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Sexual reproduction and variation in floral morphology in an ephemeral vernal lily, *Erythronium americanum*

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Summary. In a riparian population of *Erythronium americanum* (Liliaceae) in central New Jersey, experimentally self-pollinated plants produced markedly fewer fruit and fewer seeds per fruit than hand-outcrossed and open pollinated plants, even though differences were not evident between pollen tubes that penetrated stigmas from self or foreign pollen. This weak self-compatibility and a positive relation between the percentage of seeds set by outcrossed plants and the distance between pollen donor and recipient plants indicate that this population could be susceptible to inbreeding depression.

Limited resources for seed development apparently constrained maximal seed production, based on low seed set (40.6%) by hand-pollinated plants and positive correlations for these plants between plant size and the number and size of seeds set. In contrast, naturally-pollinated plants set a smaller proportion of their ovules, suggesting that limited pollinator service reduced the quantity of seeds produced in this population. Free-foraging bees usually removed more than half of the available pollen in a single visit, so that individual plants probably have few opportunities to disseminate their pollen.

Even though sexually reproductive ramets produce only a single flower per year, less than a third of variation in floral morphology is associated with variation in plant size. Within the flower, the sizes of some closely associated structures, such as the style and ovary, and the anthers and filaments, vary essentially independently of one another. Production of nectar and pollen, the ultimate attractors of pollinating insects, was positively correlated with flower size.

Most current interest in pollination centers on the physiological and ecological processes of floral biology, such as pollen tube growth, fruit development and abortion, pollinator movements, etc. (see Jones and Little 1983; Real 1983). In contrast, intraspecific variation in floral morphology has been relatively neglected. Floral morphology plays a multifaceted role in reproduction of animal-pollinated plants through its effects on pollinator attraction and handling time, pollen flow, and the incidence of selfing (Morse 1978; Schoen 1982; Harder 1983; Waser and Price 1984; Thomson and Stratton 1985). Hence morphological variation could influence reproductive success within a plant population and, if the variation was genetically controlled, it could also provide the substrate for evolutionary change. The diversity of floral forms, particularly divergent flower forms in some closely-related plants (e.g. Grant and Grant 1965; Muller 1979; Macior 1982) and convergent forms of unrelated species (e.g. Grant and Grant 1968), indicate that floral morphology is very responsive to selective forces.

In this paper we consider morphological variation within a population of *Erythronium americanum* Ker (Liliaceae – Tulipeae), a common member of the ephemeral vernal herbaceous flora of deciduous woods in the northeastern United States and southeastern Canada. Because environmental rather than genetic effects often dominate variation in plant size (e.g. Antonovics and Primack 1982), we first examine the extent to which flower size and seed production are related to plant size. We then address three specific questions related to the pollination process: whether production of the ultimate attractors of pollinators (nectar and pollen) is correlated with potential proximate cues for flower choice, such as flower size; how stylar exsertion, a feature which affects the likelihood of self-pollination, compares in the purportedly self-incompatible *E. americanum* (Bernhardt 1977) and a self-compatible congener, *E. grandiflorum* Pursh (see Thomson and Stratton 1985); and what proportion of available pollen do bees remove in a single visit. Interpretation of our results necessitated analysis of the breeding system of *E. americanum* which we also present here.

Materials

Sexually reproductive ramets of *E. americanum* produce two basal leaves and a single nodding flower from an annually dormant corm. The flower includes six tepals and six stamens, each in two whorls of three. Anthers of stamens associated with the outer whorl of tepals (outer stamens) dehisce synchronously shortly after the tepals reflex; the inner anthers usually dehisce one day later. Flowers persist for several days, probably lasting longer if unpollinated (cf. Schemske et al. 1978; Motten 1983). Nectar is produced at the tepal bases, and bees from several families visit the flowers for nectar, pollen, or both. Fruit are dehiscent capsules, which contain several to many large seeds.

The *E. americanum* we studied comprised part of a larger population on an island in the Raritan River near Raritan, New Jersey (40°33′ N; 74°38′ W). Although *Ery-*

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thronium grows at varying densities over most of this island, flowering occurs primarily at sites near the river which were subject to spring flooding. Silver maple (*Acer saccharinum* L.) and box elder (*A. negundo* L.) dominated the canopy at these sites and spicebush (*Lindera benzoin* (L.) Blume) formed the shrub layer.

