Molecular Phylogenetics and Taxonomy of the Genus *Thysanocarpus* (Brassicaceae)

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Communicating Editor: Daniel Potter

**Abstract**—The relationships and taxonomy of the genus *Thysanocarpus* (Brassicaceae) are reassessed based on molecular phylogenetic analyses of several nuclear ribosomal ITS and chloroplast (*trnL-F*) sequences and a critical re-examination of morphology and nomenclatural types. Based on these results, *Thysanocarpus* is well-supported as a member of tribe Thelypodieae, but no illuminating phylogenetic structure is found within the tribe. The independent origin of similar fruit morphology in *Thysanocarpus* and *Alyssanthes* is confirmed. Within *Thysanocarpus*, seven species are recognized: *T. conchuliferus*, *T. curvipes*, *T. desertorum*, *T. erectus*, *T. laciniatus*, *T. radians*, and *T. rigidus* comb. nov. *Thysanocarpus laciniatus* is found to have originated through hybridization. However, *T. desertorum* and *T. rigidus*, which have previously been included within *T. laciniatus* (as *T. laciniatus var. hitchcockii* and *T. laciniatus var. rigidus*, respectively), do not share that species’ hybrid origin and are distinct both phylogenetically and morphologically. Within *T. curvipes*, five subspecies are recognized: *T. curvipes* subsp. *amplectens* comb. nov., *T. curvipes* subsp. *amplectens*, *T. curvipes* subsp. *amplectens* comb. nov., *T. curvipes* subsp. *amplectens*, *T. curvipes* subsp. *amplectens* comb. nov., *T. curvipes* subsp. *amplectens*, *T. curvipes* subsp. *amplectens*, *T. curvipes* subsp. *amplectens*, and *T. curvipes* subsp. *amplectens*. Four subspecies are recognized based on a combination of morphology and geography.

**Keywords**—Fruit morphology; hybrid speciation; nuclear ribosomal ITS; Thelypodieae; *trnL-F*.

*Thysanocarpus* Hook. is a genus of annuals in the family Brassicaceae, found from extreme southwestern British Columbia south through the western United States to northwestern Mexico. The genus is most diverse in California, where all but one of the species (*T. erectus* S. Wats., a Baja California endemic) are found. In the most recent synoptic treatment of the genus, Rollins (1993) recognized five species with no named infraspecific taxa. However, variation within several of these taxa is substantial, and in the earlier treatment of California taxa, Munz (1959) recognized four varieties within *T. curvipes* Hook. and five within *T. laciniatus* Nutt. ex Torr. & A. Gray. *Thysanocarpus* is currently placed in the tribe Thelypodieae (formerly Schizopetaleae; see Beilstein et al. 2008 and Warwick et al. 2009) based on morphological and molecular phylogenetic investigations (Bailey et al. 2006; Al-Shehbaz et al. 2006; Alexander et al. 2006).

*Thysanocarpus* is notable for its unusual fruits, which are orbicular to obovate winged silicles, uniocular, one-seeded, and indehiscent. These fruits may be glabrous or pubescent with simple, blunt-tipped trichomes. The only other species in the western United States with similar fruits is *Alyssanthes* *pugetsii* (Hook.) Greene, which differs from *Thysanocarpus* in the following respects: 1) the silicles are pubescent with unicinate trichomes; 2) the silicles are borne in second infructescences; and 3) the foliage is pubescent with branched trichomes. Fruit similarities led A. *pugetsii* to be named initially as a species of *Thysanocarpus* (Hooker 1836). However, a careful reexamination of morphology (Al-Shehbaz et al. 2006) in conjunction with preliminary molecular phylogenetic analyses (Alexander et al. 2006; see also Results) suggests an affiliation with members of Arabidaceae and no particularly close relationship with *Thysanocarpus*. Outside of North America there are several additional genera with fruits similar to those of *Thysanocarpus* in the tribes Alysseeae, Heliothieae, and Isatideae. The similarity of *Thysanocarpus* to *Tauscheria* Fisch. (currently included in *Isatis* L.) in particular was noted by Hooker (1829), Torrey and Gray (1838–40), and Greene (1891). However, recent molecular phylogenetic investigations suggest that these taxa with similar fruits are not closely related to *Thysanocarpus* (Bailey et al. 2006; Mummenhoff et al. 2005; Warwick et al. 2008).

The goals of the present study are threefold. First, a family-wide phylogenetic analysis is presented to test the monophyly of *Thysanocarpus* and establish its position within Brassicaceae, including further confirmation of the separation of *Thysanocarpus* and *Alyssanthes*. Second, infrageneric phylogenetic analyses within *Thysanocarpus* are used to refine our understanding of the number of taxa in the genus and their relationship with each other. Third, a revised taxonomy of the genus is presented based on both the results of infrageneric phylogenetic analyses and a re-examination of morphology.

**Materials and Methods**

**Taxon Sampling and DNA Isolation**—Leaf material for phylogenetic analysis of *Thysanocarpus* was obtained from recent collections and from herbarium specimens from the following institutions: CAS, DS, JEPS, MO, NMC, RSA, and UC (see Appendix 1). Specimens were chosen to include multiple samples of all taxa recognized in treatments of the genus by Rollins (1993) and Munz (1959) and to include as much of the morphological variation within *T. curvipes* and *T. laciniatus* as possible. A total of 55 specimens of *Thysanocarpus* were used, including 29 specimens of *T. curvipes*; the geographic distribution of these samples is provided in Figs. 1 and 2. DNA was isolated following the procedures of Alexander et al. (2007), except that 10 mm Tris-HCl in 70% EtOH was used instead of 70% EtOH when washing contaminants from the silica columns at step 13.

