

Re: the de-lumping of *Leptosiphon parviflorus*

revised July 2013 – kindly discard earlier versions

Greetings fellow leptophiles,

The information presented here is a synthesis of 20-some years of attention to this problem, based on personal observation of plants in the wild and in cultivation, on the relevant literature, limited herbarium work, and most recently on a recent DNA study of the genus by Paul Hankamp. The latter provided many new insights which would have been impossible otherwise, in addition to proving (albeit inadvertently) the paraphyly of *L. parviflorus* sensu TJM.

As treated in TJM1&2, *Leptosiphon parviflorus* conflates two large, rather distantly related species-complexes, one northern and coastal (*longitubus*), the other more inland and southern (*parviflorus*). The two complexes overlap only in a narrow zone ca. 40 miles long and ca. 8 miles inland, fronting on Monterey Bay. There could be additional sympatry zones in E Bay and inner N CoR, but if so they are yet to be documented.

For many years the two lineages have been lumped together under *L. parviflorus*, apparently mainly on the basis of a glandular calyx. This sort of oversimplified diagnosis can be dangerous, particularly in a genus like *Leptosiphon*, which seems to make a specialty of convergent evolution and multiple origins of characters. For example, Hankamp's work shows that the capitate inflorescence common to many species of *Leptosiphon* arose independently no less than six times! Specifically: 1) *L. grandiflorus*, 2) *L. montanus/ciliatus*, 3) *L. nudatus/breviculus*, 4) *L. androsaceus/rosaceus/bicolor*, 5) *L. serrulatus/acicularis/parviflorus* "s.str.", and 6) *L. latisectus/longitubus/croceus*. Glandulosity arose twice, in *L. acicularis/parviflorus* and *L. latisectus/longitubus/croceus*.

At least 18 basionyms applicable to "macro-parviflorus" have been published, first in England and later in California, all but two of them prior to 1908. Twelve of these epithets apply to the southern/inland complex (= *L. parviflorus* s. str. and its close relatives), and six apply to the northern/coastal complex (= *L. latisectus/longitubus/croceus* etc.). At present, only three of the 18 basionyms are recognized, i.e. *croceus*, *latisectus*, and of course *parviflorus* itself. However, evidence discussed below should suffice to resurrect *longitubus*, and certain other names are also likely to be resurrected in future, pending further investigation.

A confusing welter of recombinations have been published during the past 100-plus years, under *Gilia*, *Linanthus*, and *Leptosiphon*, with varietal and subspecific combinations among the various basionyms. Jepson himself was the worst culprit in this regard, combining basionyms seemingly at random under both *L. androsaceus* (!) and *L. parviflorus*. Munz's treatment was hardly less confusing. Even now, there are many specimens of *L. parviflorus* s. str. listed in the Consortium as "*Linanthus androsaceus* ssp. *luteolus*", "*L. a. ssp. micranthus*" etc. Little wonder everybody was/is so confused.

And all along the main source of confusion has not been the plants themselves, but the taxonomists!, most of whom worked from a typological rather than biological perspective. Some still do - just look at the clover treatments in JM2 and all the way back.

The problem came to my attention in the 1970's, as a beginner botanist who happened to live in the narrow overlap zone of the two "parvifloruses". It was clear enough that there were two species, differing in morphology and habitat but both keying to *L. parviflorus*. The questions then were: which is the "real" *parviflorus*, and was there a name available for the other entity? For years, until these questions were answered, I went on calling them by nicknames: "sand *parviflorus*" and "grass *parviflorus*".

Fortunately, these questions turned out to be answerable without a trip to Kew. Recently, thanks to help

from Aaron Schusteff, I was able to look at photographs of the relevant types on the Kew herbarium website, and so was able to find out which name properly belongs to which species. *Leptosiphon parviflorus* was published by George Bentham, based on an 1833 collection by David Douglas from "California" – and therefore impossible to assign on the basis of location alone. Fortunately though, despite the poor condition of the holotype, it was clear that both plants (one lacking flowers!) comprising the specimen clearly belong to the southern/inland complex, which is therefore the "true" *parviflorus*.

