

POLYEMBRYONY IN EUONYMUS (CELASTRACEAE) ¹

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POLYEMBRYONY, the production of two or more embryos within a seed, is rather widely, although sporadically, distributed among the spermatophytes. Although less common than in the gymnosperms, polyembryony in the angiosperms is much more diverse in respect to the origin and mode of development of embryos. In the angiosperms, embryos may be derived from an egg cell (rarely from two or more "egg cells") and/or synergids and/or antipodals within a single reduced or unreduced embryo sac of an ovule, either following or without fertilization; from a fertilized egg cell through the cleavage of the zygote or the proembryo (cleavage polyembryony); or directly from the cells of the nucellus or the inner integument of an ovule (adventitious embryony) (Ernst, pp. 436–438; Lebègue, pp. 333–336). Although polyembryonate species or populations usually show a predominance of one type of polyembryony, there also are those (e.g., *Allium odorum* L.) which may produce seeds with embryos derived in several different ways.

Of all the types of polyembryony those involving apomixis (either gametophytic [diplo- or apospory, parthenogenesis, or apogamety] or somatic [adventitious embryony]) are of special interest because of the effects of apomixis on the groups in which it occurs. Apomixis makes possible the survival of well-adapted but sexually sterile genotypes, permits the building up of large populations of genetically similar individuals for rapid colonization of newly available habitats, and limits the genetic variability of those plants which have adopted this mode of reproduction (Stebbins, 1950, pp. 414–416). Although a rather restrictive factor in evolution, apomixis is important in the increase of polymorphism and geographic distribution of the genera in which it occurs. The study of agamic complexes, i.e., groups of closely related apomictic and sexual species, may yield valuable information on the present and past distribution of plants and may help in the determination both of centers of origin and routes of dispersal of genera and/or their sections and of the relative ages of different floras (Stebbins, 1941, pp. 533–536).

In view of the role of apomixis in evolution and distribution, and of its bearing on taxonomy, the records of polyembryony in three species of *Euonymus* L., coupled with the great polymorphism and wide distribution

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of this genus, suggested that it would be desirable to verify Braun's record (1860) of polyembryony in *E. americanus* and to investigate the distribution of polyembryony within the genus. Since only a few special seed collections were available, the necessity of using herbarium specimens for this purpose has limited investigations to those species in which the specimens have numerous loose seeds or fruits. Consequently, only a few seeds of each species could be examined, and no strictly statistical evaluation of the results can be made. Despite this limitation, the occurrence of polyembryony in several species has been detected, and the possibility of its absence or rare occurrence in other species has been indicated.

POLYEMBRYONATE SPECIES OF EUONYMUS

It is expedient to begin with *Euonymus latifolius* and *E. americanus*, in which polyembryony has long been known and thoroughly investigated by several authors. Other species are surveyed in alphabetical order. In citations of the material investigated by the writer the abbreviations "P" and "M" are used for polyembryonate and monoembryonate, respectively. In regard to size, embryos are described as full sized (3.5–3 mm.), subnormal (3–2 mm.), small (2–1 mm.), very small (1–0.5 mm.), minute (0.5–0.25 mm.), and very minute (under 0.25 mm.). The minute and very minute embryos usually are club shaped, subcylindrical, or subglobular, often notched at the apex; all the larger ones are distinctly differentiated into cotyledons and radicle and are similar in shape.

Euonymus latifolius (L.) Mill.

Du Petit-Thouars (1808, p. 199), the first to record polyembryony in the genus, wrote that in *Euonymus latifolius*, although sometimes two equally developed embryos were found in the endosperm ("perispèrme") of a seed, more commonly one was much smaller than the other. Later, Grebel (1820) and Treviranus (1838) also reported the occurrence of polyembryony in this species. The main points of Grebel's observations (pp. 324, 325) were that not rarely (but neither in every capsule nor twice in a capsule) two completely developed embryos lying side by side in the endosperm cavity of a seed were observed, but more frequently one embryo of the pair was much smaller than the other, had spread cotyledons, and was leaning to the radicle of the larger embryo; and, once, three normally developed, completely mature and two minute embryos were found in the endosperm cavity. In all the cases the embryos were lying in the seed in the same position, their radicles being directed toward the hilum (micropyle). Grebel did not mention the number of seeds examined. Treviranus (p. 556, *pl.* 3, *fig.* 40) reported that a half of nearly a dozen seeds examined by him were two-embryonate, both embryos of each pair lying in the same position in a seed.