To assess the monophyly of *Thysanocarpus* and its placement within Brassicaceae, we selected 51 samples of the family from GenBank for which both ITS and *trnL-F* spacer sequences were available. Sequences were chosen to sample broadly across the named tribes of Brassicaceae and include as many species of tribe Thelypodieae as possible (tribes follow Al-Shehbaz et al. 2006, Al-Shehbaz and Warwick 2007, Warwick et al. 2009) The complete list of accessions is provided in Appendix 1.

**Amplification and Sequencing**—Two loci were amplified and sequenced: *trnL-F* (primers F and C; Taberlet et al. 1991) from the chloroplast genome and the nuclear ribosomal ITS (primers ITS5 and ITS4, White et al. 1990). Amplification and sequencing followed previously developed protocols (Bailey and Doyle 1999; Bailey et al. 2002), and both loci were successfully amplified and sequenced for all samples except *trnL-F* for one accession of *T. desertorum* (32) and ITS for one *T. curvipes* (26) and one *T. erectus* (38). Most sequences were generated by direct sequencing of PCR products. However, initial direct sequencing attempts for ITS products in...
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The sequence data for *T. laciniatus* includes conflict between the two loci caused by hybridization (see Discussion). Consequently, application of cladistic methodology to a concatenated dataset including *trnL-F* and ITS sequences for *T. laciniatus* is inappropriate, because the resulting terminals would violate a fundamental assumption of cladistic analysis, that character state change occurs along a common bifurcating evolutionary history (Bremer and Wannbørp 1979; Brandt et al. 2006, Cronquist 1987). Matrix 1 was rooted with *Aethionema grandiflorum* Boiss. & Hohen., a member of the genus that is well-supported as sister to all other extant Brassicaceae (Al-Shehbaz et al. 2006; Bailey et al. 2006).

Matrices 2, 3, and 4 are used to investigate relationships within *Thysanocarpus*. Matrix 2 contains ITS sequences for all *Thysanocarpus* samples, including multiple sequences from accessions of *T. laciniatus* as described above. Matrix 3 contains *trnL-F* sequences for all *Thysanocarpus* samples. Matrix 4 is a concatenated data set containing both ITS and *trnL-F* sequences for all *Thysanocarpus* except *T. laciniatus*. The single accession (2b) of *T. curvipes* for which only a *trnL-F* sequence was available was also excluded from Matrix 4. Phylogenetic relationships among members of Thelypodieae are insufficiently resolved to identify the sister group of *Thysanocarpus* (Bailey et al. 2006; see Results). To root our analyses, we chose *Streptanthella longirostris* (S. Wats.) Rydb., a member of Thelypodieae that is resolved in a large polytomy with *Thysanocarpus*. However, identical interspecific relationships were recovered in analyses including all sampled members of Thelypodieae (Matrix 1; Fig. 3; see Results) suggesting that outgroup selection has not affected inferred relationships within *Thysanocarpus*.

Matrices were aligned automatically using ClustalW (Thompson et al. 1994) under default parameters. The resulting alignments were then checked and refined manually using Se-Al (Rambaut 2002). Gap characters were included for each locus using the simple indel coding method of Simmons and Ochoterena (2000) as implemented in SeqState (Müller 2005). Aligned lengths and numbers of parsimony-informative nucleotide and gap characters for each matrix are indicated in Table 1. All matrices are deposited in TreeBASE (study number S2546).

For concatenated matrices including both loci (Matrix 1 and Matrix 4), incongruence length difference tests (Farris et al. 1995) as implemented in WINCLADA (Nixon 1999–2002) were conducted to determine if there is significant incongruence between the loci. For each of these two matrices, comparison of ITS and *trnL-F* found them not to be significantly incongruent (Matrix 1, *p* = 0.0909; Matrix 4, *p* = 1.0000).

Prior to parsimony analyses, uninformative characters were removed from the matrices. For each matrix, heuristic searches for most parsimonious trees were conducted using NONA (Goloboff 2000) spawned from WINCLADA with 500 random addition sequence replicates with tree bisection and reconnection (TBR), holding 20 trees per replicate, followed by further TBR searching with a maximum of 10,001 trees. Cline support was estimated with 1,000 jackknife resampling replicates (Farris et al. 1996) under default settings in TNT (Goloboff et al. 2008) using the "new technology search", with parsimony ratchet (Nixon 1999), sectorial search, tree-drifting, and tree-fusing (Goloboff 1999) techniques activated and a 36% removal probability. Additionally, maximum likelihood analyses were conducted to test for sensitivity of the results to different methods of analysis. Maximum likelihood analyses were conducted with the online RAxML Black Box server (Stamatakis et al. 2008), which uses the GTR + *Γ* model when conducting a heuristic search and the GTR + CAT model when computing bootstraps. The matrices analyzed by maximum likelihood were identical to those included in the parsimony analyses described above except that gaps were excluded. We chose this approach because it is not clear whether the models used by RAxML, or any other available models, are appropriate for modelling the evolution of gap characters. For the concatenated Matrices 1 and 4, model parameters were estimated for each locus separately.

**Results**

**Monophyly and Phylogenetic Placement of *Thysanocarpus*—** Figure 3 shows the cladogram resulting from phylogenetic analysis of Matrix 1. *Thysanocarpus* is placed within Thelypodieae, which is found to be monophyletic with strong (87% jackknife) support. Resolution within Thelypodieae, however, is limited, with *Thysanocarpus* placed in a large basal polytomy. *Thysanocarpus* is weakly supported (>50%) as monophyletic; this low support is associated primarily with the placement of *T. ericetorum*, as the remaining species are...
monophyletic with high (94%) support. Athysanus pusillus is strongly supported (100%) as sister to Draba nemorosa L. of Arabideae.

