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'The flower is the plant's delight'
(Systema Naturae 1735)

Linnaeus' Peloria: The History of a Monster*

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Summary. The so-called Peloria case has been discussed repeatedly in world literature since the discovery of the five-spurred *Linaria* in 1742 and its description by Linnaeus in 1744. In 1742 a young Uppsala botanist found a peculiar specimen of the common toad-flax (now named *Linaria vulgaris* L.) on an island in the Stockholm archipelago. The plant, which had spread vegetatively, possessed five spurs instead of one spur, a characteristic of the common toad-flax. The material was presented to Linnaeus, who became quite excited. The finding was contrary to his concept that genera and species had universally arisen through an act of original creation and remained unchanged since then. In a famous thesis of 1744, Linnaeus called the deviating plant 'Peloria', Greek for 'monster'. The case of pelorism was discussed later on by a great number of famous writers and scientists including, for example, Goethe, Darwin, Naudin, De Vries and Stubbe. Parallel types were found in numerous species of other genera and families. Such aberrant forms are caused by spontaneous mutation. The history, mode of origin, morphology, inheritance and distribution of different Peloria mutants are discussed in the paper.

Key words: Peloria – Pelorism – Monster – Hopeful monster – Zygomorphic – Actinomorphic – *Linaria vulgaris – Antirrhinum majus*

Linnaeus is regarded in the history of biology as the brilliant classifier of nature's diversity. 'God created the world, Linnaeus put it in order.' Order presupposes a certain conformity in an existing multiplicity, thus ruling out chaos. The disturbances or deviations that appear must not be so numerous as to upset the rule. Nevertheless, as the English geneticist William Bateson expressed so aptly: 'Treasure your exceptions'. One of the most discussed exceptions in the history of biology is the Peloria discovery in Roslagen (a district northeast of Stockholm, Sweden) in 1742 by the student M. Ziöberg.

For those who also study speciation and evolution, Linnaeus has become a pioneer. This in spite of the fact that he so categorically contended that all species had arisen by divine creation and were constant from creation. Can a scientist express himself more categorically than Linnaeus did in 'Fundamenta Botanica' (1736) and 'Genera Plantarum' (1737), where he formulated his views on the reason for the multitude of species in the following way:

'There are as many species as the number of different forms created by the Infinite Being in the beginning.

These forms have then according to the inherent laws of creation always produced offspring like themselves, so that we do not now find more species than have previously existed.

Thus, there are as many species as there are different forms or structures if we exclude the non-essential deviations (varieties) that are conditioned by the habitat or by fortuities.' Indeed, his definitions were changed later on (Zimmermann 1935), but the definition on the constancy of the species was retained for a long time ('nullae species novae').

In 'Philosophia Botanica' (Linnaeus 1751) expressed, however, his doubt about the fixity of species. He referred to the botanists Marchant and Gmelin, among others, as well as to himself (Linnaeus 1744).

In his early treatise 'Systema Naturae' (1735) Linnaeus arranged all the plants according to their type of sex. His 'Sexual System' was built on a magnificent familiarity with the floral structure of all the plant species that he had investigated by then and his comprehension of the

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fact that plants are also sexual beings with a reproductive act. He cited in this connection Camerarius (1694) and, in particular, Vaillant (1718). But the precision work is his own. The plant kingdom was divided into 24 classes in which the cryptogams are relegated to one 'compartment' (class 24) while the phanerogams (The flower is the plant's delight) are divided into 23 classes on the basis of the number of stamens and the mutual arrangement of stamens and pistils.

The named Peloria paper (1744) signified a de novo contribution. But later on Linnaeus seems to have chosen to ignore it; perhaps he had been influenced by the theological criticism. His interpretation of the manner in which the Peloria arose is erroneous; on the other hand, his conclusion is correct that species are not constant and that they can arise de novo and be altered. Linnaeus' Peloria has been discussed by a great number of subsequent researchers and is also cited in modern surveys.

