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Genetic mechanism of pistillateness in castor: Challenges and needs: A review

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Abstract
Castor is a sexually polymorphic plant with two distinct sex forms: monoecious, which has staminate or male flowers at the base of the inflorescence and pistillate or female flowers at the top. Interspersed staminate flower (ISF) with sporadic male flowers and revertant and pistillate spike with all female flowers and no male flowers. Ankinnedu and Rao (1973) discovered that a monthly mean day temperature of 32 to 33^0C was ideal for inducing ISF and maintaining the pistillate line in castor. As the fraction of pistillate plants increased with higher nitrogen levels, the number of ISF plants fell. Three systems of femaleness—N, S, and NES—have been identified by a comprehensive examination of the genetic and non-genetic mechanisms determining sexual polymorphism in castor (Classen & Hoffman, 1950). Temperature, photoperiods, soil fertility, plant age and nutrients are among the environmental elements that have a significant impact on castor plant sex expression (1960, Shifriss). However, the relationship between genotype and environment has received relatively little study attention and stability analysis for variables related to sex is completely absent.

Keywords: Genetic mechanism, pistillateness, castor

Introduction

Ricinus communis L., a monotypic species in the Euphorbiaceae family with 2n = 20 chromosomes, is an important non-edible oilseed plant. India is one of the world's largest producers of non-edible oilseeds. Castor beans are cultivated for oil production as their seeds contain 35-55% oil (Jeong and Park, 2009) [7]. In mature castor bean seeds, 90-95% of the total seed protein is present in the endosperm. In the endosperm, crystalloid proteins make up 70-80% of the total protein and are insoluble in water.

Ricin, a toxic substance found in castor beans, is a cutting-edge tool in neurobiology for the selective destruction of neuronal cell populations (De-La-Cruz *et al*., 1995) [6]. Castor bean oil is being used in various industries for manufacturing aviation lubricants, printing inks, ointments, varnishes, cosmetics, in textile industry for dying, for oil cloth and artificial leather and fine quality nylon threads. It is also used for medicinal and lighting purpose.

Castor beans are mainly grown in arid and semi-arid regions. Castor is grown on a commercial scale in 30 countries, with India, China, Brazil, Russia, Thailand, Ethiopia, and the Philippines being the major caster producing countries, accounting for almost 88% of global production. India accounts for almost 75-80% of the world's castor cultivated area and almost 80-85% of the world's total castor production.