**Relationships Among Species of Thysanocarpus**—Figures 4, 5, and 6 show cladograms resulting from phylogenetic analyses of Matrices 2, 3, and 4, respectively. All three analyses show *T. erectus* sister to the remainder of the genus, in agreement with Fig. 3. The other species of the genus are divided into two clades, one including all samples of *T. conchuliferus*, *T. desertorum*, and *T. rigidus* (the "conchuliferus clade") and the other including all accessions of *T. curvipes* and *T. radians*. The only hard incongruence among these analyses involves the placement of *T. laciniatus*. In the plastid data set (Fig. 5), all accessions of *T. laciniatus* are in the *curvipes* clade, either forming a clade sister to *T. curvipes* or, in the case of Accession 49, in a polytomy including all accessions of that species. In the nuclear ITS data set (Fig. 4), accessions of *T. laciniatus* fall in two distinct clades. "Laciniatus clade 1" is strongly supported (99% jackknife) as a member of the *conchuliferus* clade whereas "laciniatus clade 2" is strongly supported (97%) as a member of the *curvipes* clade. ITS sequences belonging to both of these clades (denoted by suffixes "A" and "B" after accession numbers) were recovered from five accessions (41, 44, 46, 48, and 49) of *T. laciniatus*, three of which are known polyploids (Windham et al. unpubl.).

**Phylogenetic Resolution within Thysanocarpus curvipes**—Resolution within *T. curvipes* is low, however two subclades of *T. curvipes* are found in all three analyses. The only two specimens of *T. curvipes* subsp. *longistylus* included in our sample form a weakly supported (64% jackknife) subclade in the *trnL-F* analysis, (Fig. 5) but this grouping receives strong support (> 95%) in the ITS and combined analyses (Figs. 4, 6). A "northwestern Nevada clade", including three specimens of *T. curvipes* subsp. *curvipes* from Humboldt and Washoe Cos. also is apparent in all three analyses, receiving weak support (64%) in the ITS analysis and stronger support (> 85%) in the *trnL-F* and combined analyses. A third subclade, comprising all sampled specimens of *T. curvipes* subsp. *elegans*, is strongly supported (> 95%) in the ITS and combined analysis (Figs. 4, 6) but these accessions are unresolved in the *trnL-F* analysis (Fig. 5). Additional resolution within *T. curvipes* is found in ITS and combined analyses, but is only weakly supported (< 65%).

**Discussion**

**Monophyly and Phylogenetic Placement of Thysanocarpus**—Thysanocarpus is placed in a large basal polytomy within Thelypodieae, consistent with earlier phylogenetic analysis based solely on ITS sequence data (Bailey et al. 2006). The tribe appears to be recalcitrant to phylogenetic analysis, as no published analysis has yielded significant resolution within it (Bailey et al. 2006; Beilstein et al. 2006; Beilstein et al. 2008). More precise knowledge of the close relatives of Thysanocarpus must therefore await further investigation. Support for monophyly of *Thysanocarpus* exclusive of *T. erectus* is high, but *T. erectus* is only weakly united with the remainder of the genus. This is not surprising given the poor resolution at the genus level throughout Thelypodieae. Placement of *Athysanus* in Arabideae is confirmed, consistent with earlier morphological (Al-Shehbaz et al. 2006) and phylogenetic (Alexander F4 F5 F6 Fig. 2. Geographic distribution of additional Thysanocarpus specimens used in phylogenetic analyses. A. Thysanocarpus conchuliferus, *T. desertorum*, *T. erectus*, and *T. rigidus* samples from southern California and Baja California in the U. S. A. and Mexico, respectively. B. Thysanocarpus laciniatus and *T. radians* samples from California and Nevada, U. S. A.
analyses. Similarity between fruits of the two genera is thus due to convergence, in agreement with recent suggestions that fruit morphology is a poor guide to relationships within the family as a whole (Beilstein et al. 2006; Beilstein et al. 2008).

**Relationships Among Species of Thysanocarpus**—The Baja California endemic *T. erectus* forms the earliest diverging branch in all analyses (Figs. 3–6) and is sister to the other species of *Thysanocarpus*. The remaining species are divided into two clades, one including all samples of *T. conchuliferus,*
Table 1. Aligned lengths, numbers of parsimony-informative characters, and numbers of parsimony-informative gap characters for each locus in each matrix.

<table>
<thead>
<tr>
<th>Locus</th>
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<td>211</td>
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<tr>
<td>Matrix 2</td>
<td>689</td>
<td>103</td>
</tr>
<tr>
<td>Matrix 3</td>
<td>689</td>
<td>96</td>
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T. desertorum, and T. rigidus (the conchuliferus clade) and the other including all accessions of T. curvipes and T. radians (Fig. 6). Each member of the conchuliferus clade has, at one time or another, been treated as a variety or synonym of T. laciniatus (Munz 1959; Rollins 1993). Although T. conchuliferus was considered a distinct species in the most recent synopsis of the genus (Rollins 1993), T. desertorum (occasionally recognized as T. laciniatus var. hitchcockii Munz) and T. rigidus (occasionally recognized as T. laciniatus var. rigidus Munz) have rarely been recognized except by the most avid splitters. However, the discovery of the hybrid origin of typical T. laciniatus (see below) requires a reassessment of past taxonomic treatments. If the Santa Cruz Island endemic T. conchuliferus is to be maintained as a species, as has become customary in recent years (Rollins 1993), then the equally distinct T. desertorum and T. rigidus must be afforded the same treatment. All three of these taxa are diploids (Windham et al. unpubl.) and subsuming them under T. laciniatus (a name that clearly applies to a hybrid) is both unhelpful as a representation of the evolutionary relationships of these taxa and disallowed under Article H.5.1 of the International Code of Botanical Nomenclature (McNeill et al. 2006). Thysanocarpus conchuliferus, T. desertorum, and T. rigidus are rather easily separated from T. laciniatus (and each other) and are treated below as distinct species.

