Evaluation of *Penstemon* as a host for *Castilleja* in garden or landscape

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ABSTRACT

Castilleja Mutis ex L.f. (Scrophulariaceae), or paintbrush, is seldom used in gardens or landscapes because of confusion about hosts and growing conditions. Pairing annual and perennial *Castilleja* with various *Penstemon* Schmidel (Scrophulariaceae) species, however, was shown to be successful over a 2-y period. The most effective host was *P. strictus* Benth., particularly with *C. integra* Gray and *C. indivisa* Engelm. Such pairings now allow horticulturalists a way to incorporate paintbrush into a variety of growing areas. For best results, the microenvironment may need to be balanced to satisfy the growth requirements of both plants.

KEY WORDS
hemiparasite–host relationship, growth response,
paintbrush, Scrophulariaceae

NOMENCLATURE
USDA NRCS (2004)

Figure 1. Castilleja miniata with *Penstemon fruticosus* host in Mt Rainier National Park.
Photo by DA Nelson

Castilleja Mutis ex L.f. (Scrophulariaceae), or paintbrush, is usually not grown by horticulturalists because of its reluctance to survive under garden conditions. Although *Castilleja* can be grown alone because of its photosynthetic capability, it usually requires a companion plant to serve as host for its hemiparasitic needs (Adler and others 2001). For instance, *Penstemon teucrioides* Greene (Scrophulariaceae) has been investigated as a host for *C. integra* Gray (Stermitz and others 1993). Although some gardeners have used grass companions, the grass hosts reseed, thus presenting the undesired requirement of weeding to avoid overcrowding of the *Castilleja* plants. For example, under growing conditions where I live in the Mid-Columbia Basin of Washington, only 23% of the *C. integra–Festuca idahoensis* Elmer (Poaceae) combinations survived the first year. Only 4 *C. integra* bloomed during the second year, and only a single plant survived 4 y with blooms. Throughout this period, *F. idahoensis* survived and spread rampantly without its companion.

Recent discussions within the North American Rock Garden Society (McGary 2003), as well as quite recent investigations (Lawrence and Kaye 2005; Luna 2005), indicate considerable interest in techniques to grow *Castilleja*. These reports confirm that a number of host plants have been suggested and tried. Matthies (1997) found that several *Castilleja* species provide strong negative growth effects on hosts, but those effects were dependent upon the specific hemiparasite–host combinations. Earlier, Dobbins and Kuijt (1973) indicate that *Castilleja* was not generally considered to be host specific. *Castilleja affinis* Hook. & Am. ssp. *affinis* (formerly *C. wightii* Elmer) has also been shown to parasitize multiple hosts to secure enhanced growth (Marvier 1996).

Further, Adler (2002) notes that a host preference may be shown in the field by *C. miniata* Doug. Ex Hook., although that preference is probably based on several factors. Complicating the relationship is the response of the host. Sweatt (1997) found that when annual *C. indivisa* Engelm. was paired with 3 Asteraceae (*Gaillardia pulchella* Foug., *Ratibida columnifera* (Nutt.) Woot & Standl., and *Coreopsis lanceolata* L.), growth of *C. indivisa* was greatly enhanced, but the growth of the Asteraceae was variably reduced. When *C. indivisa* was paired with *Lupinus texensis*

Hook. (Fabaceae), however, the relationship with the Texas bluebonnet caused mortality for the host. In contrast, Stermitz and Pomeroy (1992) indicate that *C. indivisa* and *L. texensis* have been planted together along Texas highways and appear to tolerate the intimacy by transfer of alkaloids from one to the other. An earlier observation (Atsatt and Strong 1970) suggests that specific hosts may be deleterious to annual hemiparasites such as *C. exserta* (Heller) Chuang & Heckard. Marvier (1998) further observed that the flowering rate of *C. affinis* ssp. *affinis* was not enhanced when hosted by *Lupinus arboreus* Sims (Fabaceae). Thus, the recent literature presents a number of questions concerning the adequacy of some hosts with *Castilleja*.