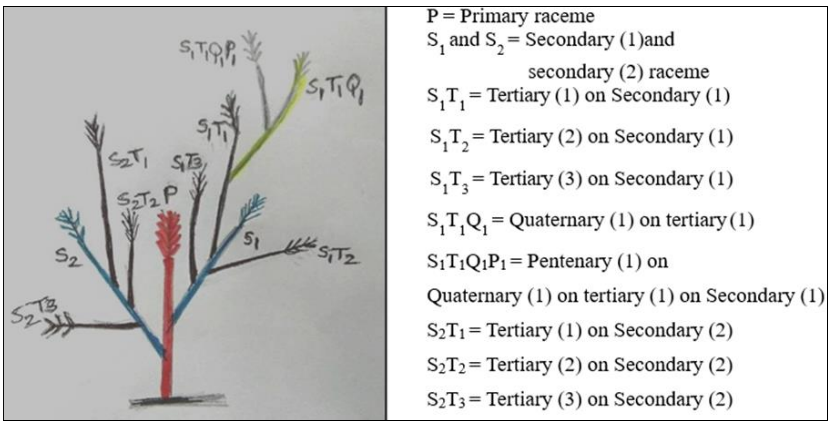


Fig 1: Different types spikes orders

Floral Biology of Castor

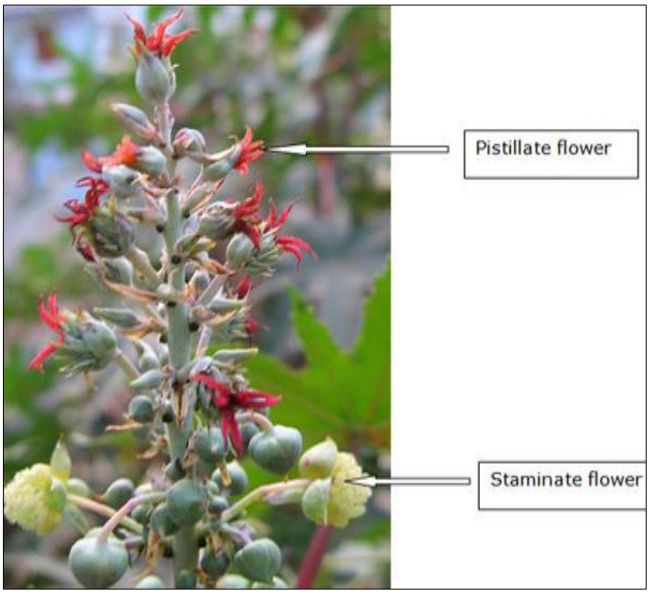


Fig 2: Floral biology of castor

- Conical, with three carpal-shaped ovaries, short style and pinnate, forked red stigma.
- Male flowers are greenish, have many stamens, and are divided into 3 to 5 aerated parts. Castor bean clusters are monoecious, with pistillate flowers in the upper 30-50% of the inflorescence and male flowers in the lower part.
- The proportion of pistillate and male flowers in grapes varies widely within and between genotypes. It is influenced by the plant's environment, genotype, and nutrition.
- Female bias is highest in winter, while male bias is predominant in summer and rainy season.
- Furthermore, the femininity of young plants with high nutrient levels is stronger than that of old plants with low nutrient levels.
- Shiny castor beans have intricate patterns. At one end is a small porous structure called a caruncle, which helps absorb water when planting seeds.
- The main stem ends in a cluster, which is the first or main cluster. After the first cluster appears, 2 or 3 branches appear at the nodes immediately below.
- Each of these branches ends up in a cluster after forming 4 or more nodes, called secondary clusters.
- Branches arise from nodes immediately below the secondary cluster, eventually terminating in the tertiary cluster. This developmental sequence (indeterminate growth habit) continues.

Pollination Mechanism

- Male flowers age immediately after releasing pollen. The opening takes place from 4:30 am to 5:00 am.
- Opens at 11:00 a.m. (4:30 p.m. to 5:00 p.m.) - reception 2 hours before opening (2-3 days).
- Pollen grains can survive for 2 days and the pistil has the ability to receive pollen for 3 days.
- The best environmental conditions for pollen dispersal are temperatures between 26 °C and 29 °C and 60% relative humidity, which may vary depending on the variety.
- Each candle takes 10-12 days to fully bloom.
- Pollination is mainly by wind and insects.
- The stigmas remain receptive after flowering for a period of 5 to 10 days.

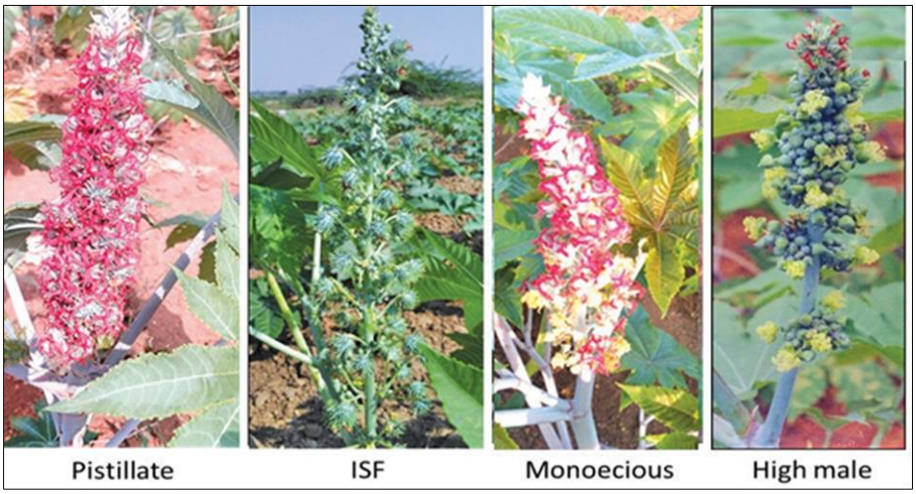
Stud of Sex Expression in Castor

Pistillate lines are the main approach for breeding high-yielding hybrid varieties, but progress has been slow due to limited knowledge of the genetic mechanisms of pistillate traits.

