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Systematics and evolution of the endemic Hawaiian genus
*Clermontia* Gaudichaud (Campanulaceae: Lobelioideae)

Lammers, Thomas Gerard, Ph.D.
The Ohio State University, 1988
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UMI
SYSTEMATICS AND EVOLUTION OF THE ENDEMIC HAWAIIAN GENUS
CLERMONTIA GAUDICHAUD (CAMPANULACEAE: LOBELIOIDEAE)

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of the Ohio State University

By

Thomas Gerard Lammers, B.S., M.A.

The Ohio State University
1988

Dissertation Committee:
Daniel J. Crawford
Tod F. Stuessy
Thomas N. Taylor

Approved by:

[Signature]
Adviser
Department of Botany
ACKNOWLEDGMENTS

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VITA

September 20, 1955 ........ Born - Burlington, Iowa

1977 ....................... B. S. Botany, Iowa State University

1980-1981 ................... Graduate Teaching Assistant, Biology
Department, University of Northern Iowa

1981 ....................... M. A. Biology, University of Northern
Iowa

1982-1988 ................... Graduate Associate, Department of
Botany, The Ohio State University

Student Alumni Research Award

PUBLICATIONS

Lammers, T. G., and A. G. van der Valk. 1977. A checklist of the
aquatic and wetland vascular plants of Iowa: I. Ferns, fern allies,

Lammers, T. G., and A. G. van der Valk. 1978 [1979]. A checklist of the aquatic
and wetland vascular plants of Iowa: II. Monocotyledons, plus a
summary of the geographic and habitat distribution of all aquatic

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Major Field: Botany

Studies in Plant Systematics with Tod F. Stuessy
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Chapter I
SYSTEMATICS OF CLERMONTIA GAUDICH. (CAMPANULACEAE: LOBELIOIDEAE)

INTRODUCTION

The Hawaiian Islands have long been recognized as an exceptional natural laboratory for the study of evolution. In the preface of the first flora of the archipelago, published just 30 years after Charles Darwin and Alfred Russell Wallace read their papers on evolution before the Linnean Society, William Hillebrand wrote (1888: xxix):

In fact, the evolution theory could hardly find a more favorable field for observation than an isolated island-group in mid-ocean, large enough to have produced a number of original forms and at the same time so diversified in conditions of temperature, humidity, and atmospheric currents as to admit an extraordinary development in nearly every direction of vegetable morphology, uninfluenced by intercrossing with foreign elements.

More recently, Simon (1987) identified three characteristics responsible for the archipelago's preeminence as a laboratory for the study of evolution: (1) the islands are of known age and arranged in a linear chronological sequence; (2) the vast majority of the biota is endemic; and (3) insular phenomena such as adaptive shifts, arborescence, and loss of dispersibility (cf. Carlquist 1974) are developed to an extraordinary degree. The first characteristic is the
result of the mode of geological origin of the archipelago (cf. MacDonald & Abbott 1970), and the latter two to its extreme isolation and physiographic diversity (cf. Wagner, Herbst & Yee 1985).

Despite this acknowledged suitability, detailed studies of evolutionary patterns and processes among the Hawaiian biota are only beginning (Crawford, Whitkus & Stuessy 1987; Simon 1987). For the past century, most systematic research in the islands has been descriptive (Wagner et al. 1985). Further, many of the resulting monographs and revisions are wholly unsatisfactory, being plagued by unworkable keys, unpredictable classifications, and an absurd proliferation of epithets (Fosberg 1948, Gillett 1972). In recent years, however, a number of exemplary studies of evolution in certain Hawaiian genera have been published. Prominent examples include work in Dubautia Gaudich. and its allies (Carr & Kyhos 1981, 1986); Bidens L. sect. Campylotheca (Cass.) Nutt. (Helenurm & Ganders 1985); Tetramolopium Nees (Lowrey & Crawford 1985); and Lipochaeta DC. (Gardner 1976, Rabakonandrianina & Carr 1981). It is interesting to note that in each instance, these evolutionary studies were preceded by or performed concurrently with taxonomic revisions of the taxa involved (e.g., Carr 1985a, Ganders & Nagata 1986, Lowrey 1986, Gardner 1979). The necessity of modern taxonomic revisions as a precursor to detailed evolutionary studies is apparent (Davis 1978; Prance 1985; Wagner, Herbst & Schmer 1986; Crawford et al. 1987).

These recent evolutionary studies have involved members of a single angiosperm family, the Asteraceae. The Hawaiian flora includes
numerous other families which would appear to offer excellent opportunities for systematic and evolutionary research (Carlquist 1972, 1980; Ehrendorfer 1979; Simon 1987). Prominent among these are Campanulaceae Juss., represented by seven genera (six endemic) and 110 endemic species of subfamily Lobelioideae (Juss.) Schonl. All are woody plants, growing terrestrially and epiphytically in montane forests at elevations between 150 m and 2150 m on the seven major islands of the archipelago. This abundance of Lobelioideae is remarkable, as the family is otherwise poorly represented on the islands of the Pacific (Rock 1919, Wimmer 1943, Carlquist 1980).

The vast majority of the Hawaiian Lobelioideae belong to the four endemic genera treated by Wimmer (1943) as subtribe Cyaneinae F. Wimmer of tribe Delisseaeae C. Presl: Clermontia Gaudich., Cyanea Gaudich., Delissea Gaudich., and Rollandia Gaudich. These genera are characterized by woodiness, axillary inflorescences, dorsally cleft corollas, and baccate fruits. On the basis of this unique suite of morphological features, they appear to form a monophyletic group, derived from a single ancestral colonization of the archipelago (Rock 1919, Carlquist 1980). As such, they are the most speciose lineage in the Hawaiian flora (W. L. Wagner, personal communication). When one considers that the oldest island upon which these plants grow is less than six million years old, this level of speciation is truly remarkable. One factor suggested as responsible for this prolific speciation is a coevolutionary relationship with avian pollinators (Spieth 1966, Carlquist 1974, Ehrendorfer 1979). Certain nectarivorous
species of Drepanidinae (Fringillidae) and Meliphagidae are known to have fed upon the floral nectar of these plants. It has been assumed that these passerines effected pollination and that the two groups coevolved. However, with the exception of a preliminary study by Cory (1984), there has been no experimental research on this proposed coevolutionary relationship.

The lack of evolutionary studies among the baccate lobelioids may be attributable to the lack of a modern taxonomic treatment upon which to base such studies. The classic monograph of Rock (1919) is the best available but has been outdated by the subsequent description of almost 100 new species and infraspecific taxa. Many of these new taxa are poorly defined and only vaguely distinguished from previously recognized taxa. Several factors are responsible for this proliferation of names, including extreme morphological variability of certain taxa, phenotypic plasticity, developmentally related changes in morphology, unrecognized hybridization, and divergent concepts of taxonomic categories and their circumscription. The recognition of these problems, together with the availability of additional data and new techniques of data analysis, show the need for an improvement in the taxonomy of these plants. In turn, these revisionary studies will make possible studies of evolutionary patterns and processes among these insular endemics. Because of the large number of species involved, the four genera will be revised separately. This monograph of Clermontia is intended as the first in the series. It provides a modern revision of the taxonomy of the genus together with an analysis
of phylogenetic patterns and discussion of factors which may have influenced these patterns. Future studies will provide taxonomic revisions of the remaining genera, and continue to examine the patterns and processes of evolution among these fascinating insular endemics.
TAXONOMIC HISTORY

The taxonomic history of Clermontia is associated closely with the history of scientific exploration in the Pacific. During the 18th and 19th centuries, European maritime powers (and eventually the United States of America) dispatched naval expeditions to gather information on the natural resources of the Pacific basin. Though prompted by expectations of commercial and political gain (Smith 1974), these expeditions also made known the natural history of previously unexplored regions.

Among the most famous of the early exploratory voyages were those undertaken for the British Crown by Capt. James Cook. Cook's third voyage resulted not only in the discovery of the Hawaiian Islands by non-Polynesians and in Cook's death, but also in the earliest collection of plants from that archipelago (St. John 1976a, 1979a). While the sloops Discovery and Resolution lay anchored at Kealakekua, Hawai'i, in January 1779, naturalist David Nelson and a party of crewmen attempted to ascend Mauna Loa (St. John 1976b). Among the plants collected during this ascent was a specimen of Clermontia (St. John 1979a). In 1794, when Discovery returned to Hawai'i under the command of Capt. George Vancouver, naturalist Archibald Menzies collected the same plant in the same region (St. John 1977). Both specimens were deposited in the British Museum but were not examined by
botanical scholars until many years later. They are identified here as Clermontia clermontioides (Gaudich.) A. Heller subsp. clermontioides.

Fifty years elapsed before the genus Clermontia was formally established. Charles Gaudichaud-Beaupré served as pharmacy botanist on the French corvette Uranie, under the command of Capt. Louis Claude de Freycinet. In August 1819, the Uranie visited the Hawaiian Islands, with calls at Kailua, Hawai‘i; Lahaina, Maui; and Honolulu, O‘ahu (Lasegue 1845, St. John & Titcomb 1983). Gaudichaud was able to spend only seven days collecting on shore. Among the specimens obtained during these forays were representatives of an undescribed genus of Lobelioideae. The new genus differed from all others in the subfamily by its unusual calyx, with deciduous connate lobes as long as the corolla and matching it in color, shape, and texture. Gaudichaud (1826-30) christened the new genus Clermontia in honor of Aimé-Marie-Gaspard, Marquis de Clermont-Tonnerre (1779-1865), who served as France’s Minister of the Navy at the time of the Freycinet expedition (Prevost & D'Amat 1959). As originally constituted, the genus included three species: Clermontia grandiflora Gaudich., C. oblongifolia Gaudich., and C. persicifolia Gaudich.

Franz Julius Ferdinand Meyen, naturalist aboard the Prussian ship Prinzess Luise, visited O‘ahu in 1831. He discovered a fourth species at Pu‘u Kakea, which he named Clermontia kakeana Meyen. Because the description was published as a brief footnote in his narrative account of the expedition (Meyen 1835), it was overlooked by several subsequent botanists. Consequently, the species received two additional baptisms
before the priority of Meyen's name was recognized. Thomas Nuttall, who visited O'ahu aboard the brig May Dacre in early 1835 (Graustein 1967, St. John 1979b), collected the same species and published it (Nuttall 1842) as Clermontia macrophylla Nutt. Gaudichaud, during his return to the archipelago aboard the corvette Bonite in October 1836 (Lasegue 1845), also collected this common species. A plate illustrating this plant and labelled Clermontia macrocarpa Gaudich. was published in 1842 in a folio atlas without accompanying text (Gaudichaud s.d., cf. Stafleu & Cowan 1976).

