

**NEW VARIETAL COMBINATIONS IN *DIPLACUS*
FOR THE SHRUBBY MONKEYFLOWERS,
THE *DIPLACUS AURANTIACUS* COMPLEX (PHRYMACEAE)**

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ABSTRACT

New combinations are made at the varietal level within *Diplacus aurantiacus* (Phrymaceae) for eight taxa previously treated at the species level in *Diplacus* and/or at the varietal level in *Mimulus*: ***Diplacus aurantiacus* (Curtis) Jeps. var. *aridus* (Abrams) D.J. Keil, comb. nov.; *Diplacus aurantiacus* (Curtis) Jeps. var. *calycinus* (Eastw.) D.J. Keil, comb. nov.; *Diplacus aurantiacus* (Curtis) Jeps. var. *grandiflorus* (Lindl. & Paxton) D.J. Keil, comb. nov.; *Diplacus aurantiacus* (Curtis) Jeps. var. *linearis* (Benth.) D.J. Keil, comb. nov.; *Diplacus aurantiacus* (Curtis) Jeps. var. *lomolocensis* (Munz) D.J. Keil, comb. nov.; *Diplacus aurantiacus* (Curtis) Jeps. var. *longiflorus* (Nutt.) D.J. Keil, comb. nov.; *Diplacus aurantiacus* (Curtis) Jeps. var. *parviflorus* (Greene) D.J. Keil, comb. nov.; and *Diplacus aurantiacus* (Curtis) Jeps. var. *puniceus* (Nutt.) D.J. Keil, comb. nov.** Lectotypes are designated for *Diplacus calycinus* Eastw., *Mimulus linearis* Benth., *Diplacus longiflorus* Nutt., and *Diplacus puniceus* Nutt.

The bush monkeyflowers are prominent, showy, and often common components of various widespread plant communities in California and the adjacent regions of southwestern Oregon and northwestern Baja California that together form the California Floristic Province. Although displaying considerable similarity in vegetative form, with some variation in leaf shape and pubescence, these plants show diversity in floral form and color. Since the introduction of bush monkeyflowers to European gardens in the late 1700s, taxonomists have proposed many names to account for the variation. During the past century taxonomists have attempted to bring order to these plants in floras and in more focused studies, but to date there is not a consensus about how to classify them.

Thompson (2005) published a monograph of subg. *Schizoplacus* A.L. Grant of what was at the time treated as the large genus *Mimulus* L., then placed in Scrophulariaceae. He had previously treated *Mimulus* for *The Jepson Manual* (Thompson 1993). The cohesiveness of the Scrophulariaceae was already in question (Olmstead et al. 2001), and the placement of *Mimulus* into a redefined Phrymaceae soon followed (Beardsley & Olmstead 2002). Beardsley and Barker (2005) provided evidence that *Mimulus* (sensu lato) is not monophyletic. Barker et al. (2012) presented a revised generic conspectus of Phrymaceae in which *Mimulus* was broken apart, and the plants that Thompson had treated as *Mimulus* subg. *Schizoplacus* were reassigned to a resurrected and expanded genus *Diplacus* Nutt.

The shrubby monkeyflowers, which Thompson (2005) treated as *Mimulus* sect. *Diplacus*, have been variously classified in past studies. Some authors have recognized them as the genus *Diplacus* along with an herbaceous relative, *D. clevelandii* (Brandege) Greene. Jepson (1925) recognized *Diplacus* with six species in California, and McMinn (1939) recognized seven species. In his revision of *Diplacus* (McMinn 1951b) and in the second edition of his *Illustrated Manual of California Shrubs* (McMinn 1951a), McMinn accepted *Diplacus* as a genus of 14 species and

stabilized hybrids including the herbaceous *D. clevelandii* and acknowledged a plethora of additional natural and artificial hybrids. However, he noted this:

I have chosen to treat all these field entities (taxa) simply as binomials. Inasmuch as binomials to most botanists indicate species, I have endeavored not to use the word species when writing of these various entities. I must point out, however, that if sterility and geographical distribution tests were the main criteria applied in delimiting species and subspecies, then the field entities of the genus *Diplacus* probably would be classified as two taxonomic species [*D. aurantiacus* and *D. clevelandii*], eleven subspecies, and numerous hybrids.