Therefore, the heredity or genetics of sex expression is of particular importance in the development of hybrids.

A Basic Sex Form in Castor

1. **Monoecious (M):** It is the most natural occurrence of annual and perennial castor. The spike has basal 1/3rd to 1/2 male flowers while the top portion has female flowers. In between these few whorls have both male and female flowers in an interspersed fashion.
2. **Pistillate (P):** It occurred as a rare recessive mutant with the spike having female flowers throughout the spike. It may be 100 percent pistillate or <100 percent (70-90%) having a few male flowers in the basal portion.
3. **(c) Interspersed staminate flower (ISF):** This is a modification of the pistillate with male flowers interspersed between the female flowers on the stem.
4. **Sex revertants:** In later stages, females become monoecious.



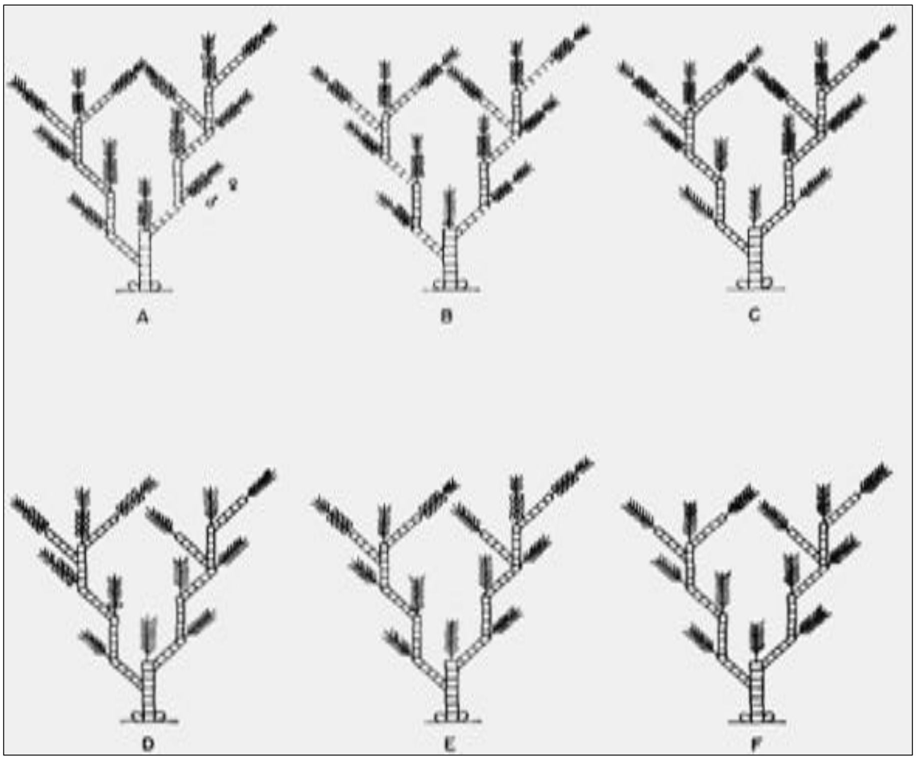


Fig 3: Diagrams of some developmental patterns of sex expreaasion in Ricinus. A, a monoe-cious individual; b to e, sex reversals; f, steictly female at this stage, but capable of reverting to monoecism depending on genotype

Types of sex promoting environments

Different writers classify the basic sex types in different ways since the expression of sex in different areas is heavily impacted by environmental conditions.

- **Female promoting environment:** Winter, low temperature <(30 °C), immature plants, early order spikes, high nutrition, and a smaller temperature difference between maximum and minimum temperature favour female flowers and change the balance of a spike towards femaleness.
- **Male promoting environment:** Summer, rainy season, hot temperature (>32 °C), old plants late order spikes, insufficient nutrition, and a wide temperature difference between maximum and minimum temperature encourage male flowers on a spike and an inclination towards maleness.