Because *Penstemon* Schmidel is quite hardy and well known for its blooms during late spring and early summer, it may provide an alternative host for *Castilleja* that is preferable to grasses (Figure 1). When *Penstemon strictus* Benth. was paired with *C. integra*, *P. strictus* did not bloom the first year but *C. integra* was dramatically floriferous; that is 87% (42 of 48 plants) bloomed (Nelson 2003). Further, when *P. nitidus* Dougl ex Benth. was paired with *C. integra*, limited growth was noted and it did not bloom the first year (Nelson 2003). Aside from a dissimilar range between the pair, the results could also suggest that the seed or plant quality of *P. nitidus* was insufficient for the demands of growth and hosting, perhaps because of the wild, open-pollinated source.

My recent observations suggest that penstemons, including the robust *P. strictus*, should be examined to determine if they remain vigorous and unaffected by the demanding hemiparasitic paintbrush. My goal is to provide a recommendation for long-lived paintbrush–host pairs that have good flowering characteristics. I attempt to determine if dissimilar ranges might be a factor for the lack of vigor of selected pairs. *Lupinus argenteus* Pursh was included in the study as a comparative base for the *Penstemon* hosts because lupine was used as host in several previous studies.

METHODS AND MATERIALS

Deno's (1993) stratification procedure was used to overcome delayed germination for *Castilleja* and *Penstemon*. This process, confirmed by Lawrence and Kaye (2005) and Luna (2005), generally requires that seeds be set on a damp paper towel in a loose plastic bag (mid-January) within a refrigerator (5 °C [40 °F]) until small roots are observed (4 to 6 wk). Germinating seeds were placed within 15 x 20 cm (6 x 8 in) peat containers containing Premier Pro-Mix BT (Premier Horticulture Inc, Red Hill, Pennsylvania) that had been diluted with 50% sterilized, sharp sand (sand exposed to 150 °C [300 °F] for 24 h). Outside, daytime exposure was usually started in late February to avoid fungal predation. Once most seedlings had attained their first true leaves (mid-March), they were individually removed from the larger container, combined singly with the companion *Penstemon*, and transplanted to peat pots. Most combined seedlings were adjacent or within 1 cm (0.4 in). Two extra groups of *C. integra*, however, were combined within 2 or 4 cm (0.8 or 1.6 in) of either *P. strictus* or *P. hirsutus* (see Table 1 for all species used in the study). A series of solitary *C. integra* were grown as a control for this experiment. Permanent garden placement (sandy loam with low humus) was usually performed after the companion plants had been together for approximately 8 to 10 wk (generally, late May). Initiation of bloom was defined as onset of bract coloration.

Lupinus argenteus seeds were treated with an aqueous spray (distilled water) of *Rhizobium* spp. (Nitragin, Brookfield, Wisconsin) before stratification. Germination occurred within 3 wk with direct transfer of seedlings to large pots to reduce root damage. Plants were given outside exposure as soon as above-freezing, daytime conditions allowed (mid-February). Combination with *Castilleja* was performed by mid-March.

Penstemon strictus was used as host for all *Castilleja* in the study because of its robust characteristics, whereas *C. integra* was used to parasitize all *Penstemon*. *Castilleja miniata* was paired with *Penstemon* that may require more moisture. *Castilleja haydenii* was included in the study because the violet bracts may offer special value to gardeners. The choice of *Penstemon* was based on availability (*P. rydbergii* and *P. eatonii*) as well as on distinct and varying ranges (*P. albertinus*, *P. attenuatus*, *P. hirsutus*, *P. ovatus*, and *P. serrulatus*) (see Table 1). Both *C. exserta* and *C. indivisa* were included to compare annual *Castilleja* response to the *Penstemon* host.

Because of the individual needs of diverse host–hemiparasite species, attempts were made to place the plants into desired garden microenvironments (level of light and water). This was required because of the harsh growing conditions of the Mid-Columbia Basin (eastern Washington); annual precipitation is 160 mm (6.7 in) with summer temperatures ranging from 31 to 40 °C (90 to 105 °F). Hosts that I perceived needing moist areas were provided with afternoon shade and considerable moisture (pop-up sprayer yielding 25 mm/d [0.1 in/d]); these included *P. ovatus* and *P. rydbergii*, as well as their companion *Castilleja*. All other pairs were placed in full sun under moderate xeric conditions (microsprayer yielding 1 mm/d [0.05 in/d]). Plants were irrigated twice each day, 0600 and 1600 hours, to deliver the previously described amounts. Additional water was added if wilting was observed. In all cases, these watering conditions were maintained from June through September.

