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***Jaltomata*: An Introduction, and Preliminary
Observations on the Red/Orange Floral Nectar**

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Jaltomata is a morphologically and ecologically diverse neotropical genus of about 30 species of both herbs and shrubs (Mione, 1992). Corollas may be rotate, campanulate or tubular, or even urn-shaped with a recurved limb. The genus has a broad altitudinal distribution, from near sea level to over 4000 m, and habitats vary from the fog-dependent coastal desert of Peru (lomas, see Rundel et al., 1991) to the moist and dry mountains. All 16 species tested are self-compatible (Mione and Coe, in press).

There are two monophyletic groups of *Jaltomata*. One group, here called "Mesoamerican", includes herbs with rotate corollas that produce clearish nectar in small amounts and, with few exceptions, purple/black fruits (certain accessions of two different Mexican species have green fruits; Mione and Bye, 1996). This group includes about 10 species, widely distributed from southeastern Arizona, U.S.A., to southern Bolivia, with the highest species diversity in Mexico.

The other monophyletic group, here called "South American," includes both herbs and shrubs that exhibit a broad range of corolla forms, and have orange or red fruits. These are distributed in the Andes from northern Venezuela through northern Bolivia (about 20 species), in the Greater Antilles (1 species), and on the Galápagos Islands (1 species). Corollas of the woody species tend to be campanulate or tubular. The tubular flowered species were formerly placed in the genus *Hebecladus*. This genus, however, was merged into *Jaltomata* based on morphological characters (Hunziker, 1979; Mione et

al., 1993), and chloroplast DNA characters (Mione et al., 1994). Within the "South American" group, there are two types of nectar: a) in some species clearish nectar is produced in small amounts, as in the "Mesoamerican" group, and b) in others red/orange nectar is produced in large volumes. Species having red/orange nectar are morphologically and ecologically diverse but are confined to the region extending from northern Peru through northern Bolivia.

Below, several of the species that produce red/orange nectar are discussed briefly, including distribution information and noteworthy morphological features. Floral observations were made on plants cultivated at the University of Connecticut greenhouse, and were from field-collected seed, unless indicated otherwise.

Jaltomata umbellata (R. & P.) Mione & M. Nee, a floriferous shrub of the Peruvian lomas, has small (6.5-8 mm long), tubular, cream-colored flowers. Bright red nectar partially to completely fills the corolla tube. The style protrudes from the otherwise closed corolla during the initial, pistillate phase of one to two days; during this time no reward is available to floral visitors. When the corolla opens, the anthers dehisce, with the stigma remaining exerted several mm beyond the anthers and presumably remaining receptive. Thus, dichogamy and herkogamy are evident, and both may promote outcrossing. This species was illustrated in Ruiz & Pavón's *Flora Peruviana et Chilensis* (1799, pl. 181, fig. a), and again, in Mione et al. (1993).

Jaltomata ventricosa (Baker) Mione, a floriferous shrub of northern Peru, has urn-shaped flowers that produce red/orange nectar in quantities sufficient for it to splash out when plants are disturbed, actually staining one's skin and clothing. This species is unique among *Jaltomata* in that the limb of the corolla is completely turned outward and curls back. *J. ventricosa* was described and illustrated in the 1860s; the original plate is now the lectotype (Mione et al., 1993). Collections of this species were not represented in the major

North American herbaria from which we borrowed specimens. Recently, however, we have been able to study this species because of collections from northern Peru made by A. Sagástegui A. and S. Leiva made available through M. O. Dillon of the Field Museum of Chicago.

Blood red nectar has also been observed pooling in the base of corollas of two shrubby species of the high Andes that have broad, campanulate corollas. *Saracha herrerae* Morton (not yet transferred to *Jaltomata*), of the high altitudes (e.g. 3600 m) of southern Peru and northern Bolivia, bears large pale corollas 4.5 cm wide (measured in the field). In Bolivia this species was collected near the town of Charazani (=J. José Pérez on maps; Depto. La Paz, Prov. Bautista Saavedra) where, in the heart of the village of Kanlaya, the Kallawayas Indians (see Bastien, 1987) encourage *S. herrerae* among stone retaining walls (Mione, 1992). An undescribed but similar *Jaltomata* species from northern Peru (*J. Panero et al.* 854, Depto. Cajamarca, Prov. Cajamarca, 3300 m, CONN) has green corollas also typically large (3 cm in diameter).