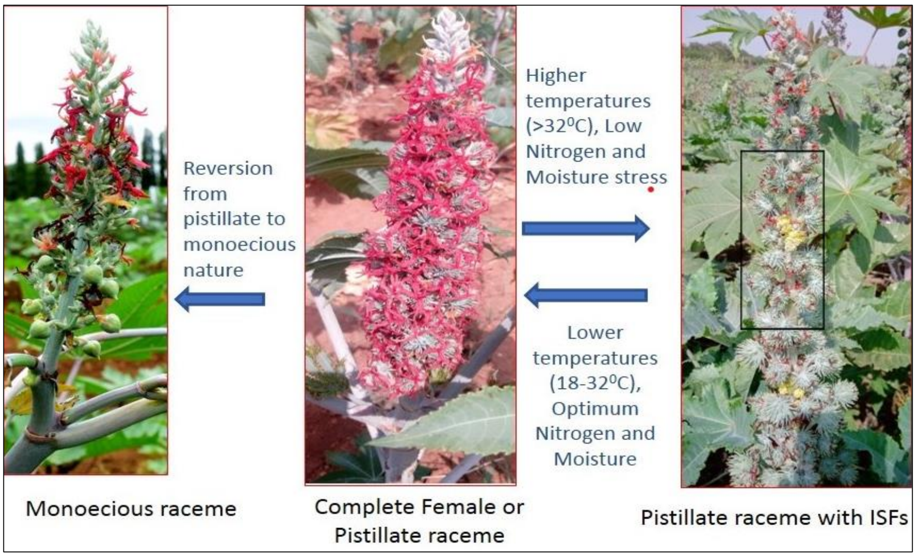


Fig 4: Classification of sex variant as per Shifriss (1960) [8]

Castor's basic sex phenotypes are characterised by the type of racemes that differentiate during development.

Type A: Monoecious

Type C: Pistillate

Type B: Sex revertant from C to A and D to E

Type D: Monoecious variant with apical interspersed raceme

Type E: Uniform interspersed raceme

Among these, type A and type Care developmentally persistent forms while others are developmentally inconsistent forms.

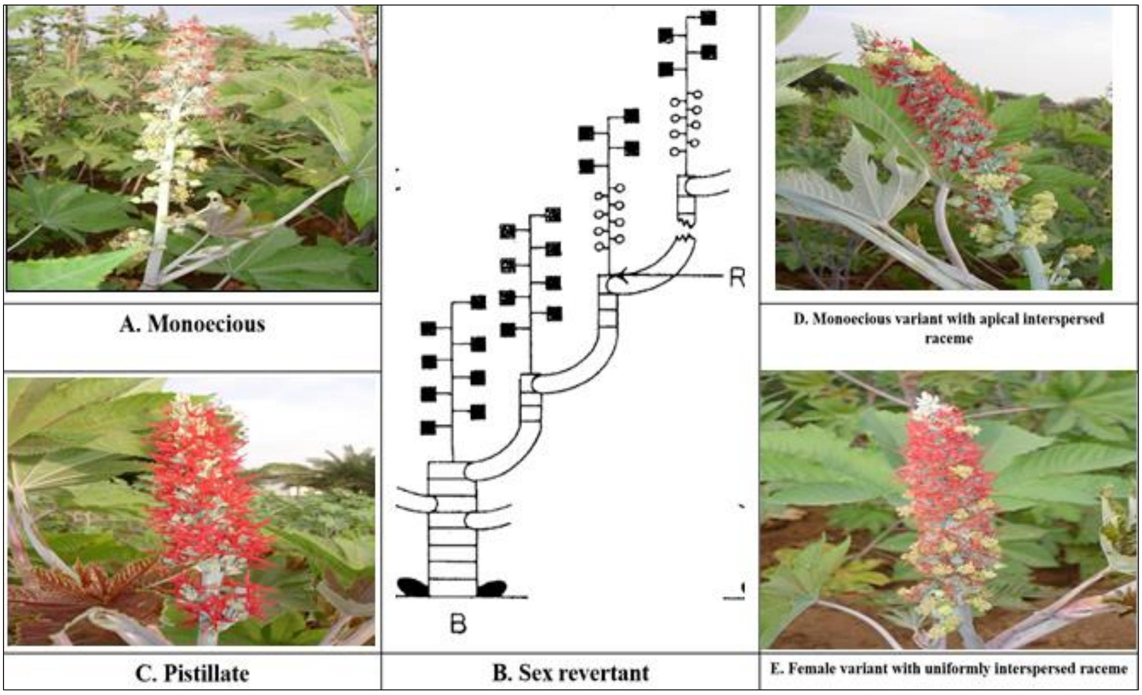


Fig 5: Classification of sex variants as conventional and unconventional system in relation to the environment, Shifriss (1960) [8]