Other botanists have retained the shrubby monkeyflowers within *Mimulus*. Grant (1924) recognized 8 species in *Mimulus* sect. *Diplacus* (Nutt.) Benth. & Hook.f. plus three additional varieties. Abrams (1951) also treated them in *Mimulus* sect. *Diplacus*, recognizing eight species in California (including *M. clevelandii* Brandege) plus two subspecies. Munz (1959) also placed these species in *Mimulus* and dealt with the variability by recognizing six species plus five additional infraspecific taxa. Thompson (1993) placed all of the California species of sect. *Diplacus* except *M. clevelandii* into synonymy under *M. aurantiacus* Curtis, acknowledging these plants to be "highly complex, with many intergrading, hybridizing, local forms." Thompson (2005), attempting to sort the variation into geographical races, recognized six varieties of *M. aurantiacus* while acknowledging that "hybridization occurs wherever any two varieties come together" and that "a large proportion of specimens are intermediate to some degree and some of these may not easily key to a recognized variety." Thompson was not the first to act on the proposition that these plants were perhaps better treated as a single highly variable species. Over 150 years earlier Lindley and Paxton (1852), noting the extreme variability of the members of the complex known to them, recognized four varieties of what was then called *Diplacus glutinosus* Nutt.

Tulig and Nesom (2012) accepted the disintegration of *Mimulus* (sensu lato) and treated the shrubby monkeyflowers plus *Diplacus clevelandii* as *Diplacus* sect. *Diplacus*. They recognized thirteen taxa, all at the species rank, including the Cedros Island endemic *D. stellatus*, and hypothesized three of these to be nothospecies: *D. ×australis* (McMinn ex Munz) Tulig [putatively *D. longiflorus* Nutt. × *D. puniceus* Nutt.], *D. ×linearis* (Benth.) Greene [putatively *D. calycinus* Eastw. × *D. aurantiacus* (Curtis) Jeps.], and *D. ×lompocensis* McMinn [putatively *D. aurantiacus* × *D. longiflorus* Nutt.]. Nesom (2013) backed away from the idea that *D. linearis* is of hybrid origin. Although they hypothesized three taxa as nothospecies, Tulig and Nesom downplayed hybridization in advocating for recognizing multiple species: "Each of the taxa of sect. *Diplacus* has a distinct geographic range and for the most part is clearly defined (Fig. 4), and throughout most of the range of sect. *Diplacus*, hybridization appears to be limited."

Stankowsky and Streisfeld (2015) and Chase et al. (2017) investigated the relationships of the taxa comprising *Mimulus* sect. *Diplacus* using a variety of methods including phylogenetic analyses of genomewide single nucleotide polymorphism data, population genomic analyses, tests for hybridization, and multivariate analyses of floral trait data. Chase et al. (2017) compared the classification hypotheses presented by Thompson (2012), Tulig and Nesom (2012), and earlier investigators in terms of the results of their analyses. The Chase et al. (2017) study included all of the taxa recognized as varieties of *M. aurantiacus* by Thompson and all recognized as species or nothospecies in *Diplacus* by Tulig and Nesom except the insular *D. stellatus*. Phylogenetic analyses identified four highly supported primary clades within the bush monkeyflowers plus the herbaceous *M. clevelandii* as their sister group. Chase et al. found evidence for recent gene flow between closely related subclades and populations and discordance between floral trait characters and molecular data that provides evidence for divergent and convergent phenotypic evolution. The taxonomies of both Thompson (2012) and Tulig and Nesom (2012) were reflected in the phylogenetic analyses with some exceptions. *Diplacus australis*, *D. rutilus* (A.L. Grant) McMinn, and *D. calycinus*, all recognized by

Tulig and Nesom appear in the analyses to be polyphyletic. Southern California plants treated by Thompson as *M. aurantiacus* var. *aurantiacus* (and by Tulig and Nesom as *D. ×australis*) were phylogenetically isolated from the remainder of *M. aurantiacus*. The hypotheses by Tulig and Nesom that two species, *D. linearis* and *D. australis*, were of hybrid origin were not supported by other analyses in the Chase et al (2017) study. Instead *D. linearis* was resolved as a monophyletic sister group of *D. grandiflorus*, and samples of *D. australis* were interdigitated among samples of *D. puniceus*, with no indication of hybridization involving *D. longiflorus*. Two samples of *D. calycinus* were phylogenetically isolated from the remaining samples of that species. Additional analyses in the Chase et al. study indicate that these two samples are probably of hybrid origin.