Hybrid Origin of Thysanocarpus laciniatus—A hybrid origin for T. laciniatus is indicated by two related lines of evidence: 1) differing placement of some sequences from this species in cladograms inferred from plastid and nuclear sequence data, and 2) polymorphism among copies of ribosomal DNA within individuals of T. laciniatus. Ten out of eleven samples of T. laciniatus exhibit incongruence between analyses based on trnL-F and ITS sequences. In the trnL-F cladogram (Fig. 5), all accessions of T. laciniatus are strongly supported as members of the curvipes clade (93% jackknife support). This placement is in conflict with the ITS cladogram (Fig. 4), which indicates that all accessions but one (Accession 42) of T. laciniatus contain an ITS sequence type derived from the conchuliferus clade, most of these forming laciniatus clade 1. For Accession 42, the only specimen lacking conflict between ITS and trnL-F, both loci indicate membership in the curvipes clade. Given the similarity between the sequences recovered from Accession 42 and those obtained from several putative allopolyploids (Accessions 41, 44, and 46), it is possible that this specimen lost the ITS sequence representing the conchuliferus clade through concerted evolution (e.g., Wendel et al. 1995; Rauscher et al. 2004).

Polymorphism among nuclear ribosomal ITS copies was detected in six accessions of T. laciniatus (Fig. 4), providing further evidence for a hybrid origin of this taxon. Cloning and restriction site analyses revealed that four accessions (41, 44, 46, and 48) contain one ITS sequence type derived from the conchuliferus clade (“laciniatus clade 1”), and a second type derived from T. curvipes (“laciniatus clade 2”). Two accessions, 47 and 49, show different patterns. Although one ITS sequence type from the conchuliferus clade and one from the curvipes clade were recovered from Accession 49, these sequence types do not group with either laciniatus clade 1 or laciniatus clade 2. The two ITS sequence types recovered from Accession 47 are both derived from the conchuliferus clade, one within laciniatus clade 1 and the second associated with T. desertorum.

These results provide strong evidence that nearly all individuals of T. laciniatus included in our sample represent hybrids between the conchuliferus clade and the curvipes clade, and that T. laciniatus has arisen more than once, potentially as many as three times among the specimens examined in the present study. Further, the hybridization event giving rise to the lineage represented by Accessions 41, 44, 46, and 48 may have occurred after the more rapid coalescence of organellar loci but before the slower coalescence of nuclear loci that results from the four-fold greater effective population size of the latter (Birky et al. 1983). This would explain the reciprocal monophyly of T. curvipes and this lineage of T. laciniatus in analysis of trnL-F sequences (Fig. 5), but the absence of reciprocal monophyly between laciniatus clade 2 and T. curvipes in analysis of ITS sequences (Fig. 4). However, the apparent lack of coalescence of ITS sequences for T. curvipes could also be confounded by recombination or a lack of sufficient informative variation at this level of analysis. Additional chromosome counts and a more detailed examination of the origins of T. laciniatus are ongoing to better understand both the complex, multiple origins of T. laciniatus and cytological evolution in the genus as a whole. Similar complicated histories have been documented in a variety of allopolyploid taxa (Werth et al. 1985; Wyatt et al. 1988; Solits and Solits 1999; Rauscher et al. 2004), and a more complete exposition of the evolution of T. laciniatus will be the subject of a future paper.

Phylogenetic Resolution within Thysanocarpus curvipes—There is strong support for monophyly of T. curvipes subsp. elegans from ITS (Fig. 4) but not from trnL-F (Fig. 5). The lack of support for this group in trnL-F data apparently results from the lower variability of trnL-F compared to ITS (see Table 1). Assessment of herbarium specimens suggests that subsp. elegans introgresses regularly with other infraspecific taxa. Although subsp. elegans is readily recognizable in its extreme form, a substantial number of herbarium specimens are morphologically intermediate between this subspecies and subsp. curvipes. It nonetheless is distinct at one of the two sampled loci, is generally recognizable morphologically, and is here given subspecific status.

The T. curvipes subsp. longistylus clade appears in all analyses with strong support. Subspecies longistylus is poorly represented in the current sequence data, with only two specimens. Although this taxon is here given subspecific status, more extensive sampling of individuals and loci would be required to establish with greater certainty whether this taxon is genetically distinct from other T. curvipes.

The northwestern Nevada clade of T. curvipes provides the only strongly-supported phylogenetic resolution in the species that has no apparent correlation with morphology. These are typical members of subsp. curvipes, essentially indistinguishable from plants occurring in northern California, Idaho, Oregon, and Washington. None of the other members
Fig. 4. Strict consensus of 54 most parsimonious trees (length = 176, CI = 0.75, RI = 0.96) from parsimony analysis of ITS sequences of *Thysanocarpus*, rooted with *Streptanthella longirostris*. Numbers above branches indicate parsimony jackknife support, while numbers below branches indicate maximum likelihood bootstrap support. Support values below 50 are not shown, and a “-” indicates that the node in question did not occur on the best tree from maximum likelihood analysis. Accessions of *T. laciniatus* falling outside of *laciniatus* clade 1 and *laciniatus* clade 2 are marked with asterisks.
Fig. 5. Single most parsimonious tree (length = 35, CI = 0.94, RI = 0.98) from parsimony analysis of trnL-F sequences of *Thysanocarpus*, rooted with *Streptanthella longirostris*. Numbers above branches indicate parsimony jackknife support, while numbers below branches indicate maximum likelihood bootstrap support. Support values below 50 are not shown, and a “–” indicates that the node in question did not occur on the best tree from maximum likelihood analysis. An accession of *T. laciniatus* falling outside the main *T. laciniatus* clade is marked with an asterisk. Note also that incongruence between parsimony and maximum likelihood analyses regarding the monophyly of the two samples of *T. desertorum* apparently results from the inclusion of gap characters in the former analysis but not the latter. Gap characters provide two synapomorphies joining these two samples, but in the absence of gaps there are no synapomorphies for *T. desertorum*. 
of subsp. curvipes (accessions 15, 16, 25 and 31) is resolved with these plants in any analysis. The genetic distinctness of the northwestern Nevada clade most likely reflects historical isolation that has not been accompanied by any readily apparent morphological divergence.