Conventional system

Conventional variations are mostly monoecious, with only a few recessive females. These traditional versions are grouped according to

1. **Variation in sex tendency:** The proportion of male: female on a spike is the sex tendency *i.e.* if male flowers are more than female flowers, it is maleness; while female flowers are more than male flowers, it is femaleness. This proportions mainly vary due to environmental conditions like seasons, photoperiods, nutrition, temperature, etc.
2. **Variation in sex pattern:** The distribution of male and female flowers on a spike is known as the sex pattern.

Form 1: Monoecious, non-interspersed apical area, interspersed middle portion of spike, exclusively female flowers in apical region, staminate blooms in lower portion.

Form 2: A monoecious variety with apical interspersion, similar to type D. Although governed by a single recessive gene, the apically interspersed nature can be modified by the environment (environment sensitive and environment resistant).

Form 3: Monoecious, terminal hermaphrodite, e.g., an inbred 97 that is strongly male.

Form 4: Female, identified as regulated by a single recessive gene in a backcross. This has evolved into the 'N' kind of pistillate mechanism.

The typical variants could be controlled by two types of genes.

- **Qualitative genes:** These are the genes that decide whether flowers are male or female.
- **Polygenes:** These are genes that either accelerate or deplete a substance (which could be a growth regulator), the gradient differentiation of which determines the sex predisposition.

Unconventional system

- In environment F, this system emerges from dominant female mutants that occur spontaneously in nature from monoecious inbred of pattern A and D at a frequency of about 0.5 percent based on a huge number of varieties and over two million plants.
- Environmentally impacted and genetically unstable. Despite being a mutant, there is no difference in meiosis between normal monoecious and dominant females, and hence this variant is not connected with a breakdown in gametic fertility.
- These variants were the basis for the 'S' type of pistillate mechanism.

Unconventional variants are three types

Type 1: Occur as a series of sex reversals (C to A)

Sex reversals begin as females but eventually become monoecious. The plant may revert immediately after the primary appears.

Type 2: Non reverted female

It has evolved from inbred stock of variation Queen 162 and Adam Mistaef, which was classified previously under type of late, reverted female. Both variety having late maturity and produce their raceme at long intervals.

Type 3: Mutating recessive female

It was created by crossing female mutant 137-6 with a monoecist N-145-4, who was known to be heterozygous for the recessive female gene.

Types of pistillate lines

N type

- It is based on Shifriss's (1960) [8] description of form 4 of the standard variation.
- It was a backcross line with a 1:1 segregation ratio of monoecious and pistillate plants.
- The pistillate traits is controlled by a single sex flipping

gene, f.

- If a plant is homozygous recessive ff for sex expression, it remains pistillate, whereas a plant that is heterozygous recessive Ff is monoecious. When a female plant is crossed with a monoecious plant, the result is 1:1 monoecious: female.
- This kind can be kept alive by sib mating and harvesting seed from female plants separately. Female and monoecious plants have a 1:1 ratio of progeny from seed generated on female plants.
- N 145-4 is an inbred pistillate line of this kind.

S type

There are two mechanisms in S type: sex reversals and environment sensitive interspersed staminate flower (ISF) expression

Sex reversals

- This S type pistillate line was developed at the Weigmann institute in Israel through selection within sex reversal variants (Shifriss, 1956) [11].
- This sex reversal-based system behaves as a polygenic complex with dominant and epistatic effects.
- Sex reversals are plant varieties that begin as female and then revert to normal monoeciousness at any time after the first raceme, up to 5-10 sequential order racemes.
- Once the transition to monoecism occurs in a plant, it is ontogenetically irreversible.
- The selection of late order revertants is used to develop stable pistillate lines from S type.
- On continual inbreeding, sex revertants produce a range of sex reversals that might be early, late, or non-reverted.
- Early revertant on selfing results in >50% pistillate plant population. Late revertants (beyond the fourth order) produce > 80 to 100% pistillate populations with a very low fraction of monoecious. These pistillate lines are thereafter late reversed.
- When allowed to open pollinate, these sex revertants relapse to monoecism and must thus be maintained through ongoing selection for revertant pistillate plants.
- The late revertants are a potential source of pistillate line among the children of sex revertants - female, monoecious, early revertants, and late revertants.
- Although the genetic system that governs the timing of phenotypic reversal is unstable, reversion in and of itself is not associated with any severe breakdown in the female generating machinery.