In 1860, Braun (pp. 157, 158, *pl.* 4, *figs.* 1–12; *pl.* 5, *figs.* 1–4) examined nearly fifty seeds of *E. latifolius*. Twenty-eight of these were polyem-

bryonate (twenty-four with two embryos, three with three, and one with four). All embryos in a seed were lying in the same position in respect to, but often at different distances from, the micropyle. Strasburger (1878, pp. 658, 659, *pl.* 19, *fig.* 44) confirmed Braun's observations and stated that most seeds examined by him were polyembryonate. He also investigated the embryology of *E. latifolius* and concluded that the egg cell, although fertilized, only rarely developed into an embryo, but the adjacent nucellar tissue penetrated into the embryo sac and gave rise to adventitious embryos. Usually, only a single cell of the nucellar tissue became the initial of an adventitious embryo, which appeared to be situated similarly to an embryo developed from a fertilized egg cell, but sometimes the development of adventitious embryos began from a large cell-complex.

Most recently Andersson (1931), investigating the embryology of the same species, reported (pp. 34, 35), "In den allermeisten Samen und Samenanlagen mit Stadien nach der Befruchtung von *Euonymus latifolius*, die ich untersucht habe, kamen zwei bis mehrere Embryonen vor. In einigen Fällen habe ich feststellen können, dass die befruchtete Eizelle stirbt. Ob das aber immer der Fall ist, weiss ich nicht. Es ist aber nicht zu verneinen, dass sogar in Samen mit einem einzigen Embryo, dieser ein Adventivembryo sein kann. Auch die Eizelle wächst. Sie teilt sich erst ziemlich spät, und dann ist es sehr schwierig zu entscheiden ob sie noch da ist oder nicht. Denn zu dieser Zeit haben sich einige Zellen des inneren Integuments vorgewölbt . . . Die Zellen geben durch ihren Plasmareichtum ihren Charakter als Initialen der Adventivembryonen zu erkennen. . . . Nicht alle Adventivembryonen werden zu derselben Zeit angelegt. . . . Es scheint mir aber, dass Embryonen auch von einem schon vorhandenen Embryo hervorsprossen können, der dann als Embryoträger fungiert. . . . Einmal habe ich eine embryoähnliche Bildung wahrgenommen, von der ich geneigt bin zu glauben, dass sie aus dem Endosperm stammt." Andersson also showed that in *Euonymus latifolius*, as in *E. europaeus* L. (*q. v.*), the nucellus disintegrates, except for a negligible residue in the chalazal region, and can not be regarded as a source of adventitious embryos. Thus, according to him, in *E. latifolius* the adventitious embryos originate from the inner integument, although he once observed an embryo possibly of endospermous origin.

Euonymus americanus L.

Braun (1860, p. 159) investigated seeds of this species and stated that polyembryony in *Euonymus americanus* is even more common than in *E. latifolius*. Only five of twenty seeds examined by him were monoembryonate, six contained 2 embryos, four 3, three 4, and two 5. Two embryos in a seed often were subequal and full sized, the others gradually smaller, with one or two minute and easily overlooked. The relative position of the embryos in the endosperm was the same as in *E. latifolius*.

One hundred twenty-six seeds of nine collections of *Euonymus americanus* from various parts of its range were examined by me.