**Taxonomic Treatment**


Herbs, annual, glaucous, glabrous or pubescent. Trichomes of the foliage absent or concentrated towards the base of the plant, simple, acicular, 0.3–0.6 mm long. Stems erect, simple or branched. Basal leaves shortly petiolate, simple, entire or dentate to pinnatifid or pinnatisect, often withered by anthesis or fruiting; cauline leaves sessile, auriculate or not, entire or dentate or pinnatifid to pinnatisect. Racemes several, many flowered, corymbose, ebracteate, usually elongated considerably in fruit; fruiting pedicels slender, often recurved. Sepals greenish or purplish with pale margins, oblong to ovate, ascending, caducous, base of lateral pair not saccate; petals white to purplish, 1–3 mm long, subequaling or longer than sepals, blade spatulate to oblong, claw undifferentiated from blade; stamens 6, slightly tetradynamous; filaments slightly dilated at base; anthers ovate, yellow or purple; lateral nectaries 1 on each side of lateral stamens or semiannular, median nectaries

Fig. 6. Strict consensus of 22 most parsimonious trees (length = 180, CI = 0.83, RI = 0.96) from parsimony analysis of combined ITS and trnL-F sequences of *Thysanocarpus* (excluding *T. laciniatus*), rooted with *Streptanthella longirostris*. Numbers above branches indicate parsimony jackknife support, while numbers below branches indicate maximum likelihood bootstrap support. Support values below 50 are not shown, and a "--" indicates that the node in question did not occur on the best tree from maximum likelihood analysis.
absent. Fruits indehiscent silicles 2.5–10 mm wide, orbicular to ovate or elliptic, strongly latiseptate, sessile, unsegmented, usually pendulous; valves with a prominent midvein, glabrous or with blunt-tipped, simple trichomes; replum winged, the wing flattened, usually with radiating rays, entire or crenate, often perforate; septum obsolete; ovules and seeds 1 per fruit; style short, 0.2–1.5(–1.8) mm long, usually persistent but fragile and easily broken; stigma entire. Seeds aseriate, wingless, elliptic to orbicular, flattened; seed coat not mucilaginous when wetted; cotyledons accumbent.


Trichomes absent. Basal leaves oblanceolate to elliptic, pinnatifid or occasionally siminate-dentate, 1–3(–5) cm long. Cauline leaves lanceolate to narrowly elliptic or nearly linear, widest near base or middle, auriculate-clasping. Flowers with yellow anthers. Lower fruiting pedicels 3.5–6.5 mm long, stiffly divaricate-ascending or slightly recurved. Fruits glabrous, cymbiform, the wings strongly incurved toward the flat side of the silicle; wings divided into spatulate lobes 0.25–0.4 mm wide at the narrowest, these occasionally joined distally. Figure 7A.

**Distribution**—United States, southern California, Santa Cruz Island. Figure 8.

**Thysanocarpus conchuliferus** is the most narrowly-distributed species in the genus, found only on Santa Cruz Island. The cymbiform fruits of the species are very distinctive, although *T. curvipes* occasionally has silicles with incurred to involute wings. In addition to characters used in the key, the two are further distinguished by the much shorter, denser inflorescences of *T. conchuliferus* (internodes in the inflorescence average less than 2 mm in *T. conchuliferus* and greater than 3 mm in *T. curvipes*). Although *T. conchuliferus* has usually been considered a variety of *T. laciniiatus* in the literature, it has strongly auriculate cauline leaves, while *T. laciniiatus* has cuneate-based or minutely auriculate leaves.


**Thysanocarpus runcinatus** G. Don, A General History of the Dichlamydeous Plants, 1: 196. 1831.—LECTOTYPE, here designated: Table 18 A, W. J. Hooker, Fl. Bor.-Amer. 1: 388. 1829. Although the specimen used in producing this figure was not explicitly stated, it was likely drawn from the holotype of *T. curvipes*.

Trichomes present or absent. Basal leaves oblanceolate to obovate, subtent to sinuate-dentate, 1–6(–13) cm long. Cauline leaves lanceolate, widest at base, auriculate-clasping. Flowers with purple anthers, or rarely some flowers with infertile, whitish anthers. Lower fruiting pedicels 3–7(–12) mm, recurved in a continuous arc. Fruits with claveate hairs 0.2–0.4 mm long or glabrous, flat or plano-convex, obovate to nearly orbicular, 3.6–9 mm wide; wing entire, crenate, divided into narrow, spatulate lobes, or perforate, usually with broad (0.2–0.5 mm) rays (Fig. 9).

**Distribution**—United States (Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, and Washington), Mexico (northern Baja California and northern Sonora), and Canada (southern Vancouver Island, British Columbia); Fig. 10.

This is a variable species and many attempts have been made to divide that variation into recognizable taxa. These efforts have produced a total of 18 basionyms referable to plants here included within *T. curvipes*. Morphological characters used include pubescence of the stem, foliage, and silicle, length of the style, and size or ornamentation of the silicle wing. Of these characters, all but pubescence of the silicle show variation along geographic lines. Pubescent...

Silicles appear to be more common in the northern part of the range of *T. curvipes* but this feature is variable and, contrary to Piper’s (1906) suggestion that fruit pubescence is consistent within populations, we have seen a number of mixed populations.