Methods

Morphometry

To characterize relations between morphological features of *E. americanum* we collected plants with fully-formed flower buds on April 14 and 21, 1984. Most of the plants collected had mature, but unopened flower buds; however, 33 of the plants gathered on April 21 had fully opened flowers with dehiscent outer anthers. We picked these latter flowers in the morning before pollinators became active and measured the volume of nectar they contained with capillary tubes. The remaining plants were taken to the laboratory and placed in individual water-filled tubes where most flowers opened the next day.

For each flower collected we measured some or all of the following characters; length of an inner and outer tepal, lengths of the filament and dehisced anther from an inner and outer stamen, ovary and style length, and ovule number. Linear measurements were taken with calipers to the nearest 0.1 mm. In addition, each plant's two leaves were removed at the point where the leaf base no longer completely ensheathed the flower scape. We measured the area of each leaf with a video scanner and digitizer connected to a ModComp IV/25 minicomputer.

Before anther dehiscence we removed either the inner anthers or all anthers from about half of the flowers collected. These anthers were placed in a separate vial for each stamen whorl from each plant. After they dehisced in the vial we preserved the pollen by adding 70% ethanol. The size frequency distribution and the total number of pollen grains for each plant were estimated with the aid of a Coulter Counter (model TAII). Pollen from one whorl of stamens was suspended in 200 ml of constantly stirred salt water (0.1% NaCl). The counter draws off 2 ml subsamples of this mixture, monitors the magnitude and frequency of changes in electrical resistance as particles pass through a small aperture (400 μm), and provides the frequency of particles in 16 size classes that are equally spaced on a logarithmic scale. We counted the pollen grains (particles in five size classes between 16.0–50.8 μm) in five subsamples from each sample. The average standard error of the counts of these subsamples, expressed as a percentage, was 4.9%.

Breeding system

Some of the flowers that were emasculated prior to anther dehiscence were used to investigate the ability of the flower's own (self) pollen to produce pollen tubes in comparison to pollen from another plant (outcross). After anthesis, stigmas were pollinated with either self or outcross pollen and set aside for 24 h. The styles were then excised at the top of the ovary, fixed in 70% ethanol, slit longitudinally, stained with aniline blue (0.1% in 1 M K_3PO_4 acidified with HCl until the solution turned blue) followed by acetocarmine (45% acetic acid saturated with carmine) and mounted on a microscope slide. We assessed the length of pollen tubes relative to the length of the style at 100×.

On April 20 and 21 we hand-pollinated flowers to determine some of the reproductive characteristics of *E. americanum*. Fully-formed buds on marked plants were emasculated on April 20 and two indehiscent anthers from each bud were placed in an individual vial. These buds were then bagged to open in isolation from pollinators. The next day these flowers received one of three randomly-assigned pollination treatments; self pollen, outcross pollen, or self pollen followed by outcross pollen after 20 to 60 min (self outcross). A fourth pollination treatment (open pollinated) included unbagged, marked plants. All but the open-pollinated plants were bagged until May 26 when the nearly mature fruit were collected. At that time we opened the fruit, dried the seeds to a constant mass in a 80° C oven and weighed each seed individually.

Pollen removal by bees

To estimate the amount of pollen that can be removed by a single insect visit, we exploited the staggered anther dehiscence of *E. americanum*. On April 20, screen cages were placed over individual plants with mature flower buds to exclude insects. The next day we uncovered each plant when the outer whorl of anthers had dehisced and observed the plant until it had been visited by a bee. We then removed the anthers from each stamen whorl and placed them in separate vials. Pollen from these anthers was handled and counted as described above. Because the number of pollen grains in intact outer anthers is highly correlated with the number of grains in inner anthers ($r=0.947$, $n=48$, $P<0.001$), we could estimate the amount of pollen available in each flower before the bee visit and compare it with the amount remaining after the visit.