The *Jaltomata* species with the largest recorded flowers (e.g. 5 cm diam., herbarium specimen), *J. weberbaueri* (Dammer) Mione, also produces blood red nectar (Mione and Coe, 1992). This Peruvian species is distributed in Depto. Ancash above 3000 m. A similar species, *J. aspera* (R. & P.) Mione of the Peruvian lomas, may also produce dark nectar. The flowers were described as having "5 purple glands at base" (*Goodspeed & Metcalf 30248*, MO, US). Only nine collections of this species have been seen, all made prior to 1943 (Mione and Coe, 1992).

Some noteworthy character correlations are that red/orange nectar always occurs copiously and is characteristic of many of the larger flowered species, while clear nectar occurs in just a few droplets per flower and tends to occur in smaller flower species. In addition, it seems likely that the bright nectar showing through the partially translucent corolla-

or in the case of campanulate flowers, showing both in the front view and through the corolla--is conspicuous to pollinators. Perhaps the red/orange nectar serves as both the attractant and the reward to pollinators.

A feature of interest for the genus is that in all species of the "Mesoamerican" group, stamens markedly change angle relative to the stationary style during floral phenology (Davis, 1986; Polsgrove, Mione and Anderson, 1993), and corollas (rotate) close at night. These features are exhibited only by some of the species of the "South American" group. The species of the "South American" group that have stationary filaments all have campanulate, infundibular or tubular corollas (non-rotate corollas) that do not close at night, the latter with one exception. Thus, non-rotate corollas and stationary filaments always co-occur, and these usually co-occur with the corolla remaining open at night. These tightly correlated, derived character states (Mione, 1992) may represent a suite of characters that are associated with a certain type of pollinator or pollination system, and/or, the correlation may be due to common ancestry. The species that produce red/orange nectar are a subgroup of the species having stationary filaments and campanulate, infundibular or tubular corollas remaining open at night.

Although red/orange nectar occurs only in certain species of Peru and northern Bolivia, its presence is not correlated with habitat, nor altitude, nor with a particular corolla form. In *Jaltomata* this striking nectar is found, as far as is known, only in woody species with corollas that are either campanulate, infundibular or tubular, but red/orange nectar is not present in all of the *Jaltomata* species with both this habit and one of these corolla forms (Mione, 1992). The red/orange nectar can be considered a synapomorphy (no other groups near *Jaltomata* have it so far as known) and thus the species that share this feature are a putatively monophyletic subgroup of the "South American" clade. If so treated, then the characters for habitat, altitude and corolla form must be considered secondari

ly variable, and evolutionarily labile--at least for these species. We are considering the possibility that red/orange nectar was a "key" character that allowed entrance of an underexploited niche (perhaps hummingbird pollination?). And, perhaps this ecological and reproductive opportunity, working synergistically with a propensity for long-distance dispersal (berries are red/orange and presumably bird dispersed) fueled the adaptive radiation of the red/orange nectar lineage into various habitats and altitudes. Alternatively, if red/orange nectar evolved more than once it would represent a fascinating case of parallel evolution for floral reward, but then the morphological and ecological diversity present among these species is not an example of adaptive radiation.

Systematic studies in progress will result in a taxonomic treatment of the genus and will elucidate the remainder of the *Jaltomata* species of Peru and northern Bolivia with red/orange nectar. Combined phylogenetic and ecological studies will address: a) the monophyly of the species with red/orange nectar, b) the evolution of habitat preference (e.g., is residence in the lomas derived and if so how many times has it evolved?), and c) morphological character evolution. In particular, characters and suites of characters that relate to breeding ecology will be studied.

Red nectar in *Jaltomata*, and in much of the Solanaceae, is unusual. It may characterize pollination by hummingbirds in a family where this is not common. And it could be a synapomorphy for a variable group of *Jaltomata* species. We would be pleased if readers would share with us any comments about the above, and accounts of other dark nectars in the Solanaceae.

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