- Friesner 22624*, Jackson County, Indiana (GH): 5 seeds; 1 M; 4 P (three seeds with 2, and one with 3 embryos; supernumerary embryos small, minute, or very minute).
- Short 1855*, Kentucky (GH): 6 seeds; 2 M; 4 P (one with 2, two with 3, and two with 4 embryos; in all cases only one embryo in each seed full sized, the supernumerary small, minute to very minute).
- Fernald & Long 7522*, Nansemond County, Virginia (GH): 25 seeds; 1 M; 24 P (one with 10 embryos, one with 9, two with 8, four with 6, four with 5, three with 4, eight with 3, and one with 2; in one 6-embryonate seed the largest (full-sized) embryo reversed, with the radicle directed toward the chalaza; in one 6- and one 8-embryonate seed all the embryos small to very minute and lying in various positions both axially [with their radicles directed to opposite poles] and \pm transversely). This specimen shows not only the highest percentage (96%) of polyembryonate seeds, but also the highest number of embryos in a seed (10), the average number being 5.
- Demaree 9576*, Montgomery County, Arkansas (GH): 5 seeds, all P (two with 2, one with 3, and two with 4 embryos; in all cases only one embryo in each seed full sized, the supernumerary small, minute to very minute).
- Demaree 16568*, Grant County, Arkansas (GH): 5 seeds; 2 M; 3 P (two with 3, and one with 4 embryos).
- R. B. Channell*, 13 Sept. 1957, Davidson County, Tennessee (preserved fruits): 50 seeds; 9 (18%) M (FIG. 1, a); 41 (82%) P (nine with 2 embryos, nine with 3, fourteen with 4, four with 5, three with 6, and two with 7; in one 3- and one 4-embryonate seed one embryo reversed [FIG. 1, b, c], with the radicle directed toward the chalaza; in a 4-embryonate seed three minute embryos situated in the micropylar region and one subnormal embryo lying across the seed [FIG. 1, d]). Four was the average number of embryos in a seed. (See also FIG. 1, e.)
- Wiegand & Manning 1908*, Henry County, Alabama (GH): 5 seeds, all P (two with 2, one with 3, and two with 5 embryos; in all the cases only one embryo in a seed full sized, the supernumerary mostly minute to very minute; in a 5-embryonate seed one minute embryo situated at the reverse pole of the endosperm cavity [opposite the micropyle] immersed in the endosperm and covered with an oil droplet). An endospermous origin of the last-mentioned embryo seems to be possible.
- Palmer 6782*, Polk County, Texas (A): 5 seeds, all P (two with 2, one with 3, and two with 4 embryos; in a 4-embryonate seed two embryos full sized).
- Kral & Godfrey 3570*, Gadsden County, Florida (GH): 20 seeds; 19 M; 1 P (with one full-sized and one small embryo).

My observations show that polyembryony in *Euonymus americanus* is rather frequent, as long ago stated by Braun (1860). Ten was the highest number of embryos found in a seed. Although all supernumerary embryos usually were found in the micropylar region in normal positions, in seven seeds one or more supernumerary embryos of a seed were situated in reverse axial and/or transverse positions (FIG. 1, b-e). In six of these seeds an integumentary origin of such embryos is assumed, but in one (*Wiegand & Manning 1908*) an endospermous origin of a reverse embryo is to be suspected. The specimen *Kral & Godfrey 3570*, perhaps representing *E. americanus* var. *angustifolius* (Pursh) A. Wood or a form close to it seems to be an exception in which polyembryony is rare.