Based on concordance between morphology and geography, with insight added by phylogenetic analyses as discussed above, we recognize five subspecies within *T. curvipes*. Three of these, subsp. *amplectens*, subsp. *curvipes* and subsp. *eradiatus*, are predominantly allopatric, although overlapping in some areas of southern California. Two subspecies, subsp. *elegans* and subsp. *longistylus*, occur only within the ranges of other subspecies of *T. curvipes*. The latter two subspecies receive some support in our molecular phylogenetic analyses, while the previous three do not. Although the five subspecies recognized here are quite distinct in their extremes, there are a number of specimens of intermediate morphology, as is to be expected for infraspecific taxa. Southern California is particularly problematic, as all five subspecies overlap in this area and all appear to interbreed to some extent.
Fig. 8. Distribution of other Thysanocarpus in the western U. S. A. and Baja California in adjacent Mexico. Distribution is mapped at the county/municipio level except for T. rigidus and T. erectus, for which all specimens seen are mapped.
1. Stems pubescent basally .......................... 2
2. Fruits < 5.5 mm wide and 6 mm long, entire, incised, or perforate ........................................... 3
3. Styles ≤ 0.7 mm long .................................. 2a. subsp. curvipes
4. Styles 0.9–1.8 mm long ............................... 2b. subsp. longistylus
1. Stems glabrous throughout .......................... 4
2. Styles 0.9–1.8 mm long ............................... 2c. subsp. elegans
4. Styles ≤ 0.7 mm long ................................ 2d. subsp. eradiatus
5. Wings of the fruit radiate, entire to perforate .... 5
5. Wings of the fruit eradiate, entire or sparingly incised

Fig. 10. Map of western North America showing the distribution of the subspecies of *Thysanocarpus curvipes*. Distribution is mapped at the county/municipio level except for Canada, which lacks equivalent political units.
Thysanocarpus hirtellus Hook. var. Thysanocarpus ramosus
Thysanocarpus filipes
Thysanocarpus affinis
otherwise distinct. The names overlap in southern California and central Arizona but are
range of brous-stemmed plants found in the southeastern part of the
er Sonora). Figure 10.

Arizona, and southwestern New Mexico) and Mexico (north-
rate, the style 0.2–0.7 mm long. Figure 9A.

2. Thysanocarpus curvipes Hook. subsp. curvipes

This and Thysanocarpus curvipes subsp. eradiatus are gla-
brous-stemmed plants found in the southeastern part of the
range of T. curvipes. The two intergrade where their ranges
overlap in southern California and central Arizona but are
otherwise distinct. The names T. amplectens and T. filipes
denote plants with glabrous, imperforate-winged silicles and
those with pubescent, perforate-winged silicles, respectively,
variants that do not appear to warrant recognition.

2b. Thysanocarpus curvipes Hook. subsp. curvipes

Thysanocarpus curvipes Nutt. ex Torr. & A. Gray, Fl. N. Amer. 1: 118. 1829.—TYPE: U. S. A. California: Santa Barbara Co.: Santa Barbara, s. d., T. Nuttall s. n. (holotype: BM!, iso-
types: NY!, US!).

Thysanocarpus pulchellus Fisch. & C. A. Mey., Index Seminum
[St. Petersburg], 2: 50–51. 1835; Thysanocarpus curvipes
Hook. var. pulchellus (Fisch. & C. A. Mey.) Greene, Fl. Francisc. 276. 1891.—TYPE: U. S. A. California: Sonoma: Circa coloniam rutherfordian Ross, cult. in horto bot. imp. Petropol. [cultivated at the St. Petersburg Botanical Garden from material collected near the Russian Fort Ross], 1835, F. P. Wrangel s. n. (holotype: LE!).

Thysanocarpus curvipes Hook. var. involutus Greene, Fl. Francisc. 276. 1891.—TYPE: U. S. A. California: Sonoma Co.: 10 Mar 891, Bioletti s. n. (holotype: NDG!).

Thysanocarpus hirtellus Greene, Pittonia 3: 86. 1895.—TYPE: U. S. A. California: Napa: Wooded cañon tributary to Dry Creek, 12 May 1895, Greene s. n. (lectotype, here designated: NDG 4137!, isotypes: NDG 4136!, NDG 4138!).

types: BKL, DS, GH, NY!, UC!, US!).


Trichomes present. Fruits 3–5.5 mm wide, the wings radiate, entire, crenate, divided into spatulate lobes, or perforate, the style 0.2–0.6 (–7) mm long. Figure 9B.

Distribution—United States (California, Idaho, southwestern Montana, northern Nevada, Oregon, and Washington), Mexico (northern Baja California and northern Sonora), and Canada (southern Vancouver Island, British Columbia). Figure 10.

This is the most widespread subspecies of Thysanocarpus curvipes and further shows the greatest sympatry with other subspecies. The ranges of both subsp. elegans and subsp. longistylus are included almost entirely within the distribution of subsp. curvipes. Stems of these three subspecies are pubescent basally (with rare exceptions in subsp. longistylus), distinguishing them from the two southeastern subspecies, subsp. amplectens and subsp. eradiatus. Specimens intermediate between subsp. curvipes and subsp. elegans are encoun-	ered throughout areas of sympatry, and these often cannot be assigned confidently to either subspecies. Plants morphologi-
cally intermediate between subsp. curvipes and subsp. longistylus are, however, rare in herbarium collections.

Variation within populations of T. curvipes subsp. curvipes can be substantial. For instance, silicles may be either gla-
brous or pubescent, and either perforate or imperforate, at a single site. As here defined, subsp. curvipes includes: var.
cognatus (plants with cuneate-based silicles), subsp. madocar-
pus (plants with glabrous silicles), var. involutus (plants with
strongly involute wings on the silicles), T. hirtellus (plants
with particularly abundant pubescence), and T. pulchellus
(plants with petals longer than the sepals). None of these
characters, however, seem to provide a sound basis for distin-
guishing taxa. Thysanocarpus curvipes usually has been listed
as a synonym of T. lacinuatis (e.g., Rollins 1993), but the type
material at BM and NY has prominently auriculate leaves and
pubescent stems, closely resembling plants here assigned to
T. curvipes subsp. curvipes.