The United States Exploring Expedition under the command of Commodore Charles Wilkes visited the Hawaiian Islands aboard the sloop Vincennes during 1840-41. Naturalists William Brackenridge and Charles Pickering collected numerous botanical specimens which were subsequently studied by Asa Gray (Mann 1867-68). In his synopsis of Clermontia, Gray (1861) reduced the four species recognized by previous monographers (Presl 1836, de Candolle 1839) to synonyms of three varieties of Clermontia grandiflora: C. grandiflora var. brevifolia A. Gray (C. grandiflora s. str.), C. grandiflora var. longifolia A. Gray (C. kakeana), and C. grandiflora var. oblongifolia (Gaudich.) A. Gray (C. oblongifolia and C. persicifolia). One new species, Clermontia parviflora Gaudich. ex A. Gray, was described on the basis of a specimen collected by Gaudichaud in 1836. Gray's synopsis was followed by Mann (1867-68).
Hillebrand (1888) expanded the circumscription of *Clermontia* by including species which did not have the distinctive calyx of the original species, but which shared with them a distinctive branching habit and few-flowered inflorescences. Two infrageneric groups of unspecified rank were recognized on the basis of calyx lobe morphology. Species that fit the original circumscription of the genus were treated as *Clermontia genuinae*. This group included the original four species recognized by Presl (1836) and de Candolle (1839), Gray's (1861) novelty, plus two new species and five new varieties. The newly added species with short, free, persistent, green calyx lobes made up the *Clermontioideae*. This group was formed by transferring *Cyanea arborescens* H. Mann and *Delissea clermontioides* Gaudich. into *Clermontia* and by describing two new species. With this expansion, a total of 11 species and five varieties were recognized in the genus. Subsequently, four more species were added to the genus by Forbes (1912) and Léveillé (1911, 1913).

Rock (1919) formalized the infrageneric groups of Hillebrand (1888) as sections and recognized 23 species and six infraspecific taxa. Subsequently, an additional 11 species and eight infraspecific taxa were added by Degener (1937), Forbes (1920), Hochreutiner (1934), St. John (1939a, 1939b), Skottsberg (1926), and Wimmer (1929). Wimmer (1943) recognized 27 species and 18 infraspecific taxa, and maintained the sectional classification of Hillebrand and Rock. Subsequently, nine species and 21 infraspecific taxa were added by Skottsberg (1944), Degener & Degener (1956, 1958a), Rock (1957, 1962), St. John (1971),

Wimmer's monograph is the most recent critical evaluation of *Clermontia*. However, a recent enumeration of the species has been provided by St. John (1973), who recognized 40 species and 35 non-autonymic infraspecific taxa. Another 17 species and two infraspecific taxa have been described subsequently (St. John 1976a, 1978, 1983, 1987). Thus, a revised enumeration of the species of *Clermontia* according to St. John's views would include a total of 57 species and 37 additional infraspecific taxa. Altogether, 107 heterotypic taxa have been described in *Clermontia* prior to this revision. In the present treatment, the two sections are maintained, but each is divided into three series. A total of 22 species and nine additional subspecies are recognized. Of the remaining taxa, 71 are treated as synonyms of accepted taxa, two are considered to be based on interspecific hybrids, and four belong to other genera.
SYNOPSIS OF CLASSIFICATION

CLERMONTIA GAUDICHAUD

I. Section Clermontioideae (Hillebrand) Rock

A. Series Clermontioideae

1a. *C. clermontioides* (Gaudichaud) A. Heller subsp. *clermontioides*

1b. *C. clermontioides* (Gaudichaud) A. Heller subsp. *rockiana* (F. Wimmer) Lammers

2. *C. pyrularia* Hillebrand

3. *C. waimeae* Rock

B. Series Sarcanthae Lammers


4c. *C. arborescens* (H. Mann) Hillebrand subsp. *arborescens*

5. *C. tuberculata* C. Forbes

C. Series Unilabiatae Lammers

6a. *C. peleana* Rock subsp. *singuliflora* (Rock ) Lammers

6b. *C. peleana* Rock subsp. *peleana*

7. *C. fauriei* A. Léveillé
II. Section Clermontia

A. Series Dupliciflorae Lammers

8. **C. kakeana** Meyen
9. **C. lindseyana** Rock
10. **C. persicifolia** Gaudichaud
11. **C. pallida** Hillebrand
12. **C. kohalae** Rock
13. **C. montis-loa** Rock
14. **C. drepanomorpha** Rock

B. Series Parviflorae Lammers

15. **C. multiflora** Hillebrand
16. **C. micrantha** (Hillebrand) Rock
17. **C. parviflora** Gaudichaud ex A. Gray
18. **C. calophylla** F. Wimmer

C. Series Clermontia

19a. **C. oblongifolia** Gaudichaud subsp. **oblongifolia**
19b. **C. oblongifolia** Gaudichaud subsp. **mauiensis**
   (Rock) Lammers
19c. **C. oblongifolia** Gaudichaud subsp. **brevipes**
   (F. Wimmer) Lammers
20a. **C. grandiflora** Gaudichaud subsp. **munroi**
   (H. St. John) Lammers
20b. **C. grandiflora** Gaudichaud subsp. **grandiflora**
20c. **C. grandiflora** Gaudichaud subsp. **maxima** Lammers
21a. **C. samuelii** C. Forbes subsp. **hanaensis**
(H. St. John) Lammers

21b. *C. samuelii* C. Forbes subsp. *samuelii*

22. *C. hawaiensis* (Hillebrand) Rock
ETHNOBOTANY

Prior to Cook's discovery of the Hawaiian Islands, the indigenous Polynesians were quite familiar with Clermontia. As a generic term, they called the plants haha, 'ohaha, 'oha, and 'oha-wai (Rock 1919; Pukui & Elbert 1971; Degener, Degener & Pekelo 1975). The first two names sometimes were applied to species of Cyanea and other genera of Lobelioideae as well. Only a few specific names have been recorded. It is possible that others were forgotten as Hawaiian language and culture declined during the nineteenth century. Those known include haha-'ai-a-kamanu ("haha, food of the birds") for Clermontia fauriei; 'oha-wai-nui ("big 'oha-wai") for C. arborescens; and 'oha-kepau ("gum 'oha") for C. hawaiiensis (Pukui & Elbert 1971, Degener et al. 1975).

The vernacular name 'oha-kepau refers to the copious white latex found in all species, and used in various ways by the Hawaiians. The latex of Clermontia arborescens was administered to asthmatics (Nagata 1971). Preliminary assays (Swanholm, St. John & Scheuer 1959, 1960) have shown Clermontia species to be rich in alkaloids, presumably pyridine alkaloids related to lobeline (Hill 1970, Gibbs 1974). Such alkaloids commonly accumulate in the latex of Lobelioideae (Vagujfalvi 1971) and may be of some efficacy in the relief of bronchial asthma symptoms (Blacow 1972). This latex was also used as a galactagogue (Nagata 1971), a use presumably based in sympathetic magic rather than
pharmaceutical efficacy, as the latex resembles mothers' milk in color. Because of its viscosity, it was an important component of pilali, the bird-lime used to snare small forest birds in the practice of kia manu or bird-catching (Perkins 1903, Munro 1944, Berger 1981). Munro (1944) also has described the use of Clermontia flowers as a lure in snaring birds. The brightly colored feathers thus obtained were fabricated into exquisite cloaks, capes, helmets, lei (necklaces and chaplets), and kahili (royal standards).

Despite the abundance of alkaloidal latex in all plant parts, certain species reputedly produce comestibles. The leaves of Clermontia hawaiiensis reportedly were boiled and eaten (Kunkel 1984). The large orange berries of Clermontia fauriei, C. kakeana, and others were consumed by the natives (Wimmer 1943, Kunkel 1984). Rock (1919) described them as "sweet", though Hillebrand (1888) found them "insipid". Personal experience supports Hillebrand's appraisal. Nuttall (1842) also reported seeing these fruits strung as lei on O'ahu.
CONSERVATION

Fourteen hundred years of human occupation have effected major changes in the terrestrial Hawaiian ecosystem (Carlquist 1974, 1980; Berger 1981; Kirch 1982; Olson & James 1982; Wagner, Herbst & Yee 1985). The two major types of changes that have occurred are (1) the physical destruction of native communities by alteration of the landscape to suit human activities; and (2) the introduction and establishment of competitive, predatory, or pathogenic alien organisms (Jacobi & Scott 1985). The most obvious threats to species of Clermontia are loss of habitat through clearing of the forests; predation by herbivorous mammals such as pigs, deer, goats, sheep, and cattle; and competition with aggressive aliens, such as Clidemia hirta (L.) D. Don (Melastomataceae), Passiflora mollissima H. B. K. (Passifloraceae), and Psidium cattleianum Sabine (Myrtaceae).

A first step in any conservation effort is to inventory and categorize the species at risk (Wagner et al. 1985). The publication of St. John's (1973) checklist of Hawaiian plants prompted Fosberg and Herbst (1975) to attempt such an assessment. Their list included 42 of the 75 taxa recognized in Clermontia by St. John (1973). Two-thirds of these were placed in category "U" (status uncertain), due to taxonomic problems and (or) insufficient ecological data. However, sufficient information was available for the authors to suggest that Clermontia
Pursuant to the Endangered Species Act of 1973 (16 U.S.C. 1531 et seq.), the United States Fish and Wildlife Service (USFWS) began compiling information on imperiled species (Lamberton 1980, Arnett 1983). Information on Hawaiian species at risk was derived primarily from the list of Fosberg and Herbst (1975). Five species of Clermontia are currently under review by USFWS for possible listing as threatened or endangered: C. drepanomorpha, C. lindseyana, C. loyana, C. munroi, and C. pyrularia. Two others, Clermontia haleakalensis and C. konaensis, are regarded as already extinct. Two taxa listed by Fosberg and Herbst (1975), Clermontia hawaiiensis var. hawaiiensis and C. peleana, have been deleted from further consideration, in the belief that the extant populations are in no immediate danger.

New information on the conservation status of several Clermontia species has resulted from field and herbarium studies undertaken as part of my research on the systematics of the genus. Further, this research has also resulted in a classification of the genus that is far more conservative than that of St. John (1973). Some of these changes affect species listed by USFWS, and require a brief explanation.

The following species appear to be reasonably secure throughout their respective ranges: Clermontia clermontioides (including C. konaensis and C. loyana), C. hawaiiensis, C. kakeana, C. montis-loa, C.
parviflora, and C. persicifolia. These species occur on two or more islands, or occupy a major portion of a single island. Further, there is no evidence of a major reduction in range in historical times, nor did I experience undue difficulty in locating extant populations. The following species also appear secure at present, but merit special attention because of their highly restricted distributions: Clermontia calophylla, C. drepanomorpha, C. kohalae, and C. waimeae (endemic to the Kohala Mountains of Hawai'i); C. pallida (endemic to Moloka'i); and C. samuelii (endemic to the windward slopes of Haleakala, East Maui). Although their ranges are quite small, there is no evidence of major range reductions in historical times.

In two instances, a species is relatively common on one island but very rare on another. Clermontia fauriei has been collected many times on Kaua'i. Its occurrence on O'ahu is documented by just two specimens, collected in 1950 and 1956. Similarly, Clermontia micrantha is common in the bogs of West Maui. Its occurrence on Lana'i is documented by a few specimens collected during the 1930's. Two possible interpretations of this pattern may be proposed. First, the species was formerly common on both islands, and the observed pattern is due to differential extirpation. Alternatively, the species never was common on the one island, and the few populations there are the products of a relatively recent dispersal event.