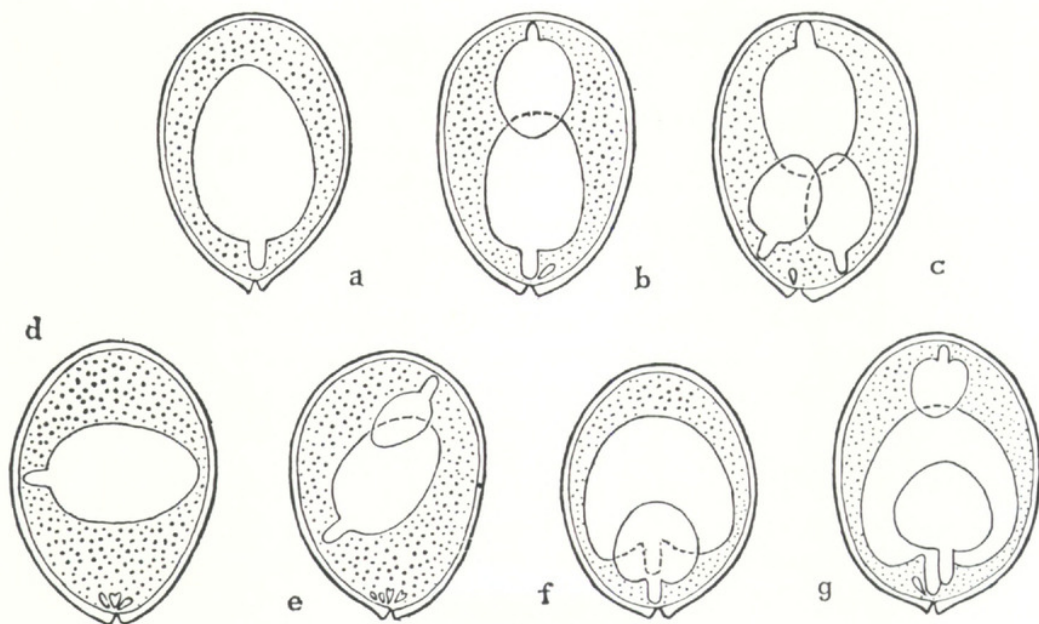


FIG. 1. Longitudinal sections of seeds of *Euonymus* to show arrangement of embryos. Drawings diagrammatic, the micropyle below, double seed coat not indicated, endosperm stippled, ca. $\times 5$. a-e, *E. americanus* (Channell, Tennessee, 1957): a, monoembryonate seed; b, three-embryonate seed with embryo at chalazal end in reversed position; c, four-embryonate seed with nearly full-sized embryo in reversed position; d, four-embryonate seed with subnormal embryo horizontal, three minute ones in micropylar region; e, six-embryonate seed with one subnormal and one small embryo lying in opposite directions and four minute embryos around micropyle. f, g, *E. alatus* var. *apterus*: f, two-embryonate seed with cotyledons of smaller embryo clasping radicle of larger (Sargent, Japan, 16 Sept. 1892); g, four-embryonate seed with one small embryo in reversed position (Arnold Arb. no. 14543-B).

Euonymus alatus (Thunb.) Regel var. *apterus* Regel

Thirteen seeds of three herbarium collections, and 200 seeds of a living cultivated plant were examined.

W. T. Tsang 23362, Kwangsi, China (A): 3 seeds; 1 M; 2 P (each with one full-sized and two somewhat smaller embryos).

Wilson 354, Western Hupeh, China (A): 10 seeds; 8 M; 2 P (each with two subequal, slightly undersized embryos).

Sargent, 16 Sept. 1892, Sapporo, Japan (A): 3 seeds, all P (two with 2 subequal embryos in each; one 4-embryonate seed with one embryo in a reverse position at the chalazal end of endosperm [FIG. 1, g]).

Arnold Arboretum; no. 14543-B (grown from seeds sent from Korea, by J. Jack): 200 seeds; 166 (83%) M; 34 (17%) P (twenty-eight 2-embryonate and six 3-embryonate; in all cases embryos located in the micropylar region [FIG. 1, f]).

Euonymus dielsianus Loes.

Stewart, Chiao, & Cheo 811, Kweichow, China (A): 4 seeds; 1 M; 3 P (all 2-embryonate; in each of two seeds both embryos subequal and nearly full sized but lying in reverse positions with their radicles directed toward micropyle and chalaza respectively).

***Euonymus macropterus* Rupr.**

Dorsett & Morse 1336, Odomari, Sakhalin (A): 10 seeds; 1 M; 9 P (six with 2, and three with 3 embryos).

***Euonymus oxyphyllus* Miq.**

Wilson, 1914, Hondo, Japan (A): 5 seeds, all from the same capsule; 2 M; 3 P (one with 2, one with 3, and one with 4 embryos).

***Euonymus vagans* Wall. ex Roxb.**

(*E. bockii* Loes.; *E. hupehensis* var. *brevipedunculatus* Loes.)

Seven seeds of two herbarium specimens were investigated.

C. S. Fan & Y. Y. Li 673, Hunan, China (A) [determined as *E. bockii*]: a single seed examined contained two subequal, full-sized and one minute embryo.

Henry 9106B, Yunnan, China (A) [determined as *E. hupehensis* var. *brevipedunculatus* Loes.]: 6 seeds; 2 M; 4 P (all 2-embryonate).

***Euonymus verrucosoides* Loes.**

Sixteen seeds of two herbarium specimens were examined.