Discovery of Peloria

The background of the original Peloria is as follows:

In the summer of 1742 a student, Magnus Ziöberg – who subsequently became a jurist and later a presiding judge and who died in Stockholm in 1779 – visited his birth place in the archipelago of Roslagen and took the opportunity to collect plants. He found among other things a strange toad-flax-like plant which he had not previously seen. He pressed it for his herbarium 'unaware of its nature and character and of the great value of his collection' (Fries 1908). The herbarium was given to the renowned professor in Uppsala, Olof Celsius, who found that 'here was something remarkable' and gave the peculiar plant to Linnaeus for identification. The latter remarked first that the plant was a *Linaria* but suspected that flowers from another species had been glued to the herbarium specimen in order to deceive the specialist. Linnaeus, however, opened one of the flowers and observed a floral structure that had never before been observed by botanists. The flowers were so divergent that Linnaeus believed that the plant had come from the Cape of Good Hope, Japan, Peru, or some other distant part of the country rather than from Roslagen. 'Thus, he experienced incredible longing to see this plant alive.'

Ziöberg was prevailed upon to collect new specimens with roots and stems from the remote, original collection locality (Södra Gåsskäret, not far from the island Nord-Ljusterö, Fig. 3). Although this was done and a living collection was planted in the botanical garden at Uppsala, the transplant nevertheless languished.

Linnaeus succeeded, however, in studying the details of a plant before it died. His dissertation on 'Peloria', which was defended by the student Daniel Rudberg – later a physician in the province of Dalsland, where he died in 1797 – was based on it. The disputation took place on December 19 1744. The thesis (in Latin) was written by Linnaeus himself. The respondent Rudberg never saw the plant in the living state.

Linnaeus' enthusiasm, which was easily ignited, had no bounds in relation to this new find. He found the plant to be one of the most amazing he had come into contact with up to this time. And he expressed it in his very personal way. What he said sounded unquestionably dramatic even in Swedish (and in English): 'Nothing can, however, be more fantastic than that which has occurred, namely that a malformed offspring of a plant which has previously always produced irregular flowers now has produced regular ones. As a result of this, it does not only deviate from its mother genus but also completely from the entire class and *thus is an example of something that is unparalleled in botany* so that owing to the difference in the flowers no one can recognize the plant anymore'. And so the famous words of the Peloria find (Fries 1908): 'This is certainly no less remarkable than if a cow were to give birth to a calf with a wolf's head.' (Hoc certe non minus prodigium est, quam si vitulum, capite lupino praeditum, vacca pareret.)

Naming

The plant was called Peloria after the Greek word for monster. 'If we maintain that Peloria had arisen and had been procreated by *Linaria*, we would, not without justification, be inclined to maintain something strange and unbelievable. And it would not appear to be a greater miracle than if apple trees were to produce narcissi, thistles figs and dog-roses grapes.' And naturally Linnaeus referred to Plutarch: 'We cannot seek figs or olives on grape-vine and the common reed forms no figs'.

But is was *Linaria* that gave rise to the monster 'Peloria'. *Linaria*, in English toad-flax, has irregular so-called zygomorphic flowers with four stamens and a single spur (Fig. 1). It belongs to Linnaeus' class Didynamia (family Scrophulariaceae in present-day systems of plant classification). Peloria has a regular, symmetrical corolla with five spurs ('honey houses' or nectaries) and five equally long stamens (class Pentandria) instead of an irregular corolla with one spur and two pairs of stamens of different lengths.

It can be of certain historical interest to mention here that the 'great Goethe' (1820) depicted normal and peloric *Linaria* (Fig. 2). He considered that Linnaeus most aptly designated the find as a monster, i.e. Peloria (p. 241).

How this completely deviating plant arose from the basic type *Linaria*, Linnaeus, of course, did not know.