2c. Thysanocarpus curvipes Hook. subsp. elegans (Fisch. & C. A. Mey.) P. J. Alexander & Windham, comb. nov. Thysanocarpus elegans Fisch. & C. A. Mey., Index Seminum


Thysanocarpus foliosus Heller, Muhlenbergia 2: 47–48. 1905.—
TYPE: U. S. A. California: Kern Co.: On the side of a ravine
back of Girard Station in the Tehachapi Mountains, 18 Apr 1905, A. A. Heller 7719 (holotype: CAS!; isotypes: AC, BKL, DS, GH, NY!, UC!, US!).

Trichomes present. Fruits 5.5–7 (–9) mm wide, the wings
radiate, perforate, the style 0.4–0.8 (–1) mm long. Figure 9C.

Distribution—United States (California) and Mexico
(northern Baja California). Figure 10.

As mentioned above, this subspecies appears to hybrid-
ize with Thysanocarpus curvipes subsp. curvipes on a regular
basis. Plants that may result from hybridization with subsp.
amplectens or subsp. eradiatus can be found in the southern
part of the range from Kern County to Santa Barbara County
in southern California. Plants in the type collection of T. folio-
sus resemble these putative hybrids and, although tenta-
ively
included here, are not readily assignable to any one subspecies. Morphological intermediates involving subsp. elegans are responsible for most of the apparent intergradation among subspecies of *T. curvipes*. Our molecular phylogenetic analyses provide support for the recognition of this subspecies, although it is resolved as a clade only in the ITS data.

Among plants here referred to *Thysanocarpus curvipes* subsp. *elegans*, the name *T. deppii* refers to plants with pubescent silicles. As discussed above, silicle pubescence shows a high degree of local variation independent of other characters and does not appear to be useful in naming taxa.


Trichomes absent. Fruits 3–5(–6) mm wide, the wings eradiate, entire or sparingly incised, the style 0.2–0.7 mm long. Figure 9D.

**Distribution**—United States (northwestern Arizona, southwestern California, northwestern Colorado, southern Nevada, and southwestern Utah). Figure 10.

Specimens intermediate between this subspecies and subsp. *amplectens* occur in southern California and central Arizona, and apparent hybrids with subsp. *longistylus* are found in southern California (Kern and San Bernardino Counties). Subspecies *eradiatus* is, however, uniform outside these areas. Although *T. trichocarpus* is the older name and would have priority at species rank, this taxon is usually referred to in the literature as var. *eradiatus*, so the latter name is used here at the subspecies level. The types of var. *eradiatus* and *T. trichocarpus* differ in the pubescence of the silicle (glabrous in the former, pubescent in the latter) but are otherwise similar.


Trichomes present or, rarely, absent. Fruits 3.4–5(–5) mm wide, the wings indistinctly radiate and entire to distinctly radiate and divided into spatulate lobes, or perforate, the style 0.9–1.5(–1.8) mm long. Figure 9E.

**Distribution**—United States, California (Tuolumne Co. south to Kern Co.). Figure 10.

Although this subspecies was named based on style length alone, it overlaps slightly with subsp. *elegans* in this character. Nonetheless, subsp. *longistylus* is readily separated from that subspecies by its smaller, imperfect fruits. Subspecies *longistylus* occurs almost entirely within the range of subsp. *curvipes*, as mentioned above, but plants intermediate between the two are rarely collected. However, narrow-winged, relatively long-styled plants of subsp. *eradiatus* occurring along the southern periphery of the distribution of subsp. *longistylus* may result from introgression between these two subspecies. Subspecies *longistylus* is the only subspecies for which both ITS and *trnL-F* sequences form monophyletic clades, but our sampling for this subspecies is limited and none of the potential hybrids with subsp. *eradiatus* were included.


Trichomes absent or, rarely, plants sparsely hirsute at base. Foliage greenish to purplish throughout. Basal leaves oblancocele to elliptic, subentire, sinuate-dentate, or, rarely, pinnatifid, 1–4(–5) cm long. Cauline leaves narrowly elliptic, widest near the middle, base cuneate, with small, inconspicuous auricles that do not extend around the stem, or, rarely, with conspicuous auricles extending around the stem. Flowers with yellow anthers. Lower fruiting pedicels 1.5–4(–5.5) mm, stiffly spreading or recurved in a continuous arc. Fruits usually pulvinate with minute (0.05–0.1 mm) clavate hairs, sometimes glabrous, flat or plano-convex, obovate to nearly orbicular, 2.5–4 mm wide; wing shallowly to deeply crenate, rarely entire, usually with ± indistinct rays 0.2–0.5 mm wide. Figure 7B.

**Distribution**—United States, southern California (Inyo, Kern, Los Angeles, Riverside, San Bernardino, and Santa Barbara Counties). Figure 8.

Munz named *T. lacinianus* var. *hitchcockii* based on the minutely pubescent silicles of the type. Later, Munz (1959) listed *T. desertorum* as a “probable synonym”, although the silicles of type material of *T. desertorum* are glabrous. Among specimens currently included in *T. desertorum*, most have pubescent silicles but a minority have glabrous silicles; variation in this character is unsurprising given that no taxon in the genus has uniformly pubescent silicles (see also discussion under *T. curvipes*). Although anther color has not been used previously in *Thysanocarpus* taxonomy, the yellow anthers of *T. desertorum* provide a means of distinguishing glabrous-fruited plants from otherwise similar taxa, notably *T. lacinianus* and *T. rigidus*.


Trichomes absent or, rarely, plants sparsely hirsute at base. Basal leaves oblancocele to obovate, sinuate-dentate, 2.5–5(–6) cm long. Cauline leaves lanceolate, widest at base, auriculate-clasping, often toothed, sometimes entire. Flowers with yellow anthers. Lower fruiting pedicels 2.5–5 mm long, erect to ascending proximally but often reflexed distally. Fruits with clavate hairs 0.2–0.4 mm long or glabrous, flat or plano-convex, nearly orbicular, 3.4–5.5 mm wide; deeply notched at base and apex, otherwise entire or occasionally shallowly incised. Figure 7C.