Plant pairs of selected *Penstemon*–*Castilleja* species were shared with gardening colleagues within the Mid-Columbia Basin in an attempt to reduce the environmental bias of a single growing area.

RESULTS

First-season results with perennial *Castilleja* were obtained in 2 consecutive years (2003 [Table 2] and 2004 [Table 3]) to see if results were similar among years despite varying weather and multi-colleague's garden areas. In 2003, first-year growth and flowering were particularly superior with *C. integra* paired with either *P. strictus* or *P. eatonii*, while no *Castilleja* blooms were noted with either *P. hirsutus* or *P. ovatus*. During 2004, both *P. strictus* and *P. eatonii* provided even better growth and flowering (Figure 2). Although *P. hirsutus* did enhance blooms for *C. integra* in 2004, *P. ovatus* did not contribute to *C. integra* flowering. Other *Penstemon* providing flowering during the first year with *C. integra* were *P. attenuatus, P. rydbergii, and P. serrulatus* (Tables 2 and 3). However, *P. albertinus* performed poorly both years. Enhanced flowering was noted with *C. miniata* paired with *P. ovatus* or *P. stric-*

Photo by DA Nelson

Figure 2. First-year season (from left to right): *P. serrulatus* and *P. eatonii* with *C. integra* and *P. strictus* with *C. hayderii.*

TABLE 1

Various ranges of Castilleja *and* Penstemon *(Scrophulariaceae) and* Lupinus *(Fabaceae) used in the study.*

	General range [z]	Source [y]
Host		
P. albertinus Greene	Northern Rocky Mountains (Montana, Idaho, Alberta)	APS
P. attenuatus Doug. ex Lindl.	Northwestern US and Wyoming	APS
P. eatonii Gray	Southwestern US	APS
P. hirsutus (L.) Willd.	Alabama to Wisconsin and eastern US	HPSO
P. ovatus Dougl. ex Hook.	Washington and Oregon including British Columbia	APS
P. rydbergii A. Nels.	Western US	APS
P. serrulatus Menzies ex Sm.	Washington and Oregon	HPSO
P. strictus Benth.	Rocky Mountains	HPSO
L. argenteus Pursh	Western US	commercial
Hemiparasite		
C. exserta (Heller) Chuang & Heckard	California, Arizona, New Mexico, and Idaho	commercial
C. haydenii (Gray) Cockerell	Colorado and New Mexico	commercial
C. indivisa Engelm.	Texas, Oklahoma, Missouri, and Louisiana	commercial
C. integra Gray	Colorado, New Mexico, Arizona, and Texas	commercial
C. miniata Doug. ex Hook.	Western US and North Dakota	commercial

[z] USDA NRCS (2004).
[y] APS is American Penstemon Society; HPSO is Hardy Plant Society of Oregon.

tus, as well as with *P. hirsutus* during 2003, the only year this pair was evaluated. *Lupinus argenteus* was a much poorer host than the *Penstemon* (Table 3) in terms of *Castilleja* flowering, and only 37% of the lupine hosts survived through the first season.

The first bloom of *C. integra* (paired with *P. strictus*) occurred 8 wk after their combination in both 2003 and 2004. Rapid growth and blooming of *C. integra* continued sporadically for an additional 16 wk. This extended period occurred for nearly all *Castilleja* that bloomed during their initial season.

The annual *Castilleja* also provided unexpected results. Although *C. exserta* showed some enhancement from 2003 to 2004 (Tables 2 and 3), its bloom period in both years occurred within 30 d of pairing with *P. strictus* and lasted only 2 to 3 wk. *Castilleja indivisa* required 87 d to bloom after pairing with *P. strictus*, but that bloom lasted over 8 wk. *Castilleja indivisa* grown without hosts only reached an average height of 24 cm (9.5 in) with 69% bloom.

A further aspect of pair growth was examined by transplanting the host and hemiparasite at measured distances from each other (Table 4). The *C. integra*–*P. strictus* pairs placed 2 cm (0.8 in) from the hosts generally underwent a growth surge 12 wk after pairing but did not bloom. When separated by 4 cm (1.6 in), all but a single *C. integra* died. The paintbrush transplanted 4 cm from established (2-y-old) *P. strictus* generally died (89% mortality). *Castilleja integra* transplanted without a host also faired poorly: only 5 of 11 plants survived after 2 mo in the garden placement and none was taller than 2 cm after 4 mo of growth.