In her treatment of Phrymaceae for the Jepson eFlora, Fraga (2018), although aware of the Chase et al (2017) study, chose to treat the various shrubby monkeyflowers at the species level. Fraga (pers. comm.) believes that contrary to the conclusions of its authors "the Chase et al. paper provides evidence for recognition of several taxa as species." In her treatment Fraga recognized nine California species: *Diplacus aridus*, *D. aurantiacus*, *D. australis*, *D. calycinus*, *D. grandiflorus*, *D. linearis*, *D. longiflorus*, *D. parviflorus*, and *D. puniceus*. In contrast to Tulig and Nesom, she treated *D. australis* and *D. linearis* as full species, but agreed with them that *D. ×lompocensis* is a hybrid between *D. aurantiacus* and *D. longiflorus*. She did not comment on the results of the Chase et al. study that indicated *D. australis* is polyphyletic.

Though the overall outline of relationships in the shrubby monkeyflowers has been established, it remains necessary to ask the question of taxonomic rank for the various morphotypes. Chase et al. (2017) addressed this issue, first by quoting the same passage from McMinn (1951) that is presented above and then directly addressing the issue:

In most of the previous treatments of this group, the rank employed appears arbitrary and often was not justified by the authors. However, given the interfertility, natural hybridization, and shared genomic variation present among taxa, we support the view by McMinn (1951), and more recently by Thompson (2012), who treated the taxa (with the exception of *M. clevelandii*) as intraspecific subspecies or varieties of *M. aurantiacus*. This view, which acknowledges the reproductive continuity and close relationships among these taxa, emphasizes our need to understand how and why so much diversity arose and has been maintained within this group.

I agree with Chase et al. that treating the shrubby monkeyflowers as variants of a single species is to be preferred. Over my career as a field botanist and herbarium curator in California, I've attempted to use both the multispecies approach, especially as applied by Munz (1959) and Hoover (1970), and Thompson's (1993, 2012) *Jepson Manual* treatments of the variants as part of a single species, and I much prefer the latter. I view these plants as a partially differentiated assemblage of races that have not reached the level of stability that is usually associated with the concept of species. Certainly there is much variation within the group that deserves a level of taxonomic recognition, or at least should be mentioned, but I think it more prudent to recognize varieties—entities that may be expected to freely intergrade—than species. From a practical standpoint as a curator, I know that using a multispecies taxonomy results in forcing many specimens into inappropriate pigeonholes plus a large number of intermediate specimens unassignable to species and not readily fileable.

I'm nearing completion of the second edition of the Vascular Plants of San Luis Obispo County, California (Keil & Hoover in prep.), and I want to treat the shrubby monkeyflowers with nomenclature that is both up to date and practical. I welcomed Thompson's taxonomic approach as a realistic acknowledgement of the complex patterns of variation in these plants, but I accept the breakup of the monkeyflowers into segregate genera. The authors of the Chase et al. 2017 paper have communicated that they do not plan to propose any nomenclatural changes based on their research (Streisfeld, pers. comm.). Therefore I propose new combinations at the varietal level in *Diplacus aurantiacus* to accommodate the taxa that form this wonderful example of evolution in progress. I

use the varietal rank rather than subspecies because this is the rank that has been applied in most past studies in this group that recognized infraspecific taxa. Most plant taxonomists treat these ranks as taxonomically interchangeable, though nomenclaturally they are not.

DIPLACUS AURANTIACUS (Curtis) Jeps. var. **ARIDUS** (Abrams) D.J. Keil, **comb. nov.** *Diplacus aridus* Abrams, Bull. Torrey Bot. Club 32: 540. 1905. *Mimulus aridus* (Abrams) A.L. Grant, Ann. Missouri Bot. Gard. 11: 336. 1925. *Mimulus aurantiacus* Curtis var. *aridus* (Abrams) D.M. Thompson, Syst. Bot. Monogr. 75: 158. 2005. **TYPE: USA. California.** San Diego Co.: "Jacumba, near the [U.S.A. boundary] monument," 31 May 1903, *L. Abrams* 3656 (holotype: NY 68331, image!); isotypes: BM, CAS, E, GH2, K, MO, PH-2, POM, RSA, UC-2, US).