In three instances, a species comprises three subspecies, some of which are secure, and some of which are at risk. Clermontia arborescens comprises subsp. arborescens of southern West Maui, subsp.
waihiae of the remainder of Maui, and subsp. waikoluensis of Moloka'i
and Lana'i. The restricted range of the first is cause for some
concern. The latter two are relatively common throughout their ranges.
Clermontia oblongifolia comprises subsp. oblongifolia of O'ahu, subsp.
brevipes of Moloka'i, and subsp. mauiensis of Maui and Lana'i. The
first appears to be relatively common, although the ratio of
recent-to-early collections suggests a possible decline. The Moloka'i
subspecies has been collected only once since 1938, in 1962. The third
subspecies was last collected on East Maui in 1927 and on Lana'i in
1913. The only extant population is on West Maui. Clermontia
grandiflora comprises subsp. grandiflora of West Maui; subsp. munroi
(including C. munroi) of Moloka'i, Lana'i, and Maui; and subsp. maxima
of East Maui. The first two are reasonably secure, but the last is
known only from the recently collected holotype.

Three species currently under review or reviewed formerly by USFWS
appear to be appropriate candidates for listing as threatened or
endangered species. Clermontia lindseyana is known from only eight
widely scattered populations on Hawai'i and from two specimens
collected in 1910 and 1920 on leeward East Maui. Clermontia peleana
comprises two subspecies: subsp. peleana of North Hilo and Puna
Districts, Hawai'i; and subsp. singuliflora of Makawao District, East
Maui, and Hamakua District, Hawai'i. Only two populations of the
former are extant, and the latter is probably extinct. It was last
collected on Maui in 1920 and on Hawai'i in 1909. Although this
species is no longer under review by USFWS (Lamberton 1980), it clearly
should be reinstated. *Clermontia pyrularia* is known from only a few specimens collected at scattered localities on Hawai‘i. Probably only one or two of these populations are extant. *Clermontia tuberculata*, known from just a few populations on windward East Maui, should be added to the list of species under review. The other species currently under review should be dropped, as they are either synonymous with relatively common taxa (*Clermontia loyana*, *C. munroi*) or exist in greater numbers than originally thought (*C. drepanomorpha*).

The only extinct species is *Clermontia multiflora* of O‘ahu and Maui. The only known specimens were collected before 1871. *Clermontia haleskalensis* has been extinct since 1910 (Rock 1913, 1919). However, this unusual species is more appropriately classified as a species of *Cyanea* (Lammers 1988b). This low percentage of extinct species in *Clermontia* (less than 5%) contrasts sharply with the situation in related genera. Approximately 30% of the currently recognized species of *Cyanea* are presumed extinct while nearly 78% of the species of *Delissea* have vanished (Lammers 1988a). Factors responsible for these differential extinctions are not immediately apparent.
GENERIC RELATIONSHIPS

_Clermontia_ possesses several character states unusual among Lobelioideae. While most lobelioids are herbs with dehiscent fruits and terminal inflorescences or solitary axillary flowers, the species of _Clermontia_ are trees and shrubs with baccate fruits and axillary inflorescences. This suite of features is shared with just three other genera: _Cyanea_ Gaudich., _Delissea_ Gaudich., and _Rollandia_ Gaudich. All four are endemic to the Hawaiian Islands and are judged to form a monophyletic group, which Wimmer (1943) classified as subtribe _Cyaneinae_ F. Wimmer of tribe _Delisseaeae_ F. Wimmer.

_Clermontia_ is distinguished from the other three by its distinctive bushy habit that results from repeated branching of the stems; stems and leaves without epidermal murications; latex white; leaves simple, petiolate, callose-toothed; racemes 2(-10)-flowered, subumbellate; corolla dorsally cleft nearly to base, tube terete or tallest at base or middle; staminal column free from the corolla; berries orange or yellow, (1.2-)2-4 cm long; and seeds dark-colored, glossy, minutely foveate-reticulate, 0.2-0.5 mm long. The majority of the species are characterized by a "double-flowered" perianth, in which the calyx lobes are connate, deciduous, and mimic the corolla in size, shape, color, and texture. This type of perianth is unique among Campanulaceae. Further, there is a strong tendency toward epiphytism.
and no tendency to produce distinctive juvenile stages.

*Delissea* differs from *Clermontia* by its habit, in which branches are few (or none), erect to ascending, and unbranched or only sparingly branched after departing the trunk; racemes 5-20-flowered; corolla dorsally cleft to about the middle, with a small knob at the terminus of the cleft (sometimes with two additional lateral knobs), tube laterally compressed, tallest toward the orifice; berries purple, 6-16 mm long; and seeds pale-colored, dull, transversely rugose, 0.7-1.5 mm long. The knobs on the corolla and the seed features are unique among Lobelioideae.

*Rollandia* differs from *Clermontia* by its unbranched, often subherbaceous habit; stems and leaves sometimes muricate, especially in juveniles; racemes 5-20-flowered; corolla dorsally cleft to about the middle, tube laterally compressed, strongly sigmoid, tallest toward the orifice; staminal column dorsally adnate to the corolla; and berries 10-20 mm long.

*Cyanea* is morphologically very diverse. The genus has been divided into three (Hillebrand 1888, Wimmer 1943, St. John 1969) or five (Rock 1919, Stone 1967) sections. Neither arrangement satisfactorily reflects relationships within this complex genus and a revised infrageneric classification is needed. Overall, the genus is characterized by racemes 5-25(-40)-flowered; corolla dorsally cleft to about the middle, lacking dorsal or lateral knobs; staminal column free from the corolla; and seeds dark-colored, shiny, minutely foveate-reticulate, 0.2-0.5 mm long. Although it is not yet possible
to proffer a revised classification, it is possible to discern informal
groups of closely related species. These informal groups, and their
possible relationships to Clermontia, are outlined here.

*Cyanea* sect. *Palmaeformes* (Hillebr.) Rock is a patently unnatural
assemblage of tall species that share an unbranched palm-like habit and
a tendency to produce juvenile plants with lobed or parted leaves. On
the basis of floral and additional vegetative characters, at least four
palmiform groups may be recognized: (1) species with tan latex, sessile
leaves, clustered inflorescences, stout unilabiate corolla, and purple
berries, e.g., *Cyanea hamatiflora* Rock; (2) species with yellow latex,
 sessile leaves, clustered inflorescences, slender unilabiate corolla,
and purple berries, e.g., *C. leptostegia* A. Gray; (3) species with
yellow latex, sessile leaves, pendent inflorescences, slender
unilabiate corolla, and purple or orange berries, e.g., *C. superba*
(Cham.) A. Gray; and (4) species with white latex, petiolate leaves,
clustered inflorescences, stout bilabiate corolla, and orange berries,
e.g., *C. macrostegia* Hillebr. None of these groups is close to
*Clermontia*.

Similarly, *Cyanea* sect. *Cyanea* is an unnatural assemblage of
unbranched or sparingly branched shrubby species with epidermal
murications on stems and leaves at some stage of development, white
latex, petiolate leaves, a pronounced tendency toward lobed or parted
leaves, and orange berries. Within this assemblage, at least three
groups may be distinguished: (1) species with a corolla similar to that
of *Rollandia*, anthers with apical tufts of white hair on all five, and
berries 18-30 mm long, e.g., *Cyanea grimesiana* Gaudich.; (2) species with a corolla similar to that of *Delissea* but lacking the knobs, anthers with apical tufts of white hair on the lower two, and berries 8-15 mm long, e.g., *C. platyphylla* (A. Gray) Hillebr.; and (3) species with the corolla tube terete, suberect or gently curved, anthers with apical tufts of white hair on the lower two, and berries 11-15 mm long, e.g., *C. solanacea* Hillebr. None of these is closely related to *Clermontia*.

*Cyanea* sect. *Pilosae* Rock comprises a group of species that resemble certain Hawaiian species of *Cyrtandra* J. R. & G. Forst. (Gesneriaceae) in habit and floral morphology. The group includes species with an unbranched subherbaceous habit; non-muricate stems and leaves; simple, petiolate, callose-toothed leaves; small, slender, bilabiate corolla with suberect terete tube; and orange berries 4-15 mm long; e.g., *Cyanea pilosa* A. Gray. These species are not closely related to *Clermontia*.

*Cyanea* sect. *Delisseoideae* (Hillebr.) Rock (including *Cyanea* sect. *Hirtellae* Rock; cf. Wimmer 1943, St. John 1969) comprises several species with stems and leaves lacking epidermal murications; white latex; simple, petiolate, callose-crenulate leaves; corolla tube terete or taller at middle or base; staminal column free from the corolla; and seeds dark-colored, shining, minutely foveate-reticulate, 0.2-0.5 mm long. Further, there is some tendency toward epiphytism and the production of subumbellate racemes in this section, and no tendency toward the production of distinctive juvenile forms. In these
features, the species of Cyanea sect. Delisseoideae closely resemble those of Clermontia. They differs from Clermontia by their unbranched or sparingly branched habit; 5-40-flowered racemes; typically smaller flowers with corolla tube dorsally cleft only to the middle; and purple berries, 0.5-1.5 cm long. Species of Kaua'i with sparingly branched stems and relatively few large flowers per inflorescence, e.g., Cyanea hirtella (H. Mann) Hillebr. and C. sylvestris A. Heller, most closely resemble Clermontia.
CHROMOSOME NUMBERS

Chromosome number determinations serve as an important source of data for biologists seeking answers to various evolutionary and taxonomic questions. Carr (1985b) has emphasized the special need for such cytological study among Hawaiian angiosperms. Chromosome numbers previously have been published for only five species of Clermontia (Skottsberg 1955, Carlquist 1956, Carr 1978). Thus, an effort was made to secure materials for cytological study.

Floral buds were collected and fixed in the field in modified Carnoy's solution (6 chloroform: 3 ethanol: 1 glacial acetic acid, v/v), and subsequently refrigerated in 70% ethanol. Anthers were stained with acetocarmine and squashed in a drop of Hoyer's solution. Chromosome numbers were determined from meiotic microsporocytes via phase contrast microscopy and documented by camera lucida drawings.

All known chromosome numbers in Clermontia are listed in Table 1. Of the 22 species and nine non-autonymic subspecies in Clermontia, chromosome numbers are now known for nine species and one additional subspecies. Both sections and all but two of the series are represented among the counts. All species that have been examined are \( n = 14 \) or \( 2n = 28 \). A single count of \( 2n = 22 \) in Clermontia oblongifolia (Carlquist 1956) is rejected as probably erroneous on the basis of a subsequent count of \( n = 14 \) by Carr (1978).
Chromosome numbers were not previously known for Clermontia calophylla, C. clermontioides, C. grandiflora subsp. grandiflora, and C. parviflora. These include first counts for sect. Clermontioideae and ser. Parviflorae. Determination of chromosome numbers in Clermontia kakeana X C. micrantha and C. montis-loa X C. parviflora represent the first cytological examination of putative interspecific hybrids in the Hawaiian Lobelioidae. Meiosis appeared regular in all microsporocytes examined. This allows one to infer that Clermontia micrantha, the only one of the parental species not examined, is also $n = 14$. In addition, previously reported numbers were confirmed for Clermontia drepanomorpha and C. montis-loa.