Wilson 3102, Western Szechuan, China (A): 7 seeds; 1 M; 6 P (two with 2, three with 3, and one with 5 embryos; one 3- and the single 5-embryonate seed with only minute embryos).

Rock 14978, Southwestern Kansu, China (A) [determined as *E. verrucosoides* var. *viridiflorus* Loes. & Rehd.]: 9 seeds; 2 M; 7 P (one with 2, five with 3, and one with 4 embryos; one 3-embryonate seed with two equal, full-sized and one minute embryo).

MONOEMBRYONATE SPECIES OF EUONYMUS

Since *Euonymus europaeus* has sometimes been mentioned as polyembryonate, the question of polyembryony in this species should be considered in some detail. Jäger (1814, p. 202) listed this species among a few plants in seeds of which two embryos occur. In order to verify Jäger's record Braun (1860, p. 156) examined seeds of *E. europaeus* and remarked, "Wenn hier nicht eine Verwechselung mit der folgenden Art [*E. latifolius*] im Spiel ist, so ist ein solches Vorkommen jedenfalls sehr selten, denn mir gelang es nicht bei dieser Art mehr als einen Keimling zu finden, wiewohl ich mehr als ein halbes Hundert Samen zergliederte."

In 1916, however, Bally reported the occurrence of polyembryony in *E. europaeus*. According to his observations, sometimes the embryo sacs in this species degenerate in an earlier or later stage of development. The space which was occupied by the embryo sac becomes surrounded by the nucellar tissue. The cell walls of these "tapetum-cells" dissolve themselves, and their naked contents wander into the cavity and soon fill in the latter with a homogeneous tissue as has been observed in the pollen sacs of certain monocotyledons. When the cavity is almost completely filled with nucellar tissue, the exterior layers of the latter in the micropylar region begin to execute divisions which lead to the development of one or more

embryos growing into the endosperm tissue. However, Andersson, on the basis of his own study of embryology in *E. europaeus*, criticized Bally's observations, saying (p. 30), "The nucellar cells can not be involved at all, because the nucellus disintegrates early and its small chalazal remainder is of no significance. . . . I believe that Bally's statement is to be attributed to defective staining" (translation supplied). Regarding Bally's explanatory account of the occurrence of adventitious nucellar embryony in *E. europaeus*, Andersson (p. 32) further remarks, "The formation of embryos in the micropylar region from the cells of the nucellus is impossible, since even this part of the nucellus disintegrates early. The origin [of embryos] from the cells of the inner integument would perhaps be possible [in this species], but I have never observed it. I also have not found polyembryony, and to my knowledge the latter has been observed [in this species] otherwise only once by Jäger (1814)."

The writer examined 30 seeds from each of two living cultivated specimens of *Euonymus europaeus* (Arnold Arboretum no. 18253, and Fairfield Garden Apts., Watertown, Mass., Brizicky, Oct. 1963) and found no evidence of polyembryony. Since Braun, Andersson, and the present writer have not found polyembryony in this species, one may assume either that Jäger's and Bally's records were based on misidentified material or that polyembryony in *E. europaeus* is extremely rare.

The following species investigated by the writer showed no polyembryony:

Euonymus bungeanus Maxim.: 30 seeds of a living specimen, Arnold Arboretum no. 2128-D (grown from seeds received from J. Hers, China, 1919).

Euonymus maackii Rupr.: 30 seeds of a living specimen, Arnold Arboretum no. 14563-1.

Euonymus sachalinensis (Schmidt) Maxim.: 15 seeds of a living specimen, Arnold Arboretum no. 13213-A.

Euonymus semiexsertus Koehne: 50 seeds of a living specimen, Arnold Arboretum no. 99-35-B.

Euonymus yedoënsis Koehne: 150 seeds of three living specimens, Arnold Arboretum no. 34340-A (cutting from Arnold Arboretum no. 14576-1-A), thirty seeds; Fairfield Garden Apts., Watertown, Mass., Brizicky, Oct. 1963, tree no. 1, ninety seeds, and tree no. 2, thirty seeds.

Although a few seeds, taken from random herbarium specimens of *E. atropurpureus* Jacq., *E. obovatus* Nutt., and *E. occidentalis* Nutt., were all monoembryonate, no conclusion can be made about the nature of these species until adequate material is investigated. Seeds of *E. fimbriatus* Wall. and *E. verrucosus* Scop. were found to be monoembryonate by Braun (1860).