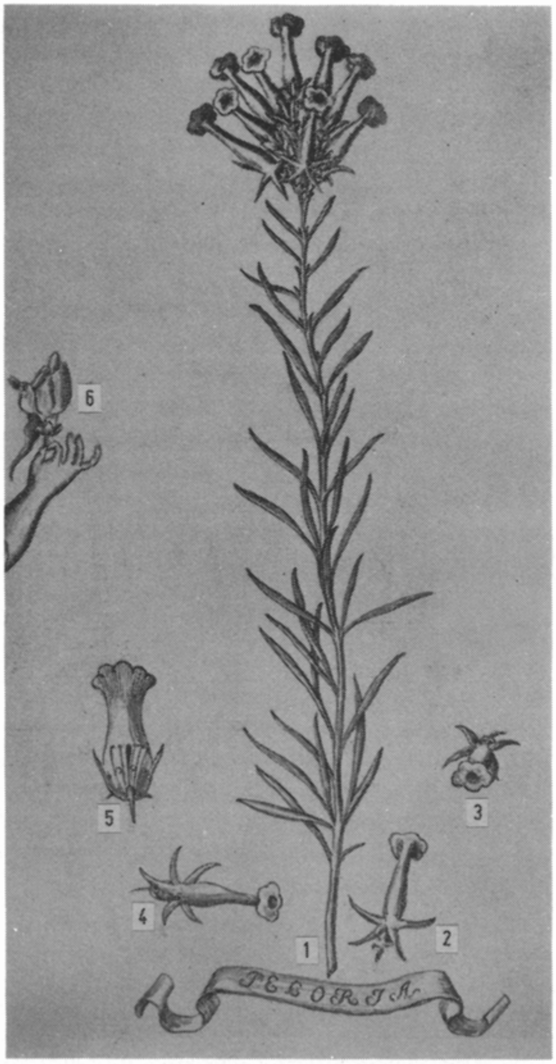

Fig. 1. The original picture of the Peloria, collected the first time in 1742 and then described by Linnaeus in 1744. Note the zygomorphic flower in (6) with one spur and the actinomorphic radial flower in (3) with five spurs

'Quaenam *mutatae* in Peloriam Linariae causa sit, nos adhuc fugit' (Amoenitates acad. 1749). ('The cause of the transformation of *Linaria* into Peloria is to us still unknown.') The italicized word 'mutatae' suggests immediately that Peloria arose as a mutation, which was later confirmed by De Vries (elaborator of the mutation concept, 1901-1903). Linnaeus, of course, was unaware of the existence of genes or chromosomes. He advanced, however, as an explanation of Peloria's origin an extremely daring hypothesis for his day, namely that Peloria has arisen as a result of *Linaria* having been fertilized by pollen of an alien species. 'And yet we could not comprehend that Peloria had arisen in any other way than by such a pollination.' The conclusion was in two ways daring, first because Linnaeus, of course, never could report the other partner in the cross, and secondly – and this is historically essential – because nature, then, would be able to give rise to new species after 'copulation' between known species, yes, even new genera in different classes.

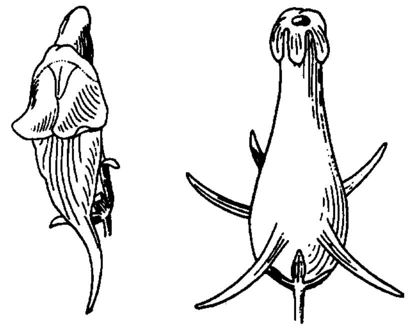

Fig. 2. Goethes illustration of normal-flowering *Linaria vulgaris* (left) and his view of the five-spurred Peloria (right)

Linnaeus' earlier thesis of the constancy of the species and the impossibility that species are created de novo were now invalidated. All species do not derive from the beginning of time and therefore cannot either be direct products of an 'Infinite Being'. In another dissertation by Linnaeus titled 'Plantae Hybridae' (Linnaeus 1751), a number of remarkable plant forms were reported that were held to be species hybrids, among them *Trifolium hybridum* (alsike clover) from *Trifolium pratense* and *T. repens* (red and white clovers), and also some quite impossible hybrids – e.g. hybrids between water clover (*Menyanthes*) and water lily (*Nymphaea*) or lilac (*Syringa*) and jasmine (*Jasminum*).