DIPLACUS AURANTIACUS (Curtis) Jeps. var. **CALYCINUS** (Eastw.) D.J. Keil, **comb nov.** *Diplacus calycinus* Eastw., Bot. Gaz. (Crawfordsville) 41: 287. 1906. *Mimulus longiflorus* (Nutt.) A.L. Grant ex L.H. Bailey var. *calycinus* (Eastw.) A.L. Grant, Ann. Missouri Bot. Gard. 11: 331. 1924. *Diplacus longiflorus* Nutt. var. *calycinus* (Eastw.) Jeps., Man. Fl. Pl. Calif. 919. 1925. *Mimulus longiflorus* (Nutt.) A.L. Grant ex L.H. Bailey subsp. *calycinus* (Eastw.) Munz, Aliso 4: 99. 1958. **LECTOTYPE** (here designated): **USA. California.** Tulare Co.: "So. Fork Kaweah River, 6000 ft," 22 Jul 1904, *Culbertson s.n.* (*C.F. Baker* 4407) (CAS 28303, image!; isolectotypes: CAS, GH, K, MO, NY, PH, POM, UC).

Eastwood (1906) cited the type collection of *Diplacus calycinus* as follows: "The type is 4407 of C. K. Baker's distribution, collected by Culbertson in the south fork of Kaweah River, 1800^m altitude, July 22, 1904." Thompson (2005) cited CAS 28303 as the holotype of *Diplacus calycinus*. However, Eastwood did not designate the herbarium in which the specimen(s) she examined were deposited. According to ICN Art. 40, Note 1 (Turland et al 2018), because there are duplicates of this collection, the specimen(s) Eastwood examined and the duplicates are to be treated as syntypes. Had Thompson made this error prior to 1 Jan 2001 this designation would have been a correctable error (ICN Art. 7.11, Ex. 13; 9.10) with Thompson's citation of CAS 28303 as holotype correctable to lectotype (sometimes described as inadvertent lectotypification (Prado et al. 2015)). However, ICN Art. 7.11 and 9.23 require that on or after 1 Jan 2001 designation of lectotype must be specifically indicated. I therefore am designating CAS 28303 as lectotype of *D. calycinus*.

DIPLACUS AURANTIACUS (Curtis) Jeps. var. **GRANDIFLORUS** (Lindl. & Paxton) D.J. Keil, **comb. nov.** *Diplacus glutinosus* (J.C. Wendl.) Nutt. var. *grandiflorus* Lindl. & Paxton, Paxt. Fl. Gard. 3: 96, plate 92. 1852. *Mimulus aurantiacus* var. *grandiflorus* (Lindl. & Paxton) D.M. Thompson, Monogr. Syst. Bot. 75: 158. 2005. **NEOTYPE** (Thompson 2005): **USA. California.** Butte Co.: "Between Chico and Forest Ranch, elev. 2000 ft," 18 May 1914, *A.A. Heller* 11407 (UC 196052); isoneotypes: A, CAS, CU, DS, E, F, GH, MO, ND-G, NY, OSC, PENN, PH-2).

DIPLACUS AURANTIACUS (Curtis) Jeps. var. **LINEARIS** (Benth.) D.J. Keil, **comb. nov.** *Mimulus linearis* Benth, Scroph. Ind. 27. 1835. *Mimulus glutinosus* J.C. Wendl. var. *linearis* (Benth.) A. Gray, Proc. Amer. Acad. Arts 11: 97. 1876. *Diplacus linearis* (Benth.) Greene, Pittonia 2: 156. 1890. *Mimulus glutinosus* J.C. Wendl. forma *linearis* (Benth.) Voss in Vilmorin, Vilm. Blumengartn. (ed. 3) 1: 762. 1895. *Mimulus longiflorus* Nutt. var. *linearis* (Benth.) A.L. Grant, Ann. Missouri Bot. Gard. 11: 334. 1924. *Diplacus longiflorus* (Nutt.) A.L. Grant ex L.H. Bailey var. *linearis* (Benth.) McMinn, Man. Calif. shrubs (ed. 1) 498. 1939. **LECTOTYPE** (here designated): **USA. California.** Without locality, 1833, *D. Douglas s.n.* (K-herb. Bentham (K 001079320, image!); isolectotypes: BM, E, GH, K-herb. Hooker, NY, OXF).