Results

Morphological relations

Variation in floral morphology such as that evident in *E. americanum* (see Table 1) could result from variation in overall plant size, and from sources unique to the flower. To assess the proportion of floral variation due to plant size, we analyzed the canonical correlation between several floral characters (style, ovary and inner tepal length, ovule number and the number of pollen grains in the inner anthers) and the areas of the two leaves (all variables were $\log_{10}$ transformed to normalize their distributions). Because total leaf size is highly correlated with total plant biomass (*E. americanum*, $r=0.98$, Wolfe 1983: *E. japonicum*, $r=0.92$, Kawano et al. 1982), we use leaf area as an indicator of plant size. Only one of the two possible pairs of canonical variates for 54 plants had a canonical correlation significantly different from zero ($R_c=0.695$, $F_{10,94}=3.723$, $P<0.001$). Based on redundancy analysis of these results, the first canonical variable for leaf area explained 86.0% of the combined variation in the leaves, but only 31.5% of the floral variation. In particular, canonical leaf area accounted for the following proportions of variation in floral characters: style length, 0.5%; ovary length, 39.2%; inner tepal length, 36.7%; ovule number, 37.1%; pollen count for inner anthers, 26.8%. These results indicate that ap-

Table 1. Some morphological features of sexually reproductive *Erythornium americanum* plants collected near Raritan, New Jersey. Descriptive statistics were estimated from log transformed characters, hence the asymmetric standard deviations

Character	Lower standard deviation	Mean	Upper standard deviation	Sample size
Leaf area (cm^2)				
Large leaf	14.0	19.0	25.8	125
Small leaf	6.3	9.1	13.2	125
Tepal length (mm)				
Outer	23.2	26.0	29.3	89
Inner	23.6	26.9	30.6	128
Style length (mm)	10.3	11.2	12.1	97
Ovary length (mm)	5.3	6.3	7.4	97
Ovule number	36.1	44.8	55.6	127
Filament length (mm)				
Outer	9.9	10.9	12.0	35
Inner	8.1	9.0	9.9	36
Anther length (mm)				
Outer	5.3	6.4	7.6	35
Inner	5.4	6.1	6.8	36
Pollen count				
Outer	37,650	48,610	62,750	48
Inner	40,270	52,540	68,530	85
Pollen Size (μm)				
Outer	28.2	29.3	30.4	47
Inner	27.3	28.7	30.1	82
Pollen/ovule ratio	1,813	2,255	2,805	43
Nectar volume (μl)	0.024	0.059	0.143	33

proximately two-thirds of the observed variation in floral characters is independent of variation in plant size.

In addition to considering the pattern of overall variation in floral morphology we examined several specific morphological relations. The first question asked whether the floral resources sought by flower-visiting insects were quantitatively related to flower size. For the 33 flowers for which nectar was measured, nectar volume was positively correlated with the length of the inner tepals ($r=0.447$, $P<0.01$). The amount of pollen produced by inner and outer anthers was similarly correlated with tepal length ($r=0.487$, $P<0.001$, $n=79$; $r=0.360$, $P<0.025$, $n=42$, respectively: all correlations based on $\log_{10}$ transformed data).

We also considered exsertion of the style beyond the dehiscent stamens, a feature which could affect the incidence of self-pollination. In this population of *E. americanum* stylar exsertion depended on the stamen whorl considered. On average the style was equal in length to the outer stamens (mean $\pm$ SD exsertion $= -0.1 \pm 1.42$ mm, $n=35$), but was 2.2 ± 1.23 mm ($n=36$) longer than the later-dehiscing inner stamens. This difference resulted from different filament lengths of the outer and inner stamens (see Table 1). Interestingly, although outer tepal length, a measure of flower size, was significantly positively correlated with the size of all structures that contribute to stylar exsertion (lengths of the style, ovary, filaments and anthers; $P<0.005$ in all cases except inner anther length ($P<0.05$)), tepal length was not correlated with exsertion of the style relative to either the inner ($r=0.134$, $P>0.25$, $n=36$) or outer stamens ($r=-0.140$, $P>0.25$, $n=35$). This condition probably results from the small amount of variation shared by the components of the pistil (style and ovary, $r^2=0.088$, $P<0.005$, $n=97$) or the stamens (inner filaments and anthers, $r^2=0.055$, $P>0.1$, $n=36$; outer filaments and anthers, $r^2=0.003$; $P>0.5$, $n=35$).