Nevertheless, it was Linnaeus that was granted the privilege of experimentally producing a species hybrid, namely between the two salsifies *Tragopogon pratensis* and *Tragopogon porrifolius*. That this cross had succeeded was reported in a paper, 'Disquisitio de Sexu Plantarum', which was awarded a prize by the Imperial Academy in St. Petersburg in 1760. Although the purity of the hybrid was denied by the botanist and hybridizer Joseph Koelreuter, who was to become famous in later years, its authenticity is uncontestable (Glass et al. 1968; Nilsson 1953).

Linnaeus' opinion that 'new species' could be formed through crossing provoked annoyance, especially in theological circles. Zimmerman (1953) mentioned a theologist with the same surname as his own that attacked Linnaeus for his view. Carl von Linné Jr. defended his father against the charge of being an atheist because of his interpretation of how Peloria arose (Gertz 1927). The later Bishop J. Browallius wrote in a letter directly to Linnaeus (Browallius 1745) that 'your Peloria has upset everyone... At least one should be wary of the dangerous sentence that this species had arisen after the Creation'.

Linnaeus concluded the Peloria dissertation with the following words: 'If with certainty it could be established that Peloria is a hybrid herb that traces its origin from Linaria and another plant, then, a new truth from this would emerge within the plant kingdom, and this of greater importance than that which has been in the animal kingdom, for in the latter the offspring lack the ability to reproduce, such as mules and hinnies, and other similar animals. That Peloria reproduces itself anew is evident in that it has fully developed seeds, and that it increases itself abundantly in its habitat.' If *Linaria* does not arise again from Peloria, a fantastic conclusion follows as a consequence, namely *that it can occur that new species arise within the plant kingdom; that genera, which as regards the organs of fruitification are different* can have the same origin and nature: yes, that in one and the same genus *different organs of fruitification* can be found' (italics by Linnaeus).

'In our Peloria all the knowledgeable persons within our science would thus with justifiable surprise observe an amazing creation of nature.'

The conclusion is there, in the clear text of Latin: 'ut novae in regno vegetabili species proveniant'.

Fries (1908) indeed remarked that Linnaeus' expectations of continued success with Peloria aborted because other specimens of toad-flax were found that had both normal and peloric-like flowers in the same inflorescence, as well as intermediate forms between the two types of flowers. And Hofsten (1959) mentioned that Linné Jr. had told the German botanist Johann Beckmann that his father, 'after Peloria had fallen short of his expectations, no longer wanted to hear any more said about this plant'. In Flora Suecica (1745), Linnaeus himself wrote: One can read 'a stupid description' of this plant's change in the dissertation on Peloria 1744. – In the same Flora, (Linnaeus 1755) it is succinctly stated: 'Peloria dicta', so-called Peloria.

The above-mentioned Beckmann wrote, however, in his diary (Schwedische Reise in den Jahren 1765-1766): 'In der That bleibt die Peloria dennoch eine ausserordentliche Pflanze, indem man noch kein ähnliches Beispiel einer selbst in der Blume so weit abweichenden Varietas weis. Scheint es nicht, dass die Varietates einmal eine ganze Veränderung und Reformation unser Botanik machen werden?' (Gertz 1927). (Actually, it is, however, so that Peloria remains a highly remarkable plant, for no one has as yet discovered any similar example of such a variety deviating even in the flower. Can it not be so that varieties at one time will totally change and renew our botany?)

For a long time, Linnaeus regarded his Peloria as a hybrid and called it still in Species Plantarum (1762/63) 'a marvel of nature'.

Linnaeus' conception of Peloria was, however, in spite of his enthusiasm so mixed with doubt and religious caution that he in later years of his life was never able to formulate an entirely new species concept; but the concept that served as the basis for his interpretation in the original edition of Systema Naturae was abandoned. Finally, he deleted in later editions also the sentence 'that no new species arise' (Hagberg 1939).