Pairs combined in 2003 were observed at the end of their second growing season (2004; Table 2). Several pairs showed excellent bloom rates during the second season. *Castilleja integra* when paired with 5 of 7 *Penstemon* spp. had bloom rates from 43% to 85%. *Castilleja miniata* paired with either *P. ovatus* or *P. strictus* also provided 50% or higher blooms. Even *C. haydenii*, combined with *P. strictus*, provided an excellent number of blooms. The remaining pairs within Table 2 showed considerable reluctance toward the promotion of *Castilleja* blooms. Interestingly, the second-year blooms started in early May and were complete by mid-July.

Although bloom rates and plant measurements are important, pair longevity (survival) is also a key component. Although most *Penstemon* hosts survived well after the second growing season, *Castilleja* survival was best when paired with *P. strictus*, but the *C. miniata*–*P. hirsutus* and *C. integra*–*P. attenuatus* pairs also did well (Table 2).

DISCUSSION

Annual Paintbrush

As noted in Tables 2 and 3, *C. exserta* was only paired with *P. strictus* and bloom rates for both years were similar (75% and

TABLE 2

First- and second-year results from Penstemon–Castilleja *pairs initiated in 2003.*

Hemiparasite	Host	2003 Number of pairs	2003 *Castilleja* bloom (%)	2003 Average height at bloom (cm)	2004 Surviving pairs	2004 *Penstemon* survival (%)	2004 *Castilleja* survival (%)	2004 *Castilleja* bloom (%)	2004 Average height at bloom (cm)
C. exserta	*P. strictus*	20	75	7					
C. haydenii	*P. strictus*	5	0	10**	3	100	60	67	26
C. integra	*P. albertinus*	8	12	7	7	87	75	71	35
	P. attenuatus	10	10	16	9	90	100	56	24
	P. eatonii	22*	32	19	9	70	40	44	23
	P. hirsutus	20*	0	12**	5	100	25	0	5**
	P. ovatus	16*	0	5**	3	93	19	0	12**
	P. rydbergia	26*	8	15	13	88	50	85	25
	P. strictus	84*	39	28	74	100	88	43	35
C. miniata	*P. hirsutus*	20*	20	18	17	100	85	6	22
	P. ovatus	15*	20	18	8	80	53	50	28
	P. rydbergii	21	0	9**	5	80	24	0	12**
	P. strictus	37	22	14	30	100	81	83	32

*Pairs shared with colleagues

**Height of non-blooming *Castilleja* spp.

TABLE 3

First-year results from Castilleja–Penstemon *or* Lupinus *pairs in 2004.*

Hemiparasite	Host	Number of pairs	*Castilleja* bloom (%)	Average height at bloom (cm)
C. exserta	*P. strictus*	20	100	12
C. indivisa	*P. strictus*	16	100	34
C. integra	*L. argenteus*	40	0.25	21
	P. albertinus	10	0	5**
	P. attenuatus	18	67	21
	P. eatonii	20	50	41
	P. hirsutus	27	22	20
	P. ovatus	20	0	6**
	P. rydbergii	16	69	38
	P. serrulatus	40	30	36
	P. strictus	108*	81	25
C. haydenii	*P. strictus*	26	69	21
C. miniata	*P. ovatus*	10	50	19
	P. strictus	20	40	19

*Pairs shared with colleagues

**Height of non-blooming *Castilleja* spp.

TABLE 4

First-year, distance-separated, pairs of perennial Penstemon–Castilleja.

Hemiparasite	Host	Distance apart (cm)	Number of pairs	*Castilleja* survival (%)
C. integra	*P. strictus*	2	8	100
C. integra	*P. strictus*	4	6	16
C. integra	*P. strictus*[z]	4	14	11
C. integra	None	—	11	45

[z] *C. integra* was placed adjacent to 2-y-old *P. strictus* after 16 wk postgermination.