Although the present investigations indicate that all the above-mentioned species may be monoembryonate, the monoembryony of at least some species, assumed on the basis of not very abundant material, should be reinvestigated. Furthermore, it seems to be of even greater importance to study the embryology of these species in order to determine the origin of the embryo, since even a single embryo within a seed could be apomictic.

SUMMARY AND CONCLUSIONS

The occurrence of polyembryony in *Euonymus latifolius* and *E. americanus*, recorded in the nineteenth century, has recently been confirmed by Andersson (1931) for the former and by the writer for the latter species. On the contrary, polyembryony in *E. europaeus*, recorded by Jäger (1814) and Bally (1916) has not been substantiated (Braun, 1860; Andersson, 1931; the writer). If these records were not due to misidentification, polyembryony in *E. europaeus* may at least be extremely rare. I have found polyembryony to be of common occurrence in *E. alatus*, *E. dielsianus*, *E. macropterus*, *E. oxyphyllus*, *E. vagans*, and *E. verrucosoides*, all of eastern Asia. In *E. bungeanus*, *E. maackii*, *E. sachalinensis*, *E. semiexsertus*, and *E. yedoënsis* only monoembryonate seeds were observed. Although no polyembryonate seeds were found in *E. atropurpureus*, *E. obovatus*, and *E. occidentalis*, the material investigated was inadequate. Braun (1860) found *E. verrucosus* and *E. fimbriatus* also to be monoembryonate.

In the polyembryonate species the number of supernumerary embryos in a seed varies from one to nine. Only rarely are two or three embryos of a seed \pm full sized and subequal; usually the supernumerary embryos are small to very minute. They are usually located with at least their radicles in the micropylar region and directed toward the micropyle (FIG. 1, a, f). In some cases, however (e.g., in *E. americanus*, *E. alatus*, *E. dielsianus*), one supernumerary embryo was lying in a reverse position with its radicle directed toward the chalaza (FIG. 1, b, c, g), and in a few cases one or more embryos were situated \pm transversely (FIG. 1, d, e). In a few instances (e.g., in *E. verrucosoides*), a full-sized embryo was absent, but there were several minute ones in the micropylar region. The cotyledons of all the embryos of a seed usually lie in nearly the same longitudinal (vertical) plane, the position of which with regard to the raphe varies from one seed to another. Although sometimes parallel to the plane of the raphe, the plane of the cotyledons is more often at an angle to it.

Since Andersson showed that in *Euonymus europaeus* and *E. latifolius* the nucellar tissue disintegrates early and the adventitious embryos in the latter species arise from the inner integument of the ovule, one may assume that the early disintegration of the nucellus is a generic character and that in all polyembryonate species the adventive embryos originate from the inner integument. In fact, the integumental origin of the supernumerary embryos located in the micropylar region in seeds of the polyembryonate species of *Euonymus* can hardly be doubted. An identical origin of the embryos found in a reverse or \pm transversal position is most probable, although the embryos at the chalazal end might also be of an antipodal origin (through apogamy). In one instance (*E. americanus*, Wiegand & Manning 1908), an endospermous origin of a reverse embryo is suspected.

Adventitious embryony from the inner integument seems to be relatively rare and has so far been recorded in only about ten species in nine

genera and eight families (Johansen, pp. 283, 284). In the family Celastraceae this kind of polyembryony is also known in *Celastrus scandens* L. It is notable that "for some reason, adventitious embryony seems to be relatively frequent in species native to warm temperate or tropical climates" (Stebbins, 1950, p. 384).

The question of whether a full-sized, normal embryo in polyembryonate seeds or a single embryo in monoembryonate seeds of *Euonymus* develops from a fertilized egg cell, or whether it is at least sometimes apomictic, can not be answered without detailed embryological study of the species involved. Andersson's statement (p. 34) regarding *E. latifolius* reads in translation, "I can ascertain that the fertilized egg cell dies in some cases. Whether it is always the case, I do not know. However, it is not to be denied that even in seeds with a single embryo this can be an adventitious one."

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