Fig. 3. The locus classicus of Linnaeus' Peloria: probably Skarpskär, in the archipelago of Roslagen, northeast of Stockholm (after Linnell 1953)

Linnell (1953) was surprised in the same way as Linnaeus by a Peloric *Linaria* in a school boy's herbarium. The locality of the find was also in this case an islet in Gälnafjärden not far from Ljusterö (Fig. 3). All the flowers in the inflorescence were regular, thus forming a complete parallel to the original specimens and in contrast to other numerous finds of mixed flower types. Linnell discusses in his paper whether the locality given by Linnaeus (Södra or Lilla Gåsskäret) is the correct one. Possibly a mixup in the name of the original Peloria locality has occurred. Linnell found, namely, that peloric *Linaria* only occurred on the islet Skarpskär north of Gåsskäret. It is not wholly certain that this conclusion is correct. But perhaps Linnell, 210 years after Ziöberg, did find the peloric Linaria specimens 'in considerable numbers' at the locus classicus, dating back to the 18th century or still earlier.

The terms 'peloria' and 'pelorism' have become accepted concepts in botany. Flowers of 'peloria character' have been found in a number of genera and species. Some of these will be mentioned below. Of special interest are those observations and investigations that have been conducted by two other great men within the theory of evolution, that is, Darwin and De Vries – by the former in his comprehensive work The Variation of Animals and Plants under Domestication (1868) and by the latter in his, in compass, equally extensive work Die Mutationstheory (1901-1903).

Charles Darwin had a great admiration for Linnaeus' contributions but in the subject index of the above-named encyclopaedic work, Linnaeus' name is mentioned in only five places: once as the 'great Linnaeus' and further, in conjunction with the cultivation of tobacco in Sweden, sterility of alpine plants in gardens, characteristics of individual reindeer, and Duchesne's discovery of the wild strawberry with entire instead of trifoliate leaves. Not once is Linnaeus mentioned under 'peloria' or 'pelorism'.

The usages 'peloria' and 'pelorism' occur, however, in several places – under *Linaria* five times in the subject index, under peloric flowers twice, peloric races once and, especially extensively, twice under pelorism. The discussions are in part quite comprehensive. For *Gloxinia speciosa* and *Antirrhinum majus*, Darwin wrote that peloric races can be reproduced by seed and that they in structure and appearance differ from the common forms of the two species 'in a wonderful manner'. In Part II of his book, Darwin cited a number of botanists that had studied the occurrence of 'pelorism'; in a large number of species belonging to the genera *Linaria, Antirrhinum, Gloxinia, Teucrium, Galeobdolon, Calceolaria* within the families Scrophulariaceae and Labiatae, but also in *Tropaeolum, Laburnum* and *Corydalis*.

New and significant is Darwin's study of the inheritance of pelorism. He crossed a peloria variant in snapdragon with the mother variety and found that the hybrid was always like the latter, thus, normal in structure. In the next generation, which arose after self-pollination, 37 of 127 investigated plants were entirely peloric. This indicates indubitably a 3:1 segregation in the Mendelian sense; that is, the pelorism in snapdragon is at least a clearly recessive character and is caused by a single gene. Darwin philosophized on this ratio – which Gregor Mendel immediately would have been able to interpret – and resorted to his strange hypothesis of pangenesis to explain how the character pelorism was able to disappear in the first hybrid generation and then appear again in the second generation. Darwin found, however, similar to present-day researchers (Stubbe 1966) that in the hybrid a certain tendency to pelorism can occur (weak 'manifestation').

It is now that a strange circumstance occurs. Mendel had critically read parts of Darwin's Animals and Plants under Domestication. In the text of Part I, Mendel made only a few notations. Mostly, Part I remained, however, 'uncut' (Orel 1971). Part II, on the other hand, was read more carefully, and Mendel made no fewer than 57 marginal notations. Unfortunately, this was mainly the case in Chapter 27 of the work, the one that treated the hypothesis of pangenesis. Mendel understood evidently the weak points in this theory. If Mendel had read Darwin's data on the cross 'peloric × normal *Antirrhinum*' and its segregation, he would certainly have realized immediately that a ratio existed here that agreed with what he himself had obtained in peas and beans. (Mendel had, moreover, used *Linaria vulgaris*, unfortunately not peloric *Linaria*, in crosses with other species of *Linaria*). Probably, Mendel missed this unique chance to elucidate Darwin's data owing to an oversight. No notations by Mendel are present in the chapter of Part II dealing with 'inheritance' (Orel 1977 personal communication).