Photo by DA Nelson

Figure 3. Third-year season of *P. strictus–C. integra.*

100%). In neither year did this annual hemiparasite show enhanced growth, but it greatly reduced host growth to a height of 1.5 to 2.5 cm, suggesting that *C. exserta* is poorly served by *P. strictus* and may be of questionable use for horticulturalists because of the short stature of the paintbrush and short bloom period. In contrast, *C. indivisa* paired with *P. strictus* grew taller and all the hemiparasites bloomed for a much longer period, despite that 3 of 16 *C. indivisa* inflicted host mortality. The longer bloom period and taller plant suggests an excellent annual for garden use.

Perennial Paintbrush

Castilleja in the field show host preference (Adler 2002) and may even show preference within a genus such as *Penstemon* (Nelson 2003). This selectivity may depend on haustorial-inducing factors or haustorial-inhibiting factors released by the host roots (Jamison and Yoder 2001). Some penstemon species contain iridoid and monoterpenoid glycosides that may inhibit *Castilleja* (Abdel-Kadar and Stermitz 1993). Consequently, *Castilleja* must compromise among host choices. Nickrent (2002) summarized that the biomass ratio of parasite to host, number of parasites attached to an individual host, length of time required for the parasite to complete its life cycle, and possible degree of coevolutionary "tuning" that has occurred over time between the host and hemiparasite all may be possible factors.

Combinations of perennial hemiparasite–host pairs examined in the first year of pair establishment (Tables 2 and 3) indicate that the perennial *Castilleja* species were amenable to most *Penstemon* hosts provided but not all pairs responded suitably for garden use. Despite an extremely hot summer in 2003 and milder summer in 2004, the most consistent, first-year bloom rates were attained with *C. integra* paired with *P. eatonii* or *P. strictus*. However, *C. integra* paired with *P. attenuatus*, *P. rydbergii*, or *P. serrulatus*; *C. miniata* paired with *P. ovatus* or *P. strictus*; and *C. haydenii* paired with *P. strictus* may provide considerable blooms during the first year if environmental conditions are favorable.

Pairs containing *C. miniata* did provide some insight into growing conditions. For instance, under the same xeric conditions, the flowering rate of *C. miniata–P. strictus* was lower (22%, 40%) than that of *C. integra–P. strictus* (39%, 81%) in 2003 and 2004, respectively. Further, when pairs of *P. ovatus* with either *C. integra* or *C. miniata* are compared in both years, *C. miniata* yielded blooms while *C. integra* did not. Based on these preliminary observations, it appears that *C. miniata* may be the paintbrush of choice when paired with a northwestern US *Penstemon* and its increased moisture requirement. A regional exception to this was *P. serrulatus–C. integra*, which provided 30% bloom. A similar preliminary conclusion concerning moisture requirements might be drawn for the *P. hirsutus* pairs with *C. integra* and *C. miniata*. Only continued slow growth was observed for the *P. hirsutus–C. integra* pairs, while *P. hirsutus–C. miniata* showed rapid growth and bloomed at 16 wk after pairing in 2003. The 2004 pairs of *P. hirsutus–C. integra* were placed in much drier conditions and provided increased growth and blooming.

Table 2 prompts a question: Why do some perennial *Castilleja* bloom precociously the first year while others wait until the second year? I believe many factors may be involved but this study can only provide some choices of successful hosts for the successive growth years. *Castilleja integra* paired with either *P. strictus* or *P. eatonii* performed well for both years, as did *C. miniata* with *P. strictus*.

Although I thought that range overlap might be involved with pair success (Nelson 2003), results of this study (Tables 1 and 2) indicate that *Penstemon* and *Castilleja* from far distant ranges can form productive host–hemiparasite pairs, at least from the perspective of *Castilleja*. Obviously, *C. indivisa* grows well when hosted by *P. strictus*. Further, *C. integra* forms productive pairs with *P. attenuatus*, *P. serrulatus*, and occasionally, *P. hirsutus*.

Matthies (1997) indicates that haustorial connections were made when the host–hemiparasite distance was 1 cm. My results suggest that an interval >2 cm between *P. strictus* and *C. integra* dramatically reduced blooming success during the initial season. Because of the difficulty of forming haustorial connections over distance, my results also indicate it may be difficult for haustoria of newly germinated *Castilleja* to penetrate into the xylem of an established host, such as *Penstemon*. This concurs with work by Stermitz and others (1993) and Marvier (1998). Even so, this growth process probably occurs sufficiently in nature because many host combinations, including *Penstemon*, are present.