As in the situation described above for *Diplacus calycinus*, Thompson's (2005) citation of the Douglas collection in Bentham's herbarium (K001079320) as holotype of *Mimulus linearis* is

incorrect, as there are several duplicates deposited in other herbaria. I therefore am designating K 001079320 as lectotype of *M. linearis*.

DIPLACUS AURANTIACUS (Curtis) Jeps. var. **×LOMPOCENSIS** (Munz) D.J. Keil, **comb. nov.** — *Diplacus lompocensis* McMinn, Madroño 11: 62. 1951. *Mimulus aurantiacus* Curtis subsp. *lompocensis* (McMinn) Munz, Aliso 4: 99. 1958. **TYPE: USA. California.** Santa Barbara Co.: "Along Highway [1] between Lompoc and Las Cruces, Santa Inez [Ynez] Mountains," 7 Jun 1949, *H. McMinn 5601* (holotype: UC 914709, image!).

Diplacus aurantiacus var. *×lompocensis* has been hypothesized by various authors (e.g., McMinn 1951, Thompson 2005, Tulig and Nesom 2012) to be a [stabilized?] hybrid between *D. aurantiacus* and *D. longiflorus* (*Mimulus aurantiacus* var. *aurantiacus* and *M. a.* var. *pubescens*) that occupies a coastal area in south-central California from southwestern San Luis Obispo Co. to western Santa Barbara Co. Evidence presented by Chase et al. (2017) supports the hypothesis that these plants are of mixed origin. Whether they represent a stabilized hybrid or recurrent recent hybrids needs further investigation. For practical considerations I am choosing to treat them as a nothosubspecies.

DIPLACUS AURANTIACUS (Curtis) Jeps. var. **LONGIFLORUS** (Nutt.) D.J. Keil, **comb. nov.** *Diplacus longiflorus* Nutt., Ann. Nat. Hist. 1(2): 139. 1838. *Mimulus longiflorus* (Nutt.) A.L. Grant ex L.H. Bailey, Gentes Herbarum 1(3): 136. 1923. **LECTOTYPE** (here designated): **USA. California.** Santa Barbara Co.: St. Barbara [Santa Barbara], "Mr. Whilatz" [± illegible; the collector?], Herb. Nuttall (BM 001025105, image!; isoelectotypes: GH, K).

As in the situation described above for *Diplacus calycinus*, Thompson's (2005) citation of the collection in Nuttall's herbarium (BM 001025105) as holotype of *Mimulus linearis* is incorrect, as there are duplicates deposited in other herbaria. I therefore am designating BM 001025105 as lectotype of *D. longiflorus*.

DIPLACUS AURANTIACUS (Curtis) Jeps. var. **PARVIFLORUS** (Greene) D.J. Keil, **comb. nov.** *Diplacus parviflorus* Greene, Pittonia 1(1): 36. 1887. *Mimulus parviflorus* (Greene) A.L. Grant, Ann. Missouri Bot. Gard. 11: 344. 1925 (nom. illeg.). *Mimulus flemingii* Munz, Man. S. Calif. Bot., 477, 601. 1935. *Mimulus aurantiacus* Curtis var. *parviflorus* (Greene) D.M. Thoms., Syst. Bot. Monogr. 75: 157. 2005. **LECTOTYPE** (Thompson 2005): **USA. California.** Santa Barbara Co.: Santa Cruz Island, Jul & Aug, 1886, *E. L. Greene s.n.* (UC 103629, image!; isoelectotypes: A, BM, DS, F, MO, ND-G-2, NY-3, PENN, PH, UC-2, US).