On the other hand, Darwin made a similar but more obvious miss when he perused a critical paper on speciation by the German botanist H. Hoffmann. Darwin cited pages of this paper where Mendel's name is also mentioned (Darwin 1876; Gustafsson 1965). Darwin missed Mendel's essay and his data; Mendel, on the other hand, missed in Darwin's work that information which could have verified his own presentation. Tragic? Or the lottery of chance that could have been turned into a historical triumph?

Through a series of investigations reported in Stubbe's monograph (1966) of 'Genetik und Zytologie von *Antirrhinum* L. sect. *Antirrhinum*', we know that in snapdragons, 'radial' (peloric) flowers are inherited in a simple fashion, but also that a series of transitional forms exist between the completely radial flowering types (with the gene cycloidea radialis cyc^{rad}) to fully normal, zygomorphic flower types (with the gene $Cyc = cyc^{+}$, Fig. 4). 'The zygomorphic flower form is transformed by multiple alleles through a series of intermediates into a radial flower form' (Stubbe 1966). The segregation occurs mostly according to a 3:1 ratio but is complicated sometimes as a result of coupling to sterility factors.

As regards pelorism and seed viability, Darwin noted a

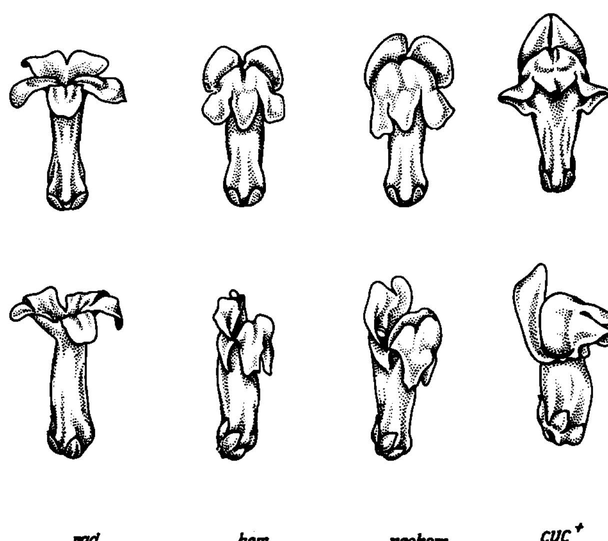

Fig. 4. The radialis series of flower morphology in *Antirrhinum majus* (cyc^{rad} is an extreme form of pelorism, cyc^{hem} and cyc^{neohem} are transitional steps to the normal type (after Stubbe 1966)

variable behaviour. In the common toad-flax (*Linaria vulgaris*) the peloric form is in most instances more or less seed-sterile, whereas in the snapdragon predominantly viable seeds are produced. *Corydalis solida* behaves like common toad-flax; *Gloxinia* like snapdragon. The number of stamens is usually increased in peloric forms: five instead of four in toad-flax and six instead of four in snapdragon.

Darwin (1868) included an interesting investigation on the anatomic-physiological background of pelorism. That species with irregular (zygomorphic) flowers can give rise to forms with regular (actinomorphic, radial) flowers, was often regarded as an atavism – a reversion to a more primitive stage. Such cases can, however, just as well be construed as disturbances during the growth of the flower, often genetically conditioned, but also modificative, that is, elicited by an altered external environment – e.g. deviating day length, unfavourable nutritional conditions. The actinomorphic flower form in the peloric variants can signify that the development of the flower is blocked at an early stage since the floral organs are regular in early stages but subsequently grow out into their zygomorphic, specialized form. In an investigation, Gentcheff and Gustafsson (1940) observed that flowers of *Pisum* varieties lost their zygomorphic structure if the plants were grown in the dark. All the stamens were then also free from one another. Darwin discussed the morphological details of peloric forms in a series of species (Darwin 1868).