**Distribution**—Mexico, Baja California (Mcpio. Ensenada). Figure 8.

Although named for the erect pedicels of the type, the species is variable in this regard. Pedicels are usually erect or
strongly ascending at the base, but may be strongly recurved distally. The fruits are much like those of *T. curvipes* subsp. *eradiatus*, except that they are deeply notched at both the base and apex, and the wings are often purplish.


Trichomes absent or, rarely, plants sparsely hirsute at base. Foliage usually greenish, sometimes purplish at base. Basal leaves oblanceolate to elliptic, often pinnatifid, sometimes sinuate-dentate or subentire, 2–6(–9) cm long. Cauline leaves linear to narrowly elliptic, widest near the middle or equally wide throughout, base cuneate or with small, inconspicuous auricles that do not extend around the stem. Flowers with purple anthers, or rarely some flowers with infertile, whitish anthers. Lower fruiting pedicels 2.5–6(–8) mm long, recurved in a continuous arc.

**Fruits** usually glabrous, sometimes with clavate hairs 0.05–0.4 mm long, flat or plano-convex, obovate to nearly orbicular, 3–5 mm wide; wing entire to deeply crenate, eradiate or with ± indistinct rays 0.2–0.5 mm wide. Figure 7D.

**Distribution**—United States, California and southern Oregon. Figure 8.

Perhaps the most visually distinctive taxon in the genus due to the large, entire-winged fruits with distinct, narrow rays, this species occurs primarily in seasonally moist, low-elevation sites. *Thysanocarpus radians* often occurs with or near *T. curvipes* subsp. *elegans*, and occasional plants approach *T. curvipes* subsp. *elegans* morphologically; whether this can be attributed to hybridization is uncertain.


Trichomes absent, or plants rarely sparsely hirsute at base. Basal leaves oblongate to sublanceolate, sinuate-dentate to runcinate-pinnatifid, 1.5–4 cm long, usually glabrous. Cauline leaves lance-ovate to lanceolate, widest at base, auriculate-clasping. Flowers with yellow anthers. Lower fruiting pedicels 7–18 mm, weakly ascending, straight or nearly so but with gernically reflexed tips. Fruits usually with clavate trichomes ±0.2 mm long, or glabrous, flat, orbicular, 7–10 mm wide; wing entire or with undulate margins, with dark, narrow (±0.1 mm) rays, these extending most or all of the way to the margins. Figure 7E.

**Distribution**—United States, California and southern Oregon. Figure 8.

Perhaps the most visually distinctive taxon in the genus due to the large, entire-winged fruits with distinct, narrow rays, this species occurs primarily in seasonally moist, low-elevation sites. *Thysanocarpus radians* often occurs with or near *T. curvipes* subsp. *elegans*, and occasional plants approach *T. curvipes* subsp. *elegans* morphologically; whether this can be attributed to hybridization is uncertain.


Trichomes absent. Foliage purplish throughout. Basal leaves oblongate to elliptic, sublanceolate, sinuate-dentate, or pinnatifid, 2–5 cm long. Cauline leaves linear to narrowly elliptic, widest near the middle or equally wide throughout, base cuneate or with small, inconspicuous auricles that do not extend around the stem. Flowers with purple anthers. Lower fruiting pedicels 1.5–6 mm long, straight and stiffly spreading to ascending. Fruits glabrous, ovobrate to nearly orbicular, 2.5–3.5 mm wide; wing entire to shallowly crenate, eradiate or with ± indistinct rays 0.2–0.5 mm wide. Figure 7F.

**Distribution**—United States, southern California (Riverside, San Bernardino, and San Diego Counties) and Mexico (northern Baja California). Figure 8.

*Thysanocarpus rigidus* is poorly represented in herbarium collections, with only five specimens known. This species can be difficult to distinguish from *T. laciniatus*, which occasionally has the branched, purplish appearance of *T. rigidus*. The stiff, straight, horizontal to slightly ascending pedicels of *T. rigidus* allow identification in these cases. This species occurs in arid mountain ranges up to moderately high elevations (2,150 m on New York Peak), and three of the five specimens were collected in May, when little else is likely to be flowering. Poor sampling of these habitats at this time of year may account for the paucity of specimens, but *T. rigidus* may be of conservation concern and should be investigated further.

**Additional Specimens**—MEXICO. Baja California: Mepio. Ensenada: 50 miles SE of Tecate, 13 May 1925, *P. A. Munz 9572* (POM!).


**Acknowledgments.** We would like to thank the following institutions for loans of specimens: California Academy of Sciences (CAS, DS), New York Botanical Garden (NY), Rancho Santa Ana Botanic Garden (POM, RSA), University of California, Berkeley (JEPS, UC), University of Notre Dame (NDG), and Utah Museum of Natural History (UT). We would also like to thank the following institutions for label information and/or photographs of type specimens: The Academy of Natural Sciences, Philadelphia (PH), Botanical Garden of the V. L. Komarov Institute of the Russian Academy of Sciences (LE), and Natural History Museum, London (BM). Thanks also to Dr. K. Gandhi for nomenclatural assistance, and to Dr. N. H. Holmgren and one anonymous reviewer for helpful comments. This research was supported by NSF DEB-0817033 & EF-054228 (CDB).


**APPENDIX 1** Voucher information for new sequence data used in this study and GenBank accession numbers for all ITS and trnL-F sequences, listed in that order. All *Thysanocarpus* sequences were generated for the present study. Among other taxa, accessions from which sequences were generated for the present study are marked with an asterisk.


5. *Thysanocarpus curvipes* subsp. amplicentis, U. S. A.: Arizona: Cochise Co.: South-west of Willcox along Stronghold Canyon East in the Dragoon Mountains c. 1.93 km southeast of Barret Spring, M. D. Windham 2929 (NMC), GU24625,