Adler (2002) indicates that hemiparasites are most successful with leguminous hosts, but my results indicate that *L. argenteus* was a poor host for *C. integra*. This suggests that an alternative growth/coupling process may be necessary, perhaps requiring joint germination conditions (Adler and others 2001). Under my garden conditions *L. argenteus* plants generally survive only about 2 to 3 y whereas *P. strictus* survive 8+ y. Thus, *Penstemon* is an alternative native host for paintbrush that has shown itself to be sufficiently hardy, long-lived, and a good host to *Castilleja* (Figure 3).

In summary, most *Penstemon*, particularly *P. strictus*, can provide host capability for *Castilleja* as long as the water requirements of both plants are somewhat similar. *Penstemon* may not represent the ultimate host for paintbrush because many other forbs may perform at a similar or higher level (Sweatt 1997). Regardless, this study shows that a *Penstemon* host should allow horticulturalists to grow paintbrush with reasonable ease.

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REFERENCES

Abdel-Kadar M, Stermitz F. 1993. Iridoid and other glycosides from penstemon species 34:1367–1371.

Adler L. 2002. Host effects on herbivory and pollination in a hemiparasitic plant. Ecology 83:2700–2710.

Adler L, Karban R, Strauss SY. 2001. Direct and indirect effects of alkaloids on plant fitness via herbivory and pollination. Ecology 82:2032–2044.

Atsatt P, Strong D. 1970. The population biology of annual grassland hemiparasites. I. The host environment. Evolution 24:278–291.

Deno N. 1993. Seed germination theory and practice, 2nd edition. State College (PA): self published. 250 p.

Dobbins D, Kuijt J. 1973. Studies on the haustorium of *Castilleja* (Scrophulariaceae). I. The upper haustorium. Canadian Journal of Botany 51:917–922.

Jamison D, Yoder J. 2001. Heritable variation in quinone-induced haustorium development in the parasitic plant *Triphysaria*. Plant Physiology 125:1870–1880.

Lawrence BA, Kaye TN. 2005. Growing *Castilleja* for restoration and the garden. Rock Garden Quarterly 63(2):128-134.

Luna T. 2005. Propagation protocol for Indian paintbrush (*Castilleja* species). Native Plants Journal 6:62–68.

Marvier M. 1996. Parasitic plant-host interactions: plant performance and indirect effects on parasite-feeding herbivores. Ecology 77:1398–1409.

Marvier M. 1998. A mixed diet improves performance and herbivore resistance of a parasitic plant. Ecology 79:1272–1280.

Matthies D. 1997. Parasite-host interactions in *Castilleja* and *Orthocarpus*. Canadian Journal of Botany 75:1252–1260.

McGary J. 2003. *Castillejas* in cultivation. Rock Garden Quarterly 61:56–57.

Nelson DA. 2003. Paintbrush: bringing a wild thing to the garden. Bulletin of the Hardy Plant Society of Oregon 19:41–42.

Nickrent DL. 2002. Parasitic plants of the world. Chapter 2. In: Lopez-Saez JA, Catalan P, Saez L, editors. Parasitic plants of the Iberian Peninsula and Balearic Islands. Madrid: Mundi-Prensa. p 7–27.

Stermitz F, Foderaro T, Yong-Xian L. 1993. Iridoid glycoside uptake by *Castilleja integra* via root parasitism on *Penstemon teucrioides.* Phytochemistry 32:1151–1153.

Stermitz F, Pomeroy M. 1992. Iridoid glycosides from *Castilleja purpurea* and *C. indivisa*, and quinolizidine alkaloid transfer from *Lupinus texensis* to *C. indivisa* root parasitism. Biochemical Systematics and Ecology 20:473–475.

Sweatt MR. 1997. The effects of various host plants on growth, water relations, and carbon balance of the hemiparasite *Castilleja indivisa* [PhD thesis]. College Station (TX): Texas A&M University. 92 p.

[USDA NRCS] USDA Natural Resources Conservation Service. 2004. The PLANTS database, version 3.5. URL: http://plants.usda.gov (accessed 22 Jun 2005). Baton Rouge (LA): National Plant Data Center.

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