Table 2. The amount of pollen removed from the inner anthers of *Erythronium americanum* flowers during a single bee visit. See Methods for an explanation of the estimation of the pollen removed

Bee species	Duration of flower visit (s)	Estimated number of pollen grains removed	Percent removed
Apis mellifera		23,910	26.8
		72,600	86.5
	70	33,740	64.6
Andrena carlini		21,650	65.9
	289	40,240	61.3
	40	39,280	45.3
	36	20,160	59.6
	12	33,620	50.3

Reproductive biology

Insects we observed visiting *Erythronium* flowers included primarily a large andrenid bee (*Andrena carlini* Cockerell), honey bees (*Apis mellifera* L.) and, less commonly, bombyliid flies (*Bombylius* sp.) and bumble bee queens (*Bombus bimaculatus* Cresson). All of these insects probed flowers for nectar and *A. carlini* females and honey bees also collected pollen. Single visits of pollen-gathering bees resulted in removal of 26.8–86.5% of the pollen available in previously caged plants (Table 2). The duration of some of these visits was abnormally long, probably due to accumulated nectar in the flowers. One honey bee in this sample interrupted her visit to hover in front of the flower, groom the pollen from her body, pack it in her corbiculae and resume feeding from the same flower.

All pollination treatments resulted in some fruit production (Table 3); however, the proportion of plants that produced fruit differed between treatments ($G=11.81$, 2 d.f., $P<0.005$). In particular, self pollinations resulted in significantly fewer fruits than outcross and self + outcross pollinations combined ($G=11.00$, 1 d.f., $P<0.001$), but these latter two treatments did not differ from one another ($G=0.81$, 1 d.f., $P>0.5$). In the pollen tube growth experiments, 2 of 6 self treatments resulted in no tube growth, but the other treatments resulted in the growth of tubes along the full length of the style which was indistinguishable from that observed in the 7 outcrossed styles.

The percentage of ovules producing seeds in flowers that developed fruit also depended on pollination treatment (Table 3). Flowers from this population contained from 29 to 80 ovules (see Table 1) and the percentage of seeds set ranged from 2.9% to 84.9%. The observed significant differences in percentage of seeds set ($F_{3,76}=8.35$, $P<0.001$) resulted from lower seed set in selfed flowers compared to other treatments (based on Tukey-Kramer multiple comparisons, $P=0.05$), and lower seed set by open-pollinated plants compared to outcrossed plants. Outcrossed and

Table 3. The effects of different pollination treatments on fruit and seed production by *Erythronium americanum*

	Pollination treatment			
	Selfed	Out-crossed	Selfed + out-crossed	Open
Fruit set				
Yes	10	24	16	
No	20	8	9	
%	33.3	75.0	64.0	
Seed set (%)				
Mean	10.5	41.2	39.6	29.4
SE	2.68	3.68	3.35	2.69
n	7	23	13	37
Average seed mass[a] (mg)				
Mean	3.8	3.6	3.6	4.5
Lower SE	3.56	3.44	3.27	4.35
Upper SE	3.98	3.78	3.91	4.75
n	5	22	13	33

[a] Based on $\log_{10}$ transformed data, hence the asymmetrical standard errors

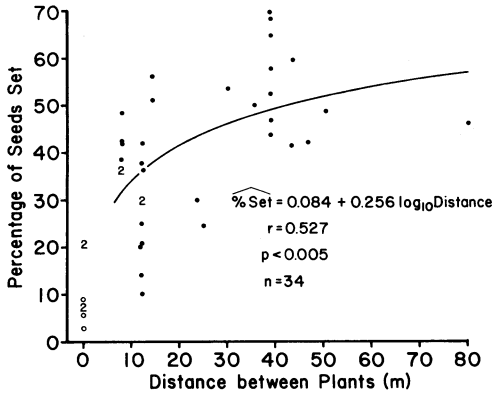

Fig. 1. Percentage of seeds set per fruit in relation to the physical distance between the pollen donor and recipient plant. Plants at 0 m were self pollinated and were not included in the estimation of regression statistics. A logarithmic model was fit to these data because it provided a slightly better explanation of the observations ($r^2=0.279$) and the 80.1 m cross had considerably less influence on the parameter estimates (Cook's $D=0.079$: Draper and Smith 1981) than for a linear model ($r^2=0.259$, $D=0.850$), due to the logarithmic scaling of distance

self+outcrossed plants set equivalent proportions of their ovules.

