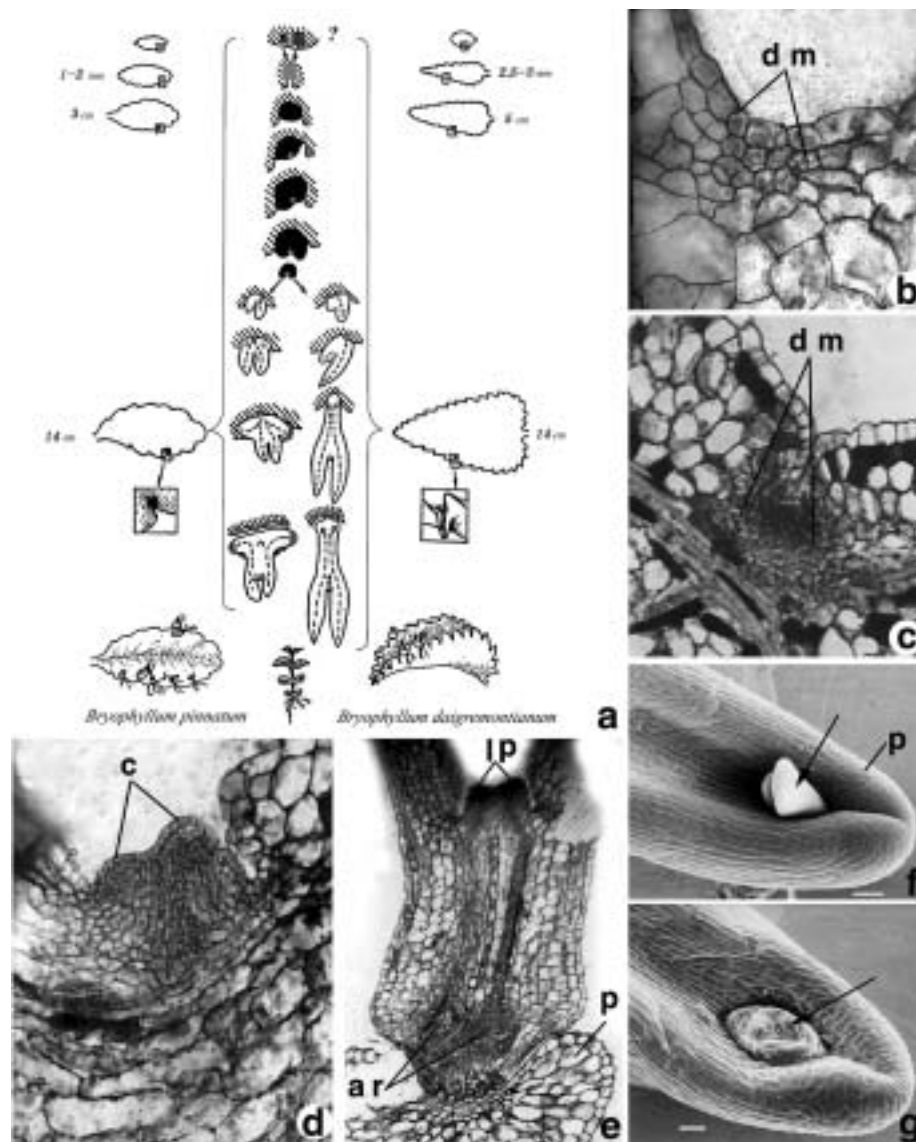
Fig. 5. Switching over of the leaf cell development program to the formation of a vegetative diaspore in *Bryophyllum pinnatum* and *B. daigremontianum*. (**a**) Development of somatic embryos on leaf in *B. pinnatum*, and transitional forms between somatic embryo and bud in *B. daigremontianum* from dormant meristem (schematic), (**b–g**) Stages of somatic embryo development: (**b**) Dormant meristem on margin of young leaf, (**c**) Dormant meristem on margin of adult leaf, (**d**) Somatic embryo at heart-shaped stage of development, (**e**) Somatic embryo at autonomous stage of development, (**f**) Somatic embryo (arrow) on peg of margin of leaf, (**g**) Trace of detachment of somatic embryo (arrow) on peg. ar – adventive root; c – cotyledon; dm – dormant meristem; lp – leaf primordium; p – peg. (b) × 1000; (c,d) × 400; (e) × 200. Bars (f, g) = 100 μm (after Batygina et al., 1996).

vivipary as well as vegetative vivipary may take obligatory or facultative forms.