The basic chromosome number of Lobelioidae has been suggested to be $x = 7$ (Mabberley 1974, Raven 1975, Thulin 1983). If this is so, Clermontia would be tetraploid. As all accepted counts from the other three genera of Cyaneinae are also $n = 14$ or $2n = 28$ (Carr 1984, Lammers 1988a), Clermontia would be best regarded as paleotetraploid. Although chromosome numbers are known for less than half of the genus, the species examined represent a broad range of morphological variation. It is suggested, therefore, that changes in chromosome number probably have not been a major factor in speciation in Clermontia.
Table 1. Chromosome numbers in Clermontia. New determinations are denoted by collection numbers; previously reported counts are denoted by bibliographic citations. Voucher specimens for all reports are included among the specimen citations (double asterisk).

<table>
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<th>Taxon</th>
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<th>Reference</th>
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<tr>
<td></td>
<td>n  2n</td>
<td></td>
</tr>
<tr>
<td>C. calophylla</td>
<td>14 28</td>
<td>Lammers 5764</td>
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<td>14 28</td>
<td>Lammers 5444</td>
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</tr>
<tr>
<td>C. grandiflora ssp. munroi</td>
<td>14 28</td>
<td>Lammers 5849</td>
</tr>
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<td>14</td>
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<td></td>
<td></td>
<td>Skottsberg (1955)</td>
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<td>Lammers 5808</td>
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CONCEPTS OF TAXONOMIC CATEGORIES

One of the primary goals of taxonomic research is to produce classifications that are the best conceptual organizations of the diversity existing in nature (Cronquist 1978). Success in achieving this goal depends in part on the taxonomic philosophy of the researcher. Some taxonomists, when delimiting species and infraspecific taxa in Hawaiian genera, have evinced a typological outlook that denies the existence of morphological variation within populations and species (Fosberg 1948, Gillett 1972, Carlquist 1974). The resulting classifications are characterized by an absurd proliferation of names and ranks, due to the formal recognition at some level in the hierarchy of virtually any detectable variation (Carr 1985a; Wagner, Herbst & Yee 1985). The predictive value (cf. Warburton 1967) of such classifications is quite low (Wagner et al. 1985). Consequently, this extreme typological approach is rejected here in favor of concepts more in accord with current practice.

Conceptually, many taxonomists adhere to a biological definition of species (Mayr 1969). Species are viewed as groups of individuals that are actually or potentially interbreeding and that are reproductively isolated from other such groups. For sexually reproducing organisms, and with reproductive isolation defined so as to include external as well as internal barriers, this is a useful
concept. Unfortunately, plant taxonomists often find it a difficult one to put into practice (Cronquist 1978). In many plant groups, data on crossability and reproductive isolation are scarce or non-existent, which precludes utilization of a biological definition of species. This is true for Clermontia.

Consequently, it has been necessary to employ a morphological definition of species in Clermontia. Here, a species is defined as an assemblage of individuals that share a set of morphological features different from those of other such assemblages (Michener 1970, Cronquist 1978, Grant 1981). Although this definition is stated in terms of comparative morphology, it is applied in the context of population structure and reproductive systems (Wagner et al. 1985). Implicit in this definition is the assumption that (1) gene flow among individuals (Mayr 1969, Grant 1980), natural selection (Carson 1985), and commonality of descent (Ehrlich & Raven 1969, Levin 1979) are responsible for the morphological features that unite a species; and (2) that partial or complete reproductive isolation is a by-product of the morphological differences used to distinguish species (Grant 1981). In other words, it is assumed that the morphological species recognized here are more or less equivalent to the biological species (or semispecies in some cases; cf. Grant 1981) that would be recognized if adequate data were available.

Often it is useful to formally recognize infraspecific patterns of morphological variation. In most groups, a single infraspecific category is sufficient (Raven, Shetler & Taylor 1974). The category
used in *Clermontia* is subspecies, which is defined here as a morphologically distinguishable group of conspecific populations, which shows geographic integrity. Geographic integrity typically is expressed as allopatry, with conspecific subspecies occupying different islands or different mountain ranges on one island. In the four most widespread species, numerical phenetic methods were used to examine infraspecific patterns of variation.

The ranks of section and series are used in classifying the species of *Clermontia*. Series previously have not been used in the genus. The supraspecific classification proposed here is based in part upon inferred branching patterns of evolution as reconstructed via cladistic analysis. However, this analysis was tempered with an intuitive assessment of morphological divergence among the lineages. As such, the resulting classification is in the time-honored tradition of the evolutionary (phyletic) school of classification (Bock 1977, Mayr 1981, Stuessy 1987). This is believed to be the most efficacious approach for the production of multi-purpose classifications of maximum predictive and heuristic value (Wharburton 1967, Buck 1986, Stuessy 1983).

This approach has necessitated the formal recognition of some paraphyletic taxa, i.e., taxa defined solely on the basis of symplesiomorphies. Such groups are anathema in a strictly cladistic classification (Nelson 1974; Farris 1979; Wiley 1979, 1981; Phillips 1984). However, cogent arguments for the taxonomic utility, biological inevitability, and philosophical acceptability of paraphyletic taxa
have been advanced by numerous authors, including Tuomikoski (1967), Ashlock (1971, 1984), Mayr (1974), Buck (1986), Cronquist (1987), and Meacham & Duncan (1987). All taxa recognized here conform to the traditional Haeckelian definition of monophyly (Ashlock 1971, 1984; Mayr 1974) and to the more recent concept of convexity (Estabrook 1978, Meacham & Duncan 1987).
MORPHOLOGY AND TAXONOMIC CRITERIA

The classification presented here is based upon macromorphological characters. In this section, the more important morphological features are described, in order to illustrate patterns of variation in these characters, and to define terms used in keys and descriptions.

Definitions of qualitative characters and their states follow Radford (1986). All measurements of quantitative characters are taken from plants in pressed and dried condition. Drying results in substantial shrinkage of the fleshy flowers and fruits. Care should be taken when identifying fresh material, as flowers and fruits will be 10-35% larger than indicated in the keys and descriptions.

The present study supports Carlquist's (1974) suggestion that floral characters are most useful for delimiting taxa within Clermontia. Qualitative features of the calyx, corolla, and androecium were used to delimit supraspecific taxa, while quantitative features of the calyx, corolla, hypanthium, androecium, peduncle, and pedicels were most useful in delimiting species and subspecies. Vegetative features vary little from one species to the next. This lack of diversity perhaps is attributable to the restriction of nearly the entire genus to a single habitat, i.e., relatively open areas in montane rain forests and cloud forests. The significant floral diversity apparently is a reflection of the importance of avian pollinators in the biology
of these plants.

Habit

All species of Clermontia are woody and share a characteristic pattern of branching that distinguishes the genus from its allies. The main stem branches repeatedly, producing numerous spreading branches, each of which branches several more times before terminating in a dense apical rosette of leaves. This pattern of branching, which Rock (1919) referred to as "candelabra-like", typically results in a rounded dense or open crown. The primary stem may not begin branching for some distance above its base, producing a tree with a definite trunk, or it may branch near ground level, producing a shrub. Most species average 1-6 m tall at maturity and include both shrubby and arborescent individuals. Less information is available on girth. Trunks of arborescent species are not uncommonly 10-12 cm in diameter, and Carlquist (1969) mentions an individual of Clermontia fauriei with a trunk over 25 cm in diameter.

Species occurring in montane cloud forests and rain forests may grow epiphytically on the moss-covered trunks and branches of large trees, such as Acacia koa A. Gray (Fabaceae), Cheirodendron trigynum (Gaudich.) A. Heller (Araliaceae), Cibotium splendens (Gaudich.) Krajina ex Skottsbr. (Thyrsopteridaceae), and Metrosideros polymorpha Gaudich. (Myrtaceae). Species of the subalpine forests of Hawai'i (Clermontia lindseyana, C. pyrularia) and montane bogs of West Maui (C. micrantha) are exclusively terrestrial, so far as known, while only
Clermontia peleana appears to be exclusively epiphytic.

Leaves

Leaves of Clermontia typically are disposed in dense rosettes at the tips of slow-growing branches. Characters of the leaves are of relatively little taxonomic utility in Clermontia, due to intraspecific variability and interspecific similarity. This contrasts sharply with the allied genus Cyanea (cf. Carlquist 1974, 1980). The lamina of most species is oblong, elliptic, or oblanceolate, 8–20 cm long, 2–6 cm wide, acute, acuminate, or cuspidate at the apex, cuneate or obtuse at base, with callose-crenulate margins. The texture of the leaf (coriaceous, chartaceous, membranaceous) and the reflectance of the upper surface (glossy, dull) are much more constant within a species and thus of greater taxonomic utility. Unlike Cyanea (Carlquist 1962), leaves of juvenile plants do not differ from those of adults.

All species of Clermontia have petiolate leaves. Two species are distinguished in part by unusual features of the petioles. In Clermontia pallida, the petioles have a distinctive yellowish-white almost chlorotic appearance and are translucent, resembling stems of Pilea pumila (L.) A. Gray (Urticaceae). Clermontia pyrularia differs from the remaining species by its winged petioles. Length of the petioles is also of some utility.
Inflorescences

The axillary inflorescences of Clermontia and its allies are unusual among Lobelioideae; in most other genera, the flowers are solitary in the leaf axils or disposed in terminal inflorescences. In Clermontia, each inflorescence typically bears just two flowers. These may be equally developed or one may lag slightly. Sometimes, one bud aborts soon after initiation. The resulting inflorescence superficially resembles a solitary axillary flower. Occasionally, as many as ten flowers are produced. Such proliferous inflorescences typically occur as sporadic aberrations on individuals with normal 2-flowered inflorescences. Only extinct Clermontia multiflora appears to have produced 7-10-flowered inflorescences consistently.

Hillebrand (1888) and Rock (1919) described the inflorescence of Clermontia as cymose, contrasting this to the racemose inflorescences of its allies. However, as shown by Wimmer (1943), the inflorescence of Clermontia is actually a few-flowered subumbellate raceae. Examination of proliferous inflorescences supports this view. Whenever a third flower is produced, it occupies a terminal position and opens after the two lateral flowers, i.e., anthesis proceeds acropetally. When four or more flowers are produced on an unbranched peduncle, the sequence of anthesis is clearly acropetal. Only when the peduncle itself branches does the inflorescence resemble a cyme. Even then, the sequence of anthesis within each branch clearly is acropetal. The 2-flowered subumbellate raceme characteristic of Clermontia is assumed to have been derived from a typical many-flowered raceme through a
reduction in the number of flowers and a concomitant condensation of the rachis.

A typical inflorescence consists of a spreading peduncle 1-5 cm long bearing a pair of scale-like bracts at the middle or apex and a pair of spreading pedicels 1-4 cm long, each with a pair of minute bracteoles and a flower. Deflexed peduncles with abruptly ascending pedicels characterize Clermontia drepanomorpha and C. pyrularia, while the entire inflorescence is pendent in C. grandiflora.