In Mutationstheorie I-II (1901-1903), as in his work Arten und Varietäten und ihre Entstehung durch Mutation (1906), De Vries thoroughly treated the concept of the constancy of species, the importance of hybridization for speciation and, above all, the great variation that appears in the morphogenesis of the peloric character. He was both more detailed and more genetically inclined than Darwin. As regards the genetic aspects, this is natural. De Vries was, of course, the first rediscoverer of Mendel's crossing analyses.

De Vries emphasized that Linnaeus, by introducing a binary nomenclature (which, however, in some measure had existed earlier, although in no way consistently effected: cf. Zimmermann 1953) created the modern species concept. Before Linnaeus the species were not regarded as being the natural units in the classification systems of organisms. De Vries also maintained that Linnaeus must have been arawe that this species were 'composite species' and not true units. He forbade his protegés to study the still smaller constituents (the varieties) that he himself in certain cases, however, assigned separate names. In this unclarified systemization of genera, species and varieties, the Peloria (*Linaria*) gave him important impulses. It fascinated him. But the cramps of old age and the constraint of religion prevented him from renewing his genial analysis of the organism world.

De Vries investigated, beginning in 1886, peloric characters in both *Linaria* and *Antirrhinum*. He had also, in his extensive cultivations, established the mutation rate of peloric *Linaria* (De Vries 1906). Of 1,750 flowering progeny plants (after crossing, because *Linaria vulgaris* is self-sterile), 16 plants were peloric, viz. a spontaneous rate of about 1%. The mutation also appears in different materials; it is thus an expression of a law-related phenomenon. Only in exceptional cases does self-pollination result in seed progeny. After open flowering of the peloric plants, 106 peloric and 13 normal individuals were obtained from the harvested seed. Unfortunately, De Vries did not determine the genetic constitution (genotypes) of the last-mentioned plants. He never cultivated their seed progeny.

Besides the extreme five-spurred mutant, De Vries (1901) described transitional forms, that is, partially peloric plants: normal-flowered individuals with occasional peloric flowers. These transitional forms were highly variable, for the most part possessing only a single peloric flower, at times two or three flowers. They occurred in garden culture as well as in nature. The variation fluctuated from year to year. These cases of pelorism were designated by De Vries as 'hemipeloria' and were assumed to have semilatent traits, which were expressed only sporadically. But 'hemipeloria' also has a genetic background. This was investigated in detail (De Vries 1901). From 'hemipeloria' the extreme peloria type can be formed. Possibly in these cases also a series of labile genes (alleles) occur which are similar to those that have been described in *Antirrhinum* (Stubbe 1966).

De Vries (1906) also detected an entirely deviating form of pelorism (Fig. 5). The floral structure in Linnaeus' Peloria (*Linaria*) can from a morphological point of view be regarded as a five-times-repeated middle part of the lower lip. In a similar way, one can, De Vries said, conceive that some other part in the corolla would be able

Fig. 5. A second type of pelorism studied by De Vries (1906). The flower entirely lacks spurs

to be repeated five times. In that case, no spur would need to be formed, not any orange pigmentation need occur in the upper part of the corolla. Such forms actually exist, even if they are rarer than the five-spurred mutants. De Vries illustrated such a regular variant with tubular flowers lacking spurs (1906). Unfortunately, the frequency of the variant and its genetic character are unknown. De Vries (1903) mentioned, however, that the French botanist Ch. Naudin carried out crosses between *Linaria vulgaris peloria anectaria* (without spurs) and *Linaria vulgaris*. The hybrids had one-spurred flowers. The loss of spurs thus seems to be a recessive trait. This form 'anectaria' produced occasional seeds that in turn gave rise to new anectaria individuals (De Vries 1901-1903).

De Vries enumerated, in his collective works, a large number of researchers that investigated the formation of peloric plants. Furthermore, he listed a large number of species in which peloric flowers were found, often induced by environmental conditions, sometimes certainly in conjunction with the genetic constitution.