So, what then is the proper name for the northern/coastal complex? *Gilia longituba* Benth., Pl. Hartw. 324 (1849) was based on an 1848 collection (Hartweg 11) from woods near Monterey. The holotype consists of three plants in good condition and unmistakable as to ID, even though the location alone would give away the identity of the plants. This is the northern species, albeit collected at the southern end of its range. The name could scarcely be more appropriate either, considering that this species, at least in its typical form, has the longest tube of any *Leptosiphon* I know of, often to 5 cm. or more. Later combinations include: *Linanthus longitubus* Heller (*Muhlenbergia* 1:43, 1904), *Gilia micrantha* Steud. var. *longituba* (Benth.) Gray (but *micrantha* = *parviflorus*), *G. longituba* ssp. *eu-longituba* Brand (=?), *G. androsacea* ssp. *eu-longituba* Brand, *G. longituba* var. *rosacea* Brand (=?). The combination *Leptosiphon longitubus* still needs to be published.

Unfortunately, *L. longitubus* has long been treated as synonymous with *L. androsaceus* and more recently *L. parviflorus*, despite many important differences from both of those spp in morphology, habitat, range, reproductive isolation etc. In fact, P. Hankamp's ITS trees prove that the two species/complexes are only distantly related, *L. parviflorus* coming out as sister to *L. acicularis*, and *L. longitubus* as very close sister to *L. latisectus* (if not even conspecific), and both equally distant from the *L. androsaceus/ rosaceus/bicolor* clade.

So there are our two "parvifloruses", each highly variable in its own right but easily distinguishable one from the other, morphologically as well as by habitat and distribution. Following are descriptions of distribution and patterns of variation within the two complexes, as best I know them at present. Any info that observers in other parts of California can contribute to this would be very welcome.

Coastwise from north to south, *L. parviflorus* s. str. begins in the sandhills of central Santa Cruz Co., where it is locally common in suitable habitat (bare sand), mixing and matching in colors from bright pink and lavender (the color arranged in longitudinal stripes) to pale pink to white, pale yellow, and bright yellow, most often white, and only one all-yellow colony known. The throat is always yellow, never dark. It should be emphasized here that, unlike most forms of *longitubus*, none of the forms of *L. parviflorus* have any trace of paired red "guidelines" on the cor lobes..

Moving south, the next "parvifloroid" to be encountered is at Ft. Ord, but this is a completely different form (if not species) than the "typical" form in the sandhills. The Ft Ord plants have a unique tricolor "bullseye" pattern, with wide, orange-yellow throat and white lobes, the two separated by a more or less conspicuous purple bar. This distinctive form occurs also at Pinnacles N.M. (including some with pink-striped lobes – see Calphotos), also near Jolon (a version with washed-out purple bars, and possibly even a yellow variant? - Calphotos again), and reported south at least to the La Panza Range (Hoover et al.). Even without the distinctive purple bar, the "bullseye parv." is easy to recognize by the yellow of the throat extending somewhat onto the lobes.

The more "typical" white/yellow/pink form continues south along the Santa Lucia Range, but soon begins to show admixture of plants with a deep purple area in throat or sometimes the entire throat, and sometimes lilac-colored lobes. This trend seems to reach an extreme in SLO and Santa Barbara Co.'s, with bluish-lilac lobes and all-black throat. At Laguna Lake near SLO this form grows on a serpentine slope, quite near to a colony of a different, white-flowered form, with no apparent mixing, possible evidence that two reproductively-isolated species may be involved.