DIPLACUS AURANTIACUS (Curtis) Jeps. var. **PUNICEUS** (Nutt.) D.J. Keil, **comb. nov.** *Diplacus puniceus* Nutt., Ann. Nat. Hist. 1: 137. 1838. *Mimulus puniceus* (Nutt.) Steud., Nomencl. Bot. (ed. 2) 2: 150. 1841. *Diplacus glutinosus* (J.C. Wendl.) Nutt. var. *puniceus* (Nutt.) Benth. in DC., Prodr. 10: 368. 1846. *Mimulus glutinosus* J.C. Wendl. var. *puniceus* (Nutt.) A. Gray, Bot. California 1: 566. 1876. *Mimulus aurantiacus* Curtis var. *puniceus* (Nutt.) D.M. Thompson, Syst. Bot. Monogr. 75: 156. 2005. **LECTOTYPE** (here designated): **USA. California.** San Diego Co.: St. Diego [San Diego], *T. Nuttall s.n.* (BM 001025107, image!; isoelectotypes: K, PH).

As in the situation described above for *Diplacus calycinus*, Thompson's (2005) citation of the collection in Nuttall's herbarium (BM 001025107) as holotype of *Diplacus puniceus* is incorrect, as there are duplicates deposited in other herbaria. I therefore am designating BM 001025107 as lectotype of *D. puniceus*.

I am not proposing varietal names in *Diplacus aurantiacus* for four of the taxa treated as species in *Diplacus* sect. *Diplacus* by Tulig and Nesom (2012). The herbaceous *D. clevelandii* is the

sister taxon to the remainder of the section, and I consider it to be a separate species. Phylogenetic evidence presented by Chase et al. (2017) indicated that red-flowered *Diplacus rutilus* does not form a lineage distinct from yellow-flowered *D. longiflorus* and recommended that it be treated as a color morph of *D. longiflorus*. The little-known *D. stellatus* was not included in the studies by Chase et al. (2017), and its status remains unclear. Thompson (2004) included it in the synonymy of *Mimulus aurantiacus* var. *aurantiacus*.

Diplacus australis presents a conundrum. Tulig and Nesom (2012) hypothesized *D. australis* to be of hybrid origin. As mapped by Tulig and Nesom (2012) these plants have a considerable range in southwestern California and northwestern Baja California, largely sympatric with *D. longiflorus* and *D. puniceus*, the putative parental taxa. However, Chase et al. (2017) found no evidence that *D. australis* is of hybrid origin. Sobel and Streisfeld (2015) presented evidence that the yellow-flowered populations treated by Tulig and Nesom (2012) as *D. australis* are differentiated from red-flowered *D. puniceus* by strong premating barriers. However, in the phylogenetic analyses of Chase et al. (2017), samples from the yellow-flowered *D. australis* are not resolved as a monophyletic lineage, but instead are interdigitated with samples of the red-flowered *D. puniceus*. Thus evidence of one sort suggests that *D. australis* is undergoing incipient speciation, which might be considered justification for recognizing these plants at the infraspecific level, but other evidence indicates that populations identified by this name do not represent a single lineage. The question of taxonomic recognition in the California flora was addressed in the Jepson Manual Contributor's Guide (Baldwin et al. 2004):

A common feature of all taxonomic concepts recognized by The Jepson Flora Project and the modern systematic community in general is that the taxa being recognized should represent natural, evolutionary lineages. Also, because TJM2 will be used (like TJM) as a definitive resource for assessing plant diversity in California (e.g., for conservation planning by state and federal agencies), we seek to capture within it all biologically meaningful, minimal-rank taxa (e.g., species, subspecies, and varieties) recognized to occur in the California flora.

Do the plants treated as *D. australis* represent a natural lineage? Or are they multiple parallel/convergent lineages? Are they a biologically meaningful taxon? Is their incipient speciation biologically meaningful?

The taxonomic rank of forma has been used in some classification schemes for entities distinguished from other members of their species by one or more noticeable features. Members of a form are not necessarily expected to constitute a clade. If the plants that have been treated as *D. australis* were given taxonomic recognition, forma would seem the appropriate taxonomic rank. However, only subspecies and varieties are recognized in the *Jepson Manual* (Baldwin et al. 2004), and I am not proposing a new combination reducing *D. australis* to the rank of forma. Chase et al. (2017) recommended that "even though no previous description of the red-flowered *M. puniceus* exists that also would include the yellow-flowered *M. australis*, we suggest that future revisions incorporate these genomic and ecological patterns into a description that recognizes this divergence in the form of "ecotypes" of the consistently recognized *M. puniceus*." Although Fraga (2018) has treated *D. australis* as a species, I prefer to accept the informal treatment for these plants proposed by Chase et al.

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