**Flowers**

In Lobelioidae, as in Orchidaceae, the flowers are resupinate, i.e., rotated 180° from their normal orientation through torsion of the pedicel. In this treatment, the terms dorsal and ventral (i.e., adaxial and abaxial) are applied to the flower as it appears at maturity, after resupination. Thus, the position of the uppermost lobe of the calyx or the three long anthers is regarded as dorsal or adaxial, despite their origin in the ventral or abaxial portion of the floral primordium.

**Hypanthium**

In all Lobelioidae, the calyx is synsepalous, with the basal portions of the five sepals connate, forming a tube. This calyx tube is adnate to the ovary, forming a hypanthium. The calyx lobes, androecium, nectary, and corolla are attached to its truncate apex. Shape and size of the hypanthium are of some utility in distinguishing
species. In most species, the hypanthium is hemispheric or obconic, while a few species (e.g., Clermontia grandiflora, C. micrantha) are characterized by an obovoid or turbinate hypanthium.

Calyx lobes

In most Lobelioidae, the free and distinct apical portions of the sepals form persistent, green, firm, more-or-less triangular calyx lobes less than half as long as the corolla. In some species of Clermontia, however, these calyx lobes are as long as the corolla (rarely as little as 2/3 its length), basally connate for 1/5-4/5 their length, deciduous with the corolla, and mimic the corolla in size, shape, color, and texture. They alternate with the corolla, creating a distinctive "double-flowered" perianth. These two types of calyx lobes have been used to divide the genus into two sections (Hillebrand 1888, Rock 1919). Species with petaloid calyx lobes are segregated as sect. Clermontia, while those with more typical lobes comprise sect. Clermontioideae. The former are discussed further under the next heading.

In each species of sect. Clermontioideae, at least some plants bear tooth-like calyx lobes approximately 1/10 as long as the corolla. In three species, one may also find plants with otherwise similar calyx lobes up to 1/2 as long as the corolla. In Clermontia arborescens and C. clermontioides, variation in the length of the calyx lobes is correlated with geographic distribution, and is used to distinguish subspecies. In Clermontia waimeae, on the other hand, short- and
long-lobed plants occur in mixed populations, and this character cannot be used to distinguish meaningful subspecies. None of the species of this section is represented solely by plants with long calyx lobes.

**Corolla**

The remarks presented here apply not only to the corolla, but also to the entire perianth in species with petaloid calyx lobes. In these species, the corolla tube and connate basal portion of the calyx lobes will be regarded as the perianth tube (actually a tube-within-a-tube), while the corolla lobes and free apical portions of the calyx lobes will be regarded as ten perianth lobes. The dorsal lobe in species of sect. *Clermontia* typically is distinct to near the base of the tube. In most species, the remaining lobes are of equal length. However, in *Clermontia arborescens* and *C. tuberculata*, the two dorsal corolla lobes are longer than the three ventral corolla lobes.

In the present treatment, each section has been divided into series, primarily on the basis of the structural type of the corolla or perianth. The structural type is a product of the curvature of the tube, posture and position of the lobes, and relative lengths of tube and lobes. Three series are recognized in sect. *Clermontioideae*. The bilabiate corolla of ser. *Clermontioideae* comprises a dorsal lip of two lobes, and a ventral lip of three. These lobes are spreading, and equal or exceed the suberect or curved tube in length. In ser. *Sarcanthae*, the corolla is also bilabiate, but the lobes are thick and fleshy, erect or slightly spreading, and of unequal length (two dorsal
longer than three ventral). The unilabiate corolla of ser. Unilabiatae has downcurved lobes 1/4-1/5 as long as the arcuate tube.

Three series are recognized in sect. Clermontia. The bilabiate perianth of ser. Dupliciflorae is essentially an elaboration of a bilabiate corolla, in which the free portion of the dorsal calyx lobe augments the dorsal lip, and the free portions of the four ventral calyx lobes alternate with the three corolla lobes. The rotate perianth of ser. Parviflorae is similar, except that the ten lobes are not gathered into two lips, but instead are evenly spaced around the mouth of the tube, like spokes around the hub of a wheel. Further, they are strongly recurved, and equal or exceed the erect or suberect tube in length. The tubular perianth of ser. Clermontia has suberect or slightly spreading lobes only 1/5-1/2 as long as the curved or arcuate tube.

At the level of species and subspecies, the length and color of the corolla or perianth are very useful taxonomically. Length of the perianth was measured from the base of the tube to the apex of the lobes along the curve formed by the median axis of the tube. Most species fall in the range from 3.5-7 cm long. Color often differs between the inner surface and outer surface. The former is less prone to intraspecific variation, making it more useful taxonomically. Various shades of green, purple, and white are commonest, while reddish hues such as magenta and rose are less common. The very dark pigmentation of species such as Clermontia kohalae and C. peleana subsp. peleana, often referred to as "black", is here termed dark
purple.

**Androecium**

In Lobelioideae as in Asteraceae, the stamens are syngenesious, with the introrse anthers and upper portions of the filaments connate, forming a staminal column. In most genera, including *Clermontia*, the dorsal three anthers are slightly longer than the ventral two, partially occluding the orifice of the anther tube, and the ventral anthers bear tufts of stiff white hairs at the apex. In *Clermontia*, there may be additional pubescence, typically shorter and softer, along the sutures separating the anthers or on the outer surfaces of the anthers.

The curvature and relative exsertion of this column help to distinguish the series recognized here. In ser. *Unilabiatae*, the staminal column is suberect, which contrasts sharply with the arcuate corolla tube. In the remaining series, curvature of the staminal column matches the curvature of the corolla or perianth tube. In ser. *Parviflorae* and *Unilabiatae*, the staminal column is strongly exserted, while in the remaining three series, it is included or only slightly exserted. At the level of species and subspecies, color of the staminal column, length of the filaments, and length and width of the anther tube are taxonomically useful.
Fruits

*Clermontia* and its allies are unusual among Lobelioideae because the pericarp is fleshy and indehiscent, i.e., a berry. In *Clermontia*, the pericarp is orange or yellow and quite thick. Following fertilization, the axile placentae enlarge greatly, filling each of the two locules with a spongy or juicy mass of tissue, orange or yellow in color and studded with numerous dark tiny seeds. The taxonomic utility of characters of the berries is reduced by their poor state of preservation on exsiccate. Size and shape appear to be of some utility, although field studies in certain species (e.g., *Clermontia kakeana*) revealed the presence of considerable intrapopulational variation in these characters. The surface texture of the berry, whether smooth or with ten longitudinal furrows or ridges, seems more constant and thus more useful for delimiting species.
NUMERICAL PHENETICS

Most species of Clermontia have very restricted distributions, being endemic to single islands. Only four species might be described as widely distributed, with populations on three or four islands: Clermontia arborescens (Moloka'i, Lana'i, and Maui); C. grandiflora (Moloka'i, Lana'i, and Maui); C. kakeana (O'ahu, Moloka'i, and Maui); and C. oblongifolia (O'ahu, Moloka'i, Lana'i, and Maui). These four widespread species assume special significance when one considers the importance of an allopatric mode of speciation in oceanic archipelagoes (Crawford, Whitkus & Stuessy 1987). Preliminary study suggests that two or more morphologically discernible and geographically isolated clusters of populations might be recognized in each of these species. From a taxonomic perspective, such clusters should be recognized formally as subspecies. From an evolutionary perspective, these subspecies may represent incipient species (Ehrlich & Raven 1969, Grant 1981, Carson et al. 1982). A better understanding of geographically correlated patterns of intraspecific variation could result in a more predictive classification at this level as well as a better understanding of the early stages of speciation. The circumscription of subspecies in Clermontia, therefore, is of special importance.

The methods of numerical phenetics (Mayr 1965, Sneath & Sokal 1963, Duncan & Baum 1981) are used here in order to best resolve
discrete clusters of populations within each of these four widespread species. This use is appropriate because these methods are most efficacious at the lower levels of the taxonomic hierarchy (Duncan & Baum 1981). Common methodological aspects of all four analyses are provided here. Results of each are presented on subsequent pages.

Although the nature of the study would have justified the use of populations as OTUs, the presence of considerable intrapopulational variation made the coding of character states representative of the entire population difficult. Consequently, herbarium specimens representing individual plants served as OTUs. The specimens used are indicated by an asterisk in the specimen citations. Between 29 and 50 OTUs were used in each analysis. Whenever possible, several individuals from the same population were scored; in this way, both intra- and interpopulational variation could be estimated. The populations sampled represent the entire geographic range of each species. Each OTU is identified by a two or three digit code. The island is indicated by an upper case letter: E = East Maui; L = Lana'i; M = Moloka'i; O = O'ahu; W = West Maui. Each population on an island is given a sequential number, and individuals within a population are denoted by a lower case letter.

The characters selected were nearly all quantitative, with continuous variables as their states. These include linear measurements of structures (as cm), ratios of such measurements, and angular measurements (as degrees). Only a few qualitative characters were employed; these usually involve the presence or absence of
pubescence or dark pigmentation. Between 36 and 41 characters were scored (Table 2) to produce a basic data matrix.

Analysis of the data was performed using NTSYS-pc, version 1.01 (Rohlf 1986), a microcomputer-implemented version of the much-used NTSYS package of numerical phenetic algorithms (Rohlf, Kishpaugh & Kirk 1979). A linear transformation was performed on the basic data matrix, in order to reduce distortion that may result from the use of different scales of measurement (cm or degrees) and from differences in the ranges of character values (Clifford & Stephenson 1975, Romesburg 1984). This standardized matrix was subjected to clustering and ordination, which are the two major types of numerical phenetic analysis (Duncan & Baum 1981). Maximum insights on taxonomic structure may be gained by using more than one numerical phenetic method (Shepherd 1980). In particular, Michener (1970) and Williams et al. (1971) have advocated the utility of performing both clustering and ordination. The specific methods employed here, hierarchical cluster analysis and principal components analysis, are the most commonly used techniques for clustering and ordination, and have proven efficacious in a variety of situations (Duncan & Baum 1981).

Cluster Analysis. First, a matrix of pairwise dissimilarity values was calculated, using average taxonomic distance as the coefficient of resemblance (i.e., dissimilarity). This coefficient provides a better estimate of relatedness than other coefficients (e.g., product-moment correlation, Euclidean distance), particularly with continuous data (Sokal 1961). Space constraints preclude the
Table 2. Characters and their states used in the numerical phenetic analyses of the four widespread species of Clermontia. States of continuous quantitative characters are cm (linear measurements) or degrees (angular measurements). States of qualitative characters are indicated in parentheses. Upper case letters in brackets indicate the specific analyses in which the character was used (A = Clermontia arborescens, G = C. grandiflora, K = C. kakeana, O = C. oblongifolia). If no letters are appended, the character was used in all four analyses.

| LEAVES. Lamina | (1) length | (2) length from base to widest point [A, K, G] | (3) width at widest point [A, K, G] | (4) width at middle [O] | (5) width halfway from middle to apex [O] | (6) ratio of length from base to widest point/length [A, K, G] | (7) ratio of length/width at widest point | (8) ratio of width halfway from middle to apex/width at middle [O] | (9) apex angle | (10) base angle | (11) pubescence of lower surface: glabrous (0), sparsely pubescent along the midrib (1). Petiole: | (12) length | (13) pubescence: glabrous (0), pubescent (1) | (14) ratio of petiole length/lamina length [O]. INFLORESCENCES. Peduncle: | (15) length | (16) pubescence. Pedicel: | (17) length | (18) number | (19) ratio of pedicel length/sum of peduncle and pedicel lengths. |
Table 2 (continued)

Calyx. Hypanthium: (20) length; (21) width at widest point; (22) ratio of length/width; (23) base angle. Calyx lobes [A]: (24) length; (25) length from base to widest point; (26) width at widest point; (27) ratio of length from base to widest point/length; (28) ratio of length/width.