The picture of Linnaeus' monster, his Peloria, the way it arose and its probable inheritance should thus now be, on the whole, evident. The original find represented a stable variant, probably strongly vegetatively spread (through adventitious buds on the roots), but also with a weak ability to form germinable seeds. This Peloria enraptured Linnaeus in the light of something entirely new, but it also changed his conception that 'all forms once had been created in paradise' (De Vries 1901). Species could be transformed into new species by 'hybridization'.

Linnaeus was not the first botanist to identify a mutation; thus, he was not the first 'mutationist'. That 'rank' must in later times be given to the pharmacist Sprenger of Heidelberg who in 1590 found a celandine (*Chelidonium majus*) with strongly lobed (laciniate) leaves in his drug garden (Roze 1895). A similar laciniate form was described by the Frenchman Marchant (1719) in a mercury species (*Mercurialis annua*). Linnaeus cited this last-named find in his Peloria paper. Later, similar laciniate mutants were observed in innumerable plant genera, trees and bushes, as well as in herbs. Duchesne's entire-leaf form of *Fragaria vesca* (monophylla) arose in 1761 (Gertz 1927; Hylander 1945). In contrast to what De Vries opined (1901), it was never collected by Linnaeus during his Lappland journey. Even if his Peloria was not the first described case of a spontaneously arisen mutant, it has, however, contributed to molding the approach that in time would lead to Darwin's Origin of Species (1859) and later on to De Vries' Mutations theorie (1901/1903).

Two hundred years after Linnaeus' Peloria, Richard Goldschmidt (1933, 1940) appropriated the term 'monster': 'hopeful monster', without citing Linnaeus in his discussions, on the mechanisms of evolution. By this expression, Goldschmidt meant that the conception of speciation that had come to dominate the theory of evolution – namely that species are formed through a successive assemblage of 'small mutations' – was inadequate. Changes in developmental rhythm and in the speed of individual physiological processes can bring about drastic reconstructions of the morphological structures (cf. Darwin's discussion on the way pelorism arises, p. 6.) 'Monsters' are thus not always doomed to a rapid extinction; they can also be 'hopeful' and effect a form of macroevolution. Goldschmidt's model received little response within zoological evolutionary theory. It is, however, possible that plant species behave differently, even though Linnaeus' Peloria cannot be labelled as a 'hopeful monster'.

Note here, however, Linnell's find again in 1953 of possibly the same population that Ziöberg observed 210 years earlier, in 1742: In certain plant species, 'monsters' can thus survive centuries also in nature. There is no reason to consider here, in detail, the extensive literature that has been amassed as regards vital and lethal mutations in cultivated and wild species. Only one reference may be cited, namely from Stubbe and Wettstein (1941; see also Stubbe 1966). They pointed out that recessive or dominant mutations drastically can change the flower structure in *Antirrhinum* and that these form transitions to other wholly independent plant genera. Thus, for example, the mutants fistulata, radialis, Hirzina and transcendens resemble members of the genera *Rhinanthus, Verbascum, Linaria, Calceolaria, Veronica*, etc., all within the family Scrophulariaceae. The mutation 'radialis' is, in its extreme form, a peloric mutant and often produces viable seeds.

Linnaeus' monster was perhaps not hopeful in the sense of Goldschmidt, but just the same no 'dead end' in the history of biological thinking. Perhaps, it hinted at those processes that have influenced the evolution of the plant kingdom throughout millions of years. In this sense, Linnaeus' dissertation on Peloria is also to be designated as one of the classics of botany.

In Forerunners of Darwin (Glass et al. 1968) and in the English edition of Stubbe's History of Genetics (1972), Linnaeus' contributions within systematics and speciation research are described briefly but satisfactorily. Peloria is discussed in both surveys. Its importance for Linnaeus' later species concept is emphasized. In Plant Hybridization before Mendel (Roberts 1929), in addition to a series of other hybrids, Linnaeus' unequivocally true, experimentally produced *Tragopogon hybrid* is discussed. Peloria is not mentioned there.

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Literature

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