The average size of seeds in fruits resulting from different pollination treatments also differed significantly ($F_{3,69}=4.98$, $P<0.005$; see Table 3). Open-pollinated plants produced significantly heavier seeds than outcrossed or self+outcrossed plants (based on Tukey-Kramer multiple comparisons, $P=0.05$). Seeds produced by selfed flowers did not differ in size from those of plants subjected to the other pollination treatments. Because average seed size was not correlated with the number of seeds in a fruit, either within pollination treatments or overall ($P>0.05$ in all cases), these results are independent of the proportion of seeds set. Because open pollinated flowers were not bagged during fruit maturation, in contrast to hand pollinated flowers, it is not possible to distinguish between whether pollination treatment or bagging was responsible for observed differences in average seed size. Pollination treatment did not affect variation in seed mass within a fruit as represented by the standard deviation of mass for each fruit (Kruskal-Wallis test, $X^2=4.96$, 3 d.f., $P>0.1$; based on $\log_{10}$ transformed seed masses to remove the dependence of the standard deviation on average seed mass).

To examine whether plant size and pollination treatment interacted to affect reproductive output by *E. americanum* we considered seed production in relation to ovule number. Because we collected fruits after the leaves had degenerated, this analysis relies on the positive correlation between leaf area and ovule number ($r=0.516$, $P<0.001$, $n=124$: see also Wolfe 1983). For both open pollinated ($n=33$) and hand-outcrossed plants (outcrossed and self+outcrossed; $n=35$) the percentage of seeds set was not correlated with ovule number ($r=0.018$ and -0.087, respectively; $P>0.5$), In contrast, the number of seeds set and their average mass were positively correlated with ovule number for hand-outcrossed plants ($r=0.436$ and 0.552, respectively; $P<0.01$), but not for open pollinated plants ($r=0.285$ and -0.008, respectively; $P>0.1$).

Within outcrossed and self+outcrossed flowers, percentage seed set was positively related to the physical distance between the pollen donor and recipient (Fig. 1). We did not observe a similar effect of outcrossing distance on fruit set. Neither average seed mass per fruit ($r=0.203$, $n=34$, $P>0.05$), nor the standard deviation of seed mass ($r=-0.033$, $n=34$, $P>0.5$) for outcrossed and self+outcrossed plants correlated significantly with outcrossing distance.

Discussion

Breeding system

Bernhardt (1977) concluded that *Erythronium americanum* from New York was self-incompatible after finding no fruit set in flowers bagged to exclude insects; however, his experiments could not distinguish between lack of self-compatibility or lack of self-pollination. Our observations indicate that "self-incompatibility" exists in the statistical sense that self-pollination produces many fewer fruits and seeds than cross-pollination, but that it is far from complete. Equivalent growth of pollen tubes following self and outcross pollinations suggests that reduced fruit production by selfed plants was not an outcome of style-pollen tube interactions. The style of *E. americanum* is hollow and pollen tubes grow along the inner wall of the central lumen, a condition associated with incompatibility systems that involve ovarian inhibition (de Nettancourt 1977). Based on the equivalent fruit and seed set we found in outcrossed and self+outcrossed hand pollinations (Table 3), prior deposition of self pollen does not appear to inhibit the success of later outcross pollen in *E. americanum*.

The positive relation between the proportion of seeds set (seeds/ovule) and the distance between parents (Fig. 1) suggests continuously varying inbreeding depression in conjunction with a restricted genetic neighborhood size as observed in *Delphinium nelsonii* and *Ipomopsis aggregata* by Waser and Price (1983). In contrast, Motten (1983) compared nearest-neighbor crosses with 50-m crosses and found

no such effect in *Erythronium umbilicatum*. Part of this difference may be due to the prolific vegetative propagation characteristic of *E. americanum* (Blodgett 1894; Holland 1981) compared with the lack of vegetative spread in *E. umbilicatum* (Parks and Hardin 1963; Motten, pers. comm.); i.e., some putative outcrosses, especially at short pollination distances, may have been geitonogamous self-pollinations within large old clones. We have no statistical evidence for outbreeding depression (Price and Waser 1979), although the highest seed sets were obtained at intermediate interparent distances (40 m).