Corolla [A]. Tube: (29) length; (30) width at widest point; (31) ratio of length/width; (32) curvature. Ventral lip: (33) length; (34) width at widest point; (35) ratio of length/width at widest point. Dorsal lobes: (36) width at widest point. General: (37) overall length; (38) ratio of tube length/overall length; (39) pubescence: glabrous (0), minutely pubescent (1).

Perianth [G, K, O]. Tube: (40) length; (41) width at base; (42) width at middle; (43) ratio of width at middle/width at base; (44) curvature. Ventral lobes: (45) length; (46) width; (47) ratio of length/width. Dorsal lobe: (48) length; (49) width. General: (50) ratio of ventral lobe length/tube length; (51) ratio of dorsal lobe length/overall length; (52) pubescence: glabrous (0), minutely pubescent (1); (53) bud apex angle [0]; (54) color: greenish white (0), rose to maroon (1).

Staminal column. Filament tube: (55) length; (56) color: greenish white or white (0), magenta or purple (1). Anther tube: (57) length; (58) width at widest point; (59) ratio of length/width;
Table 2 (continued)

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(60) pubescence: glabrous (0), sparingly pubescent (1). **General:** (61) ratio of overall staminal column length/overall perianth length.

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inclusion of these matrices here, although values from them are often cited in the discussion. Second, the OTU's were clustered by the unweighted pairgroup method using arithmetic averages (UPGMA), the commonest clustering method in current use (Duncan & Baum 1981). UPGMA is an agglomerative hierarchical technique that calculates the similarity of any two clusters as the arithmetic average of the similarities between the objects in one cluster and those in the other (Romesburg 1984). In this way, the problem of chaining that occurs in certain other methods (e.g., single linkage clustering) are avoided (Duncan & Baum 1981, Romesburg 1984). Also, dendrograms generated by UPGMA generally are the best possible graphic representation of the matrix of pairwise resemblance values (Romesburg 1984). Finally, a matrix of cophenetic values was computed and compared to the dissimilarity matrix, in order to generate a cophenetic correlation coefficient ($r$). This value $r$ provides an estimate of how well the dendrogram represents the original pairwise dissimilarity values (Farris 1969).

**Ordination.** Ordination was accomplished through Principal Components Analysis (PCA), the ordination technique most commonly used by plant taxonomists (Duncan & Baum 1981). Pearson's product-moment correlation coefficient was used in generating a matrix of pairwise correlation values for the characters. Eigenvectors (i.e., principal components of the variation) were computed from this matrix. The OTUs were projected onto the eigenvectors and the ordination plotted in two and three dimensions. How well these projections represent the actual
multidimensional configuration may be assessed from the percentage of the variation for which they account (Dunn & Everitt 1982).

**Clermontia arborescens**

This species of ser. Sarcanthae is a large shrub or small tree found in montane rain forests and cloud forests on Moloka'i, Lana'i, and Maui. Hillebrand (1888) included the common plants with short calyx lobes as well as the rarer long-lobed plants in his circumscription of this species. Subsequent authors (Rock 1919, Wimmer 1943) overlooked the latter, and interpreted *Clermontia arborescens* as a strictly short-lobed species. Years later, when long-lobed plants were rediscovered, they were segregated as *Clermontia furcata* (Wimmer in Degener & Degener 1956a) and *C. mannii* (St. John 1983). Although the short-lobed plants exhibit considerable variation in other floral and vegetative features (Degener & Degener 1960), no infraspecific taxa have been described previously.

The results of the cluster analysis are presented in Fig. 1. Two well defined clusters are apparent. The first comprises the short-lobed plants of Moloka'i, Lana'i, northern West Maui (populations W1-W3), and East Maui. The second comprises the short lobed plants of southern West Maui (populations W4-W5). The former is composed of two less well separated clusters: (1) plants of Moloka'i and Lana'i, and (2) plants of northern West Maui and East Maui.

The results of the PCA are presented as a three-dimensional ordination (Fig. 2). Characters with the highest loadings (eigenvalues
Fig. 1. Dendrogram showing relationships among OTUs of Clermontia arborescens; $r = 0.837$. 
Fig. 2. Principal Components Analysis showing relationships among OTUs of *Clermontia arborescens*. Symbols indicate geographic origin of OTUs: Moloka'i (squares), Lana'i (triangles), Maui (dots).
in parentheses) on the first principal component (21.8\% of the
variation) were corolla lip width (-0.897), width of dorsal corolla
lobes (-0.858), and length/width ratio of corolla tube (0.841).
Characters with the highest loadings on the second axis (14.4\% of the
variation) were length/width ratio of the calyx lobes (-0.923); ratio
of calyx lobe length from base to widest point, to calyx lobe length
(-0.907); calyx lobe length (-0.896); and calyx lobe length from base
to widest point (-0.896). Characters with the highest loadings on the
third axis (10.3\% of the variation) were corolla length (0.694), and
corolla tube length (0.653). The patterns revealed by ordination are
similar to those observed in the cluster analysis. Again, the
long-lobed plants of southern West Maui (populations W4-W5) form a
distinct group, while the remainder of the populations form two groups
that are less well separated: (1) plants of Moloka'i and Lana'i, and
(2) plants from the rest of Maui.

These analyses indicate that Clermontia arborescens comprises
three morphologically and geographically distinguishable clusters of
populations. Each cluster is recognized here at subspecific rank. The
long-lobed plants of southern West Maui are subsp. arborescens.
Short-lobed plants from Moloka'i and Lana'i, with the lip and dorsal
lobes of the corolla relatively narrow, are subsp. waikoluensis, while
those from the remainder of Maui, with the lip and dorsal lobes wider,
are subsp. waihiae.
**Clermontia kakeana**

This member of ser. *Dupliciflorae* is a large shrub or small tree found in montane rain forests on O'ahu, Moloka'i, and Maui. Though variable, the populations on these islands were treated as a single polymorphic species by Rock (1919) and Wimmer (1943). Subsequently, several infraspecific taxa have been recognized: *Clermontia kakeana* var. *forbesii* of Moloka'i (Degener & Degener 1958a); *C. kakeana* f. *gracilis* (Wimmer 1968) and *C. kakeana* var. *orientalis* (St. John 1971) of East Maui; and *C. kakeana* var. *rosea* of O'ahu (St. John 1987). Further, St. John (1987) recently described two new species from East Maui, *Clermontia glabra* and *C. mauiensis*, that also appear referrable to *C. kakeana*.

The results of the cluster analysis are presented as a dendrogram (Fig. 3). No geographically correlated clusters of OTUs are apparent. Although most of the OTUs from East Maui are positioned near the base of the dendrogram, for the most part they chain rather than cluster. Examination of the pairwise matrix of dissimilarity values shows that many of these OTUs are actually most similar to OTUs on other islands (distances in parentheses), e.g., E4c is more similar to OTUs from O'ahu and Moloka'i (06, 1.254; M2, 1.322; M3, 1.363) than to other OTUs from the same population (1.430-1.827). These relationships are not apparent from the dendrogram, due to limitations of the clustering algorithm.

The cluster analysis also does not support recognition of St. John's (1987) novelties from East Maui, *Clermontia glabra* and *C. 
Fig. 3. Dendrogram showing relationships among OTUs of *Clermontia kakeana*; $r = 0.745$. 
Fig. 3
mauiensis. If their types indeed represented distinct species, one would expect them to show little similarity to other OTUs, or to be part of discrete clusters well separated from other clusters. Neither pattern is seen here. The type of Clermontia glabra (E4b) is most similar to several OTUs from O'ahu and Moloka'i, including 06 (1.187), 08 (1.253), and M1a (1.279). It is also quite similar (1.390) to an specimen from the same population (E4a), which St. John (1971) earlier identified as Clermontia kakeana var. kakeana, and to the type of Clermontia kakeana (010c, 1.458). Similarly, the type of Clermontia mualiensis (E3) is most similar to a number of OTUs from O'ahu and Moloka'i, including 012 (1.503), M3 (1.514), M2 (1.552), and 010d (1.596). It is also quite similar to the type of Clermontia kakeana (010c, 1.811). Finally, the types of the two novelties are rather similar to each other, being separated by a distance of 1.995. For these reasons, Clermontia glabra and C. mualiensis are considered synonyms of C. kakeana.

Placement of Clermontia montis-loa f. molokaiensis and C. kakeana var. forbesii as synonyms of C. kakeana also is supported by the cluster analysis. The type of the first (M5) is quite similar to several specimens of C. kakeana, including 011 (0.836), 012 (0.896), 08 (0.924), and 013 (0.936). It is also rather similar to the type of Clermontia kakeana (010c, 1.478). Similarly, the type of the second (M4) is quite similar to 013 (0.850), E4e (1.040), 012 (1.060), and W2c (1.148), and to the type of Clermontia kakeana (010c, 1.440).
In the PCA (Fig. 4), characters with the highest loadings on the first principal component (16.4% of the variation) were perianth tube length (-0.769), and dorsal calyx lobe length (-0.767). Characters with high loadings on the second axis (15.8% of the variation) were the angle formed by base of lamina (-0.724) and hypanthium width (-0.705). In the three dimensional ordination, three or four groups of OTUs may be distinguished. However, none of these groups is correlated with geographic distribution. In fact, OTUs from a single population on East Maui (E4) are scattered throughout the factor space. In as much as neither cluster analysis nor PCA detected the existence of geographically discrete groups of OTUs, no subspecies are recognized within Clermontia kakeana.

Clermontia oblongifolia

This member of ser. Clermontia is the most widespread species of the genus. It grows in montane rain forests and cloud forests on O'ahu, Moloka'i, Lana'i, and Maui. The type was collected in the Ko'olau Mountains of O'ahu. Populations from the remainder of the species' range have been segregated at the rank of forma (St. John 1973): Clermontia oblongifolia f. brevipes (Moloka'i); C. oblongifolia f. kaalae (Wai'anae Mountains of O'ahu); and C. oblongifolia f. mauliensis (Lana'i and Maui).

In the dendrogram produced by cluster analysis (Fig. 5), three well defined clusters are apparent: (1) plants of O'ahu, (2) plants of Moloka'i, and (3) plants of Lana'i and Maui. Each of these clusters is
Fig. 4. Principal Components Analysis showing relationships among OTUs of *Clermontia kakeana*. Symbols indicate geographic origin of OTUs: O'ahu (dots), Moloka'i (triangles), Maui (squares).
Fig. 5. Dendrogram showing relationships among OTUs of Clermontia oblongifolia; \( r = 0.802 \).
Fig. 5
about equally distinct.