The brood bud is an organ specialized for vegetative multiplication of angiosperms, and is one of the structural units of vivipary (Batygina and Bragina, 2000a) (Fig. 4). The term "brood bud" initially was used for uni- or multicellular structures that provided vegetative multiplication in thallophytes (algae, liverworts). The structures providing this function are also inherent in higher sporiparous plants (Bryophyta, Equisetophyta, Lycopodiophyta, Polypodiophyta) and some Angiospermae. Brood buds may be of different structures: unmetamorphosed axillary or adventitious buds with an adventive root, bulblet or tubercle. In the course of brood bud development, its bipolarity is established (the initiation of adventive roots) and the new individual is formed. Brood buds arise on the plant abundantly and fall from it like seeds or spores. The similarity is enhanced by the fact that the plants formed from the fallen buds

are rejuvenated and resemble seedlings or young gametophytes.

The formation of propagules on the leaf margin and its axil is characteristic for species of *Bryophyllum* (e.g., *B. daigremontianum* is characterized by obligatory vivipary, and *B. pinnatum* by facultative vivipary) (Fig. 5). Some authors refer to these propagules as brood buds since, being on the maternal plant, they produce shoots with adventive roots. In view of their location and structure, earlier they were considered to be adventive buds (Levina, 1961; Vasilyev et al., 1978). Analysis of the literature and original data on their morphogenesis revealed a difference in their origin and development (Yarbrough, 1932, 1934; Batygina, 1989, 1990; Batygina et al., 1996). The propagule of *B. crenatum* was established to be an unmetamorphosed bud in which adventive roots develop. The propagule of *B. pinnatum* actually is an embryoid (Batygina et al., 1996). In *B. daigremontianum* the propagule is a transitional form between an unmetamorphosed bud, in which adventive roots develop, and an embryoid. Propagules are formed at a definite stage of maternal leaf development, deriving from cell groups that arise in the course of ontogenesis (dormant meristem). These cell groups are derivatives of marginal leaf meristem; they preserve the capacity for further development (Berger, 1877; Yarbrough, 1932, 1934; Batygina, 1989, 1990). These cell groups are treated as stem cells (Batygina et al., 2004).

The potential for vivipary is universal for all angiosperms. The degree of its manifestation is taxon-specific. Questions of the regulatory mechanisms of generative and vegetative vivipary, whether of hybrid origin (Ernst, 1918) or polyploid origin (Turesson, 1930), are still controversial (see: Batygina and Bragina, 2000). It is generally accepted that viviparous forms of cereals arose spontaneously and are more or less stable mutations.

The phenomenon of vivipary can be observed in plants in various ecological conditions. Together with other mechanisms, obligatory generative vivipary typical of mangroves provided an adaptation for existence in conditions of periodic flooding and high salinity. It promoted the development of salt tolerance and the ability of a seedling to root quickly. Plants' capacity for facultative generative vivipary is a reserve capability of the reproductive system. With changes in environmental conditions, some part of seeds can produce viable seedlings while still on the maternal plant.

CONCLUSIONS

Sexual and asexual processes, heterophasic and homophasic reproduction, seed and vegetative multiplication (propagation) proceed in a coordinated manner, thus enabling maintenance of the homeostasis of the species or population.

Understanding the plasticity and resiliance of reproduction systems at the level of species and populations is one of the central problems of biology today. Studies of the types, modes and forms of reproduction and their interrelations in the maintenance of biological resources are of great importance. An important trend in plant population embryology is investigation of the variability of morphogenesis and the resulting phenotype in the population (variations of the life cycle and the diversity of reproduction systems).

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