Non reverted female

- Such females are derived from inbred stock of Queen 162 and Adam Mistaef, and the population contains a high frequency of the gene for interspersed staminate flower (ISF) expression.
- The environment influences the penetrance and expressivity of ISF in these girls.
- In a female-promoting environment, only a few ISF male flowers appear, which drop prematurely due to competition with older female blooms that were fertilised by nearby monoecious pollen.
- This can be avoided by bagging the spikes to prevent cross pollination. Despite the fact that the first male flowers disappear, subsequently grown male flowers fertilise the female flowers.
- Shifriss (1960) [8] created a genuine breeding non-reverted female line with the environmentally sensitive ISF expression gene.
- The Gujarat pistillate line has both sex reversal systems, and non-reverted females have the environmental sensitive gene for ISF expression.
- The Gujarat pistillate line possesses both sex reversal systems and environmental sensitive genes for ISF expression, which provided encouragement for hybrid development programmes in India in general and Gujarat in particular.

NES type

- This type is a hybrid of the N and S types since it carries the homozygous recessive gene for pistillateness as well as environment sensitive genes for ISF that are not restricted to any raceme order and are temperature dependent. (Ankineedu and Rao, 1973; Zimmerman and Smith, 1966) [1, 10].
- Furthermore, it was discovered that temperatures above 31 C promote ISF, but temperatures below 31 C result in entirely female racemes. As a result, these pistillate lines can be maintained during the summer, whereas hybrid seed production can be done safely during normal kharif planting.
- CENES 1 developed by Zimmerman and Smith (1996) [10], and 240 developed by Ankineedu and Rao (1973) [1], JP 65 from GAU, Junagadh, and a number of pistillate lines, including VP 1, SKP 4, SKP 6, SKP 13, SKP 16, SKP 23, SKP 42, SKP 72 SKP 84, SKP 86, SKP 106, SKP 108 etc. from GAU, S. K. Nagar are NES type pistillate lines.

Constraints in use of pistillateness in castor

- Female genetic instability and unknown mechanisms of sex expression are a restriction in castor hybrid breeding efforts.
- Presently used pistillate lines are highly unstable and lot of rouging are required to be done in the hybrid seed production plots increasing cost of hybrid seed production and many times rejection of seed plots.
- Since presently used pistillate lines are highly sensitive to environment.
- The pistillates lines used presently are limited in numbers and have narrow genetic base. In these pistillate lines, reversion is a serious problem hindering the quantity and quality of seed production.

Strategies to overcome

- Development of stable pistillate lines over the environments for maintenance of high genetic purity in hybrid seed.
- The instability of sex expression (pistillateness) in castor, male sterility approach should be explored for development of stable pistillate line, if developed, would replace environmentally influenced pistillate lines in castor hybrid seed production. As CMS lines are highly stable across environments, large quantity of quality hybrid seeds can be produced at low cost of production.
- The use of varied nature of pistillate lines must be proven in multilocation or seasons, and the inflorescence development and developmental mechanism of castor flowers must be understood.

Conclusion

- The proportion of monoecious and pistillate flowers were influenced by both genetic and non-genetic factors.
- Mutational breeding is also an appropriate strategy for developing diverse pistillate lines as considering the monotypic nature and limited variability in castor.
- The castor sex type was a complex quantitative trait with 3 kinds of performance, pistillate, monoecious, and ISF.
- The new pistillate lines are S-type (Environment sensitive ISF) with stable pistillate expression across the environments without sexual reversion in any order and the maintenance of pistillate lines in summer season resulting in high genetic purity.
- The number of ISFs in each pistillate line depend not only on its genetic nature but also the maximum temperature and diurnal range of temperature.
- Environment has a strong influence on sex expression. Female expression is enhanced by moderate temperature and optimum soil fertility and moisture; male expression is enhanced by high temperature and low soil fertility and moisture.
- Female expression is greatest in spring and early summer, male expression in late summer and early fall

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