Comparison of hand-outcrossed and open pollinations suggests that both limited pollinator service and the availability of resources for fruit development can constrain the quality and quantity of seeds produced by *E. americanum*. The following observations indicate resource limitation of seed production by hand-outcrossed plants: only 4 in 10 ovules produced seeds (Table 3) even though flowers received sufficient pollen to effect full fertilization; and both the number of seeds set and their average mass were positively correlated with plant size, as represented by ovule number. In contrast, pollination limitation seems to have been a greater influence on seed production by open pollinated plants because they set a significantly smaller proportion of their ovules than hand-outcrossed plants (Table 3), and because ovule number was not correlated with the number of seeds set or their average mass.

Pollinator effectiveness

Although deposition of pollen on stigmas has recently received considerable attention (see Thomson and Plowright 1980; Motten 1983 and Thomson in press for examples involving *Erythronium*), pickup of pollen by vectors has been very poorly studied (Janzen 1983; but see Strickler 1979; Webb and Bawa 1984). The Coulter Counter makes these studies much easier. Our data (Table 2) and those of Strickler (1979) for *Echium vulgare* show that bees are effective removers of pollen, usually taking over half the available pollen in a single pollen-collecting visit. However, much of this collected pollen is quickly packed in corbiculae or scopae and is unlikely to be deposited on stigmas. A complete consideration of "pollinator effectiveness" (sensu Primack and Silander 1975; Motten 1983) must consider both pollen acquisition and donation; the best collector of pollen may do a poor job of delivering it to stigmas, and floral morphology might often represent the outcome of conflicting selection pressures on male and female functions (Janzen 1977; Lloyd and Yates 1982). Temporal separation of pollen presentation in the two anther whorls of *Erythronium* will tend to reduce the chance of a single bee removing nearly all of a flower's pollen. Extended dehiscence periods of sets of anthers [e.g. in *Aralia* (Thomson in prep.)], or "metered" delivery of fractional loads of pollen (Haynes and Mesler 1984), may reflect selection favoring pollen donations to a diversity of vectors (Thomson and Barrett 1981; Lloyd and Yates 1982).

Morphological characteristics and sexual reproduction

Exsertion of the stigma beyond the longest dehisced stamen of the outer whorl is significantly greater in the highly self-compatible *E. grandiflorum* (Thomson and Stratton 1985; $\bar{X} \pm SE = 1.5 \pm 0.17$ mm, $n = 100$) than in the weakly self-compatible *E. americanum* of this study (-0.1 ± 0.24 mm, $n = 35$; $t = 4.71$, $P < 0.001$). This result and the nocturnal closing of *E. americanum* flowers, unlike those of *E. grandiflorum*, suggest a greater likelihood of self-pollination for *E. americanum*. Greater proclivity for self-pollination in the less self-compatible plant seems unusual, but self-pollen has no detrimental effects on fruit or seed set in *E. americanum* as long as outcross pollen is also applied (Table 3). Probably very few seeds from such mixed pollinations are selfed. In contrast, *E. grandiflorum* is self-compatible, and mixed pollinations probably produce both selfed and outcrossed seeds. If stylar exsertion has a genetic basis, as in some other species (Breese 1959; Schoen 1982), and outcrossed progeny are generally more fit than inbred progeny in *E. grandiflorum*, then selection for outcrossing may maintain its greater exsertion.

In this population of *E. americanum* positive correlations between ovule number and seed size and number in plants that receive sufficient pollination both suggest that large plants function more successfully as females than do small plants. In contrast, canonical correlation analysis of overall morphological variation in *E. americanum* indicates that although a third of variation in floral characteristics is associated with variation in plant size, additional components of floral variation are independent of plant stature. Within the flower, several associated structures, such as the style and ovary, and the filaments and anthers, appear to develop independently of one another, based on their weak intercorrelations (see also Richards and Barrett 1984). The observed positive correlations between flower size and nectar and pollen production provide an inducement for selective foraging by flower-visiting insects. Because pollinators are known to feed selectively when faced with intrapopulation variation in floral morphology (Morse 1978; Harder unpubl.), heritable floral variation that is independent of plant size or the size of other flower parts would facilitate evolutionary development of new floral forms.

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