Several additional forms of *L. parviflorus* may be worth resurrecting from synonymy. One of these (from Santa Rosa Plateau – Calphotos) has white flowers and extremely long-exserted stigmas. Could this be what Munz called (*Gilia lutea* var.) *longistylis* from SD area? Another has long been known as *Linanthus parvif.* var. *laetus* (Cherokee *linanthus*). This SNF endemic is always white with yellow throat, remarkably uniform for a *Leptosiphon*, particularly one with such an extensive range; occurring sporadically along the foothills from Kern to Tehama Counties. A mysterious, possibly extinct dwarf valley form of *parviflorus* (fl tube only 1-1.5 cm) was collected by Hartweg “near Sacramento” and published by Steudel as *Gilia micrantha*. Unfortunately, this epithet has since been widely misapplied to *L. parvif.* s.str., but I know of no other records of “real” *micranthus* except for the original (type) collection. Also yet to be resolved are a series of populations extending from the East Bay area up through the inner North Coast ranges. These have been variously described as white to light violet and even pale yellow, though always with yellow throat. Presumably these are forms of *parviflorus* rather than *longitubus*, *latisectus* or *androsaceus*, but this is still unproved one way or the other, and any info about the *Leptosiphons* in that region would be very useful.

So much then for *parviflorus* "s. str." Or more likely not so str. - genetic and biological subdivisions still need to be worked out, as outlined above. At the moment it is looking like something on the order of 4 or 5 infrataxa are involved, just as in *longitubus*.

And so, on to *L. longitubus*. This consists of at least four allopatric races (sspp). Pictures of all four of these races have been posted on Calphotos (under *L. parvif.* and *L. croceus*, pending reassignment):

- 1) the widespread “typical” form of the species extends from Monterey Peninsula north to (through?) Napa Co. and inland to the Mt. Hamilton area. The northern and northeastern range limits are unresolved, presumably ending to the south of *L. latisectus* and west of *parviflorus*. It usually has white to cream-colored flowers, but it is commonly bright pink at Jasper Ridge, and occasionally so at Edgewood Park. Once saw a mostly-pink colony at Ft. Ord, although it is otherwise overwhelmingly white there, and there is also an old collection with pink flowers from Pacific Grove. In Santa Cruz Co. it tends to be cream-colored (although some individuals in a population southwest of the UCSC campus vary to light yellow);
- 2) a single isolated population in a rich mountain meadow near Boulder Creek has a unique orange-yellow limb and very long tube;
- 3) the larger-flowered but shorter-tubed, bright-yellow coastal population in San Mateo Co. currently known as *L. croceus* (but more properly *L. longitubus* ssp. *croceus*);
- 4) the fourth race/ssp. of *L. longitubus* is endemic to western Marin Co. Occurs at Mt Tam, Pt Reyes, Tiburon etc. It too has a rel. short tube, but lacks the otherwise diagnostic red “guidelines” present in the three other races (there is at least one exception to this – see Calphotos). It ranges from deep pink to white, and very rarely bright yellow. This has been for many years confused for *L. rosaceus*, and generally called “*L. parviflorus* var. *rosaceus*”. The “real” *L. rosaceus* survives at only two spots on the San Mateo Co. coast, and has white flowers (rarely pale pink), and non-glandular calyx.

Throat is yellow in all forms. Pink-fl'd forms have a white ring around the throat...absent in *parvif.*
All forms except the west Marin race have many or most individuals showing a diagnostic pair of red “guidelines” at base of each lobe; this varies from conspicuous to nearly absent within any one colony. Extreme forms (as at Jasper Ridge) can even have the marks coalesced into a single large, bilobed, deep carmine spot. The red marks are the easiest and surest way to ID this species in the field or in photos (except the W Marin form), although apparently these and most pigments tend to fade away in the herbarium. The corresponding “easy” way to identify *parviflorus* is by the palisade of stamens around the throat and absence of red marks, but they have a different overall gestalt as well, esp. in the appearance of the head: a smooth-cropped look across the top of the calyces & bracts in *longitubus*, and a more ragged irregular outline in *parviflorus*. They also differ subtly in structure of tube and throat (tube tapering to filiform distally in *parvif.*, more even in diam in *longit.*), and gen. in habitat as well (open grassland for *longitubus*, and slopes and outcrops in association with woody vegetation for *parviflorus*). A very important difference is in the shape of the cotyledons, roundish in *longitubus* and its close relative

latisectus, and linear in parviflorus and its relative acicularis.