Within the cluster of OTUs from O'ahu, there is no separation of OTUs from the Ko'olau Mountains (f. oblongifolia sensu St. John 1973) and those of the Wai'anae Mountains (f. kaalae). In fact, the type of f. kaalae (02a) is more similar to certain OTUs from the Ko'olau Mountains (06, 0.911; 011, 0.998; 07, 1.051) than to others from the Wai'anae Mountains (03, 1.069; 04b, 1.085; 02b, 1.094). Thus, the cluster analysis does not support recognition of the populations in the Wai'anae Mountains as a separate subspecies.

Within the cluster of OTUs from Maui and Lāna'i, additional geographically discrete clusters may be discerned. The two OTUs from Lāna'i (L1, L2) cluster together, as do the two from West Maui (W1a, W1b). However, all of the OTUs from East Maui do not cluster together. Examination of the pairwise matrix of dissimilarity values reveals why. Although the OTUs from Lāna'i are more similar to each other than either is to any other, and a similar condition obtains for the OTUs from West Maui, the pattern is more complex among the OTUs from East Maui. E1 is most similar to E3 (0.542), but more similar to the OTUs of Lāna'i (L1, 1.218; L2, 1.169) and West Maui (W1a, 1.170; W1b, 1.521) than to E2 (1.706). Similarly, E2 is closest to the OTUs from Lāna'i (L1, 1.118; L2, 1.158), and closer to those of West Maui (W1a, 1.402; W1b, 1.388), than to the other two from East Maui (E1, 1.706; E3, 1.505). With such reticulate patterns of relationships, it seems best to simply regard all of the OTUs of Lāna'i and Maui as a single cluster.
In the three-dimensional ordination (Fig. 6) produced by PCA, characters with the highest loadings on the first principal component (30.9% of the variation) were ratio of ventral perianth lobe length to perianth tube length (0.888), ventral perianth lobe length (0.882), ratio of petiole length to lamina length (-0.873), and staminal column color (0.867). Characters with the highest loadings on the second axis (16.6% of the variation) were peduncle length (-0.808), ratio of lamina width at middle to lamina width at 3/4 the distance from the base (0.800), and ratio of pedicel length to the sum of peduncle and pedicel lengths (0.748). Characters with the highest loadings on the third axis (10.5% of the variation) were ventral calyx lobe width (-0.697), and perianth tube width at middle (-0.671). The same three groups of OTUs revealed by cluster analysis may be discerned in the ordination. Again, there is no apparent separation of OTUs from the Wai'anae and Ko'olau Mountains, nor are all of the OTUs from East Maui positioned closely in the factor space.

The patterns revealed by both analyses suggest that Clermontia oblongifolia comprises three clusters of OTUs that are morphologically and geographically distinct. In the classification of the genus, these clusters are recognized as subspecies: (1) plants of Moloka'i with oblanceolate leaves and relatively short petiole and peduncles (subsp. brevipes); (2) plants of O'ahu with oblong or elliptic leaves rounded to acute at apex, relatively long petioles and peduncles, and green or white staminal column (subsp. oblongifolia); and (3) plants of Lana'i and Maui with oblong or elliptic leaves acuminate at apex, relatively
Fig. 6. Principal Components Analysis showing relationships among OTUs of Clermontia oblongifolia. Symbols indicate geographic origin of OTUs: O‘ahu (dots), Moloka‘i (triangles), Lana‘i (open squares), Maui (closed squares).
long petioles and peduncles, and magenta or purple staminal column (subsp. mauliensis).

**Clermontia grandiflora**

This species, a second member of ser. Clermontia, is a shrub or small tree found in montane rain forests, cloud forests, and bogs on Moloka'i, Lana'i, and Maui. Hillebrand (1888) and Rock (1919) treated the scattered populations on these islands as a single polymorphic species with no infraspecific taxa. However, St. John (1939a) segregated seven new species and one form on the basis of differences in shape, size, texture, and pubescence of leaves; lengths of peduncles, pedicels, and petioles; number of flowers per inflorescence; floral curvature; and relative lengths of calyx and corolla. Of the taxa recognized by St. John, four were endemic to Moloka'i (Clermontia forbesii, C. molokaiensis, C. subpetioluta, C. wailauensis); two to West Maui (C. grandiflora s. str., C. reticulata f. pilifera); and two to East Maui (C. hirsutinervis, C. reticulata f. reticulata); while C. munroi occurred on both Lana'i and West Maui.

Wimmer (1943) recognized only one of St. John's novelties, Clermontia wailauensis. The remainder were treated as infraspecific taxa or synonyms of Clermontia grandiflora. Wimmer also described one new form from West Maui and subsequently (Wimmer 1968) added another from Lana'i. Skottsbeg (1944) studied this complex on Maui and found that characters used to distinguish the segregate taxa often were variable within populations and even within individuals. However, he
did not suggest a revised classification. Two species recently
described from West Maui also appear referable to the complex:
*Clermontia earina* (St. John 1983) and *C. spatulata* (St. John 1987).

In the cluster analysis (Fig. 7), two large clusters are evident. The first (the lower half of the dendrogram) comprises only OTUs from West Maui. The second (the upper half of the dendrogram) comprises all of the OTUs from Lana'i, nearly all of the OTUs from Moloka'i and East Maui, and three OTUs (W1b, W1d, W2a) from West Maui.

At the base of the dendrogram are three OTUs (M2b and M3 from Moloka'i, and E4 from East Maui) that did not cluster closely with any of the other OTUs. The matrix of pairwise dissimilarity values was examined in order to better resolve the relationships of these OTUs. This showed the following relationships (dissimilarity values in parentheses): M2b is most similar to L4 (1.243) and E7 (1.265); M3 is most similar to L1 (1.370), M4 (1.525), and M5E (1.539); and E4 is most similar to E6 (1.283) and E3d (1.320). The failure of these OTUs to cluster with their nearest neighbors may be explained by the constraints of the clustering algorithm.

Because dendrograms are readily interpretable in terms of classifications (Romesburg 1984), it is appropriate to compare the results of the cluster analysis to the two previous classifications of this complex. Clearly, the dendrogram offers little support for St. John's (1939a) classification of the complex. The types of *Clermontia forbesii* (M2a), *C. molokaiensis* (M4), and *C. subpetiolata* (M5) are quite similar to one another, which fails to support recognition of
Fig. 7. Dendrogram showing relationships among OTUs of *Clermontia grandiflora*; \( r = 0.731 \).
three distinct species. St. John (1939a) indicated that Clermontia forbesii is most closely related to C. hirsutinervis, C. molokaiensis is closest to C. munroi, and C. subpetiolata is closest to C. wailauensis. None of these suggested relationships is supported by the dendrogram. Conversely, the types of Clermontia reticulata (E2) and its f. pilifera (W5b) are quite dissimilar, suggesting that segregation at a rank higher than forma might be appropriate. Further, the dendrogram suggests that the types of the two recent novelties, Clermontia earina (W6) and C. spatulata (W2h), are rather similar to one another. In fact, the latter clusters most closely with the type of Clermontia grandiflora f. hamata (W2g).

The dendrogram also offers little support for Wimmer's (1943) alternative classification. As noted above, the types of Clermontia forbesii, C. subpetiolata, and C. molokaiensis cluster closely. Wimmer recognized the first two as varieties of Clermontia grandiflora. Clermontia molokaiensis, however, was merged with C. munroi and C. reticulata f. reticulata to form a third variety, C. grandiflora var. vulgata. Clearly, the types of Clermontia munroi (L5c) and C. reticulata f. reticulata (E2) do not resemble C. molokaiensis (M4) as closely as do C. forbesii (M2a) and C. subpetiolata (M5). Further, Wimmer indicated a close similarity between the types of C. hirsutinervis (E1b) and C. forbesii (M2a) by subordinating the former to the latter at the rank of forma. Again, the dendrogram suggests that the two are less similar. The position of the type of Clermontia wailauensis (M3) might be interpreted as supporting Wimmer's
recognition of it as a species distinct from *C. grandiflora*. However, as shown above, this OTU is most similar to other OTUs from Moloka'i and Lana'i, including the types of *Clermontia molokaiensis* (M4) and *C. subpetiolata* (M5), and its basal position is the due to distortion of the similarity matrix during clustering.

Due to the large number of OTUs, the three dimensional plot showing the results of the PCA was difficult to interpret visually. Consequently, the results are presented as a two-dimensional ordination (Fig. 8). Characters with the highest loadings on the first principal component (26.3% of the variation) were length/width ratio of calyx lip (0.923), ratio of calyx tube width at middle to calyx tube width at base (-0.898), and length/width ratio of ventral calyx lobes (0.856). Characters with the highest loadings on the second axis (14.0% of the variation) are calyx tube width at base (-0.732) and filament tube length (-0.720).

In the PCA, two major groups may be distinguished: (1) the majority of the OTUs from West Maui; and (2) all of the OTUs from Moloka'i and Lanai, all but one of the OTUs from East Maui (E4), and three OTUs from West Maui (W1b, W1d, W2a). The last three clustered with the OTUs from Moloka'i, Lana'i, and East Maui in the dendrogram, and clearly are more similar to these OTUs than to the other OTUs from West Maui. The OTU from East Maui (E4) that clustered poorly in the dendrogram is positioned in the factor space at some distance from the other OTUs. This specimen differs from all other specimens examined by its exceptionally large flowers. Given the high loadings of floral
Fig. 8. Principal Components Analyses showing relationships among OTUs of *Clermontia grandiflora*. Symbols indicate geographic origin of OTUs: Moloka'i (triangles), Lana'i (squares), West Maui (open circles), East Maui (dots).
characters on the first two principal components, it is not surprising
that this unusually large-flowered specimen is well separated from the
remainder of the OTUs. The two OTUs from Moloka'i (M2b, M3) that did
not cluster well are positioned among other Moloka'i OTUs in the factor
space.

The patterns revealed by cluster analysis and ordination suggest
that the populations of Clermontia grandiflora comprise three groups
which are treated here as subspecies. Plants of bog habitats on West
Maui (populations W3-W7, plus W1 and W2 in part), with a curved
perianth tube broader at the middle than the base, comprise subsp.
grandiflora. Plants of forest habitats on Moloka'i, Lana'i, West Maui
(populations W1 and W2 in part), and East Maui (populations E1-E3,
E5-E7), with an arcuate perianth tube broader at base than middle,
comprise subsp. munroi. The plant with exceptionally large flowers
from East Maui (E4) is described as subsp. maxima.
PHYLOGENETIC RECONSTRUCTION

The several algorithms known collectively as cladistic analysis offer an explicit, repeatable, and relatively objective methodology for reconstructing the branching patterns of evolution (Funk & Stuessy 1978, Duncan 1980, Felsenstein 1982, Duncan & Stuessy 1984). Despite the suitability of the Hawaiian Islands for evolutionary studies, cladistic methods have been used in only one instance to examine phylogenetic patterns among endemic Hawaiian taxa. Gardner and La Duke (1978) utilized a character compatibility algorithm (Estabrook, Johnson & McMorris 1975, 1976a, 1976b) to test Gardner's (1976) intuitive phylogeny of Lipochaeta DC. (Asteraceae). In the present study, a parsimony algorithm is used to infer patterns of phylogeny in Clermontia. The results also are used to help construct an infrageneric classification.