The four races of *L. longitubus* appear to be completely interfertile, and therefore not separate species (contra "*L. croceus*"), but allopatric races. A good proof of this is to be found in the nursery trade, in the form of a seed strain called 'Stardust', advertised as "French Hybrid *Linanthus androsaceus*". This is actually not *androsaceus* at all but *longitubus*. You can see how some enterprising horticulturist got ahold of all the color forms of *longitubus* (incl. *croceus*, for its color and large size), grew them together and...voila! There are even bronze-colored ones from the mix of pink and yellow. The red marks and various other features tell you it is all *longitubus* - there is no trace of *parviflorus* or *androsaceus* in the mix. It still remains to be seen whether *L.latisectus* is also interfertile (and therefore conspecific) with *longitubus*. This could be easily tested by growing it outdoors for several years with *L. croceus* or the other yellow race of *longitubus*, to see whether or not a hybrid swarm is the result.

If you think any part of the foregoing sounds fishy please let me know. I think it is as good a reflection of the biological reality as can be had at this time. And the DNA evidence so far, at least as I interpret it, supports the model beautifully: one clade with *latisectus* branching off first, then *longitubus*, with its specialized local races independently diverging from the common form; then *L. parviflorus*, coming out of a completely different branch (with *acicularis*); and lastly *androsaceus*, *rosaceus*, *bicolor* and *jepsonii* on a third separate branch. It would be good to follow up with sequencing the various forms of *parviflorus* in order to understand its local variants to the same degree of detail as those of *longitubus*. In fact, several instances of more-or-less close sympatry (at Pinnacles, SLO, and Jolon area) may mean there is still another species or two hiding under *parviflorus* "s. str."

Finally, a key to separate the two species, as worked out so far:

- 1)stamens inserted high in throat, in sinuses of cor. lobes, exserted and well separated; cotyl. Linear; fl tube gen 1.5-4? cm., tapering to filiform distally; corolla lacking red marks at base of lobes; throat yellow or dark inside; plants of sandy or very light, sterile soils or serpentine; SCoR from SCo. south to SD. and north in SNF to Tehama Co. then south along inner N CoR to E Bay area*L. parviflorus* s.l. (incl. var.? "bullseye", var. *laetus*, var. *longistylis*?, var. *micranthus*? others?)
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1' stamens inserted deeper in throat, little exserted, closely grouped; cotyl. roundish; fl tube gen 3-5+ cm, uniform in diam throughout; corolla gen with paired red marks at base of each lobe; plants of finer-textured, rel. moist grassland soils and serpentine, gen on rel level sites; coast ranges from Monterey Pen. to Santa Clara and Marin to Napa Co.'s.....*L. longitubus*
 2. all fls of population yellow, most or all with red marks; south of SFBay
 3. cor rel. large but tube short; plants rel short; coastal bluff(s), San Mateo Co.....ssp. *croceus*
 - 3'. cor smaller and orange-yellow, but tube very long, forest meadow(s), SCruz Co.....ssp. xxxxx
- 2'. fls mostly white to cream or pink
 3. cor white to deep pink (rarely yellow), lacking red marks; tube rel short; w Marin Co...ssp. zzzzz
 - 3' cor white to cream to bright pink, gen with red marks; loc's other than above.....ssp *longitubus*

Well, that should just about do it, and i hope this puts the whole mess into nice sharp focus for you as it does for me. I think people overestimate the complexity of these things, mainly because they have been so badly scrambled by past taxonomic treatments. If you had to go only by the stuff that has been published you'd be permanently lost. The plants themselves seem to follow good simple biological logic. Of course this is only a rough outline; a great deal of refining and fleshing-out remains to be done. Photos and other info strongly encouraged, in particular from NCoR, E Bay, and SCoR.

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