Materials and Methods

In this study, the 22 species of Clermontia were used as OTUs. A total of 36 characters were selected, each divided into two (or less often three) states (Table 3). Character states were polarized via outgroup comparison (Crisci & Stuessy 1980; Stevens 1980; Watrous & Wheeler 1981; Stuessy & Crisci 1984; Maddison, Donoghue & Maddison 1984), using Cyanea hirtella and C. sylvestris as the outgroup. This
Table 3. Characters and their states used in the cladistic analyses of Clermontia. 0 = plesiomorphic state; 1, 2 = apomorphic states.

Habit and Leaves. 1. Habit: large shrubs and trees up to 9 m tall (0), small shrubs no more than 3.5 m tall (1). 2. Branching: sparingly (0), repeatedly (1). 3. Leaf margins: callose-crenulate (0), callose-serrulate (1). 4. Petiole color: opaque green (0), translucent yellowish-white (1). 5. Petiole shape: terete (0), winged (1). 6. Petiole length: less than 1/2 as long as lamina (0), more than 1/2 as long as lamina (1).

Peduncles and pedicels. 7. Peduncle posture: spreading (0), declinate (1), pendent (2). 8. Pedicel rigidity: stiff (0), flexuous (1). 9. Number of flowers per peduncle: 7-10 (0), 2-5 (1). 10. Peduncle length: 1/2-2 times as long as pedicels (0), less than 1/2 as long as pedicels (1), 3-5 times as long as pedicels (2).

Hypanthium. 11. Shape: widest at apex (0), widest below apex (1). 12. Length: 2.5-5 times shorter than corolla (0), 5-7 times shorter than corolla (1). 13. Surface: smooth or with 10 shallow longitudinal furrows (0), with 10 prominent longitudinal ridges (1).

Table 3 (continued)

as corolla (0), equalling the corolla (1), sometimes as little as 2/3 as long as corolla (2).

Corolla/Perianth.  20. Integrity of tube: dorsally cleft to middle (0), dorsally cleft to base (1).  21. Length of tube: 1.5-4 times longer than wide (0), 4.5-9 times longer than wide (1).  22. Curvature of tube: curved (0), erect or suberect (1), arcuate (2).  23. Posture of lobes: spreading (0), erect or suberect (1), recurved (2).  24. Arrangement of lobes: bilabiate (0), unilabiate (1), rotate (1).  25. Length of lobes: equalling or exceeding tube (0), much shorter than tube (1).  26. Length of lobes: all five of same length (0), two dorsal longer than three ventral (1).  27. Texture: firm (0), fleshy (1).  28. Overall length: 4.5-9 cm long (0), 1.5-4.5 cm long (1).  29. Surface: smooth or sparsely pubescent (0), muricate (1).  30. Internal color: green, white, magenta, or rose (0), dark purple (1).

Staminal column.  31. Exsertion: included or somewhat exserted (0), strongly exserted (1).  32. Curvature: matches corolla curvature (0), diverges from corolla (1).  33. Position: centered in tube (0), dorsally displaced (1).  34. Anther length: 3-4 times longer than wide (0), 2-3 times longer than wide (1), 4-5 times longer than wide (2).

Berries.  35. Shape: widest at middle (0), widest above middle (1).  36. Size: 0.5-2 cm long (0), 2-4 cm long (1).
outgroup was also used to root the tree. For characters with three states, the plesiomorphic state was coded as 0, but the apomorphic states (1, 2) were otherwise unordered (cf. Swofford 1985).

The basic data matrix was analyzed using PAUP version 2.4 (Swofford 1985), a microcomputer-implemented program that uses a Manhattan metric to infer phylogeny under the principle of maximum parsimony. Recent comparisons by Fink (1986) and Platnick (1987) showed this program to be the most efficacious software currently available for estimating phylogeny on the basis of a maximum parsimony criterion. Parsimony algorithms assume that the shortest tree, i.e., the one with the fewest character state changes, offers the best possible reflection of evolutionary history. Although the parsimony criterion is controversial (Felsenstein 1983, Sober 1983), in the absence of specific evidence to the contrary, it is the best possible assumption that can be made (Farris 1983, Kluge 1984).

Trees were constructed by adding OTUs according to the CLOSEST algorithm. In this method, each unplaced OTU is added to every possible position on the tree, and the resulting length of each tree calculated. The OTU that will add the least length to the tree is then added, and the process repeated with the new tree and the remaining unplaced OTUs. The MULPARS algorithm was used to find multiple equally parsimonious trees. In order to find even shorter (i.e., more parsimonious) trees, branch-swapping was effected using the SWAP=GLOBAL option. The large size of the data matrix precluded using the more rigorous BANDB (branch-and-bound) algorithm (Hendy & Penny 1982).
Results and Discussion

PAUP was able to locate over 100 equally parsimonious trees. All were redundant, i.e., the result of alternative arbitrary resolutions of polytomies (Swofford 1985). A representation of the common topology underlying these trees is presented in Fig. 9. Resolution of this cladogram involved 64 character state changes. Of these, 31 are parallelisms and three are reversals, resulting in approximately 53% homoplasy. The consistency index (Kluge & Farris 1969) is 0.672.

The cladogram contains numerous polytomies and poorly resolved clades. These may be attributed to a lack of cladistically useful characters. Cladistic methods, particularly computer-implemented ones, work best when the characters can be divided into two discrete and mutually exclusive states. Unfortunately, species of Clermontia are largely distinguished on the basis of meristic floral characters, which are not amenable to cladistic analysis. Thus, some of the taxonomically most useful characters perforce were eliminated from the cladistic analysis.

Full resolution of the cladogram was also vitiated by the numerous parallelisms. Most appear to be genuine parallel developments of derived features, due to mosaic evolution (Stebbins 1974). Although parallelisms pose a problem for the resolution of an ideal cladogram, they can be very informative regarding the selective pressures faced by the organisms involved. For example, very dark purple ("black") pigmentation has developed on the inner surfaces of the perianth in
Fig. 9. Cladogram showing cladistic relationships among species of Clermontia. OTUs are represented by an acronym derived from the first three letters of the specific epithet. Character state changes are indicated by symbols bearing the character number. Unique synapomorphies are indicated by a single bar, parallelisms by a double bar, and reversals by a dot.
three lineages: Clermontia calophylla, C. waimeae, C. peleana subsp. peleana and the clade comprising Clermontia drepanomorpha, C. kohalae, and C. montis-loa. All six species are endemic to the youngest island, Hawai‘i. On this basis, one might hypothesize that due to some pollinator endemic to that island, selection for this unique pigmentation has been so strong, that it has arisen independently four times.

Despite these problems, the cladogram provides important insights on evolutionary relationships and taxonomic structure within the genus. The holophyletic (cf. Ashlock 1971) nature of Clermontia is supported by four synapomorphies. Within the genus is a holophyletic clade of 15 species defined by six synapomorphies, which corresponds to sect. Clermontia. The remaining seven species share only plesiomorphic characters and form a tetrachotomy at the base of the cladogram.

Previous authors (Hillebrand 1888, Rock 1919, Wimmer 1943, St. John 1969) treated these species as sect. Clermontioideae. Each of these sections is made up of two relatively well supported clades plus a poorly resolved grade of plesiomorphic species.

These inferred patterns and an intuitive assessment of divergence among the lineages suggest that it would be most meaningful and useful to classify Clermontia in the following way. The two sections recognized by previous authors, sect. Clermontioideae and sect. Clermontia, are maintained. The autonymic section is holophyletic, while the more primitive sect. Clermontioideae is paraphyletic. Each section is divided into three series. Within sect. Clermontia, the
clade comprising *Clermontia calophylla*, *C. micrantha*, *C. multiflora*, and *C. parviflora* is described as ser. *Parviflorae*, while that comprising *Clermontia grandiflora*, *C. hawaiensis*, *C. oblongifolia*, and *C. samuelii* becomes the autonymic series. The remaining species of the section comprise paraphyletic ser. *Dupliciflorae*. Within sect. *Clermontioideae*, the clade comprising *Clermontia arborescens* and *C. tuberculata* is described as ser. *Sarcanthae*, while that comprising *C. fauriei* and *C. peleana* is described as ser. *Unilabiatae*. The remaining three plesiomorphic species comprise paraphyletic ser. *Clermontioideae*. All of these series are new and are described formally in the next section.
TAXONOMY


Shrubs or small trees, (0.4-)1-6(-9) m tall, terrestrial or epiphytic. Stems branched repeatedly, spreading, light gray to light brown, glabrous or rarely pubescent, with numerous helically arranged leaf scars near apex; pith solid; latex white, viscous. Leaves simple, alternate, exstipulate, petiolate or rarely subsessile; lamina oblong, elliptic, or oblanceolate, (4-)8-20(-28) cm long, (1-)2-6(-9.8) cm wide, coriaceous or chartaceous, rarely membranous, glabrous or pubescent, rarely muricate; upper surface glossy or dull; lower surface dull, paler; margin callose-crenulate, rarely callose-serrulate; apex acute, acuminate, or cuspidate, rarely obtuse or rounded; base cuneate or attenuate, rarely obtuse or rounded; petiole (0.2-)1.5-7(-13.5) cm long, terete or rarely winged, green and opaque or rarely yellowish-white and translucent, glabrous or pubescent. Inflorescences axillary 2(-10)-flowered subumbellate racemes, sometimes 1-flowered by abortion, glabrous or pubescent, rarely muricate; peduncle spreading, rarely deflexed or pendent, (0.3-)0.8-5(-12) cm long, bibracteate;
pedicels spreading, rarely ascending or pendent, (0.3—)1—4(—7) cm long, bibracteolate. Flowers perfect, epigynous, zygomorphic, resupinate, protandrous. Calyx synsepalous; tube adnate to the ovary, forming a hypanthium, hemispheric, obconic, obovoid, turbinate, or rarely oblong, (0.5—)0.8-1.5(-2.2) cm long, (0.3—)0.8-1.5(-2.2) cm wide, smooth, rarely muricate or with 10 longitudinal ridges; lobes 5, valvate, either less than 1/2 as long as the corolla, distinct or rarely connate at base, persistent, triangular or deltate, rarely oblong or ovate, firm, green, or as long as the corolla or rarely as little as 2/3 as long, connate for 1/5-4/5, deciduous, mimicking the corolla in shape, texture, and color. Corolla bilabiate, unilabiate, tubular, or rotate, (1.5—)3.5-7(-9) cm long, white, green, purple, or rose-colored; tube suberect to arcuate, dorsally cleft to near the base; lobes 5, valvate, downcurved, erect, spreading, or recurved, 1/5-3 times as long as the tube. Stamens 5, syngenesious, alternate with the corolla lobes, included or exserted; filaments connate above, free, purple, magenta, or white, (1.7—)2.5-6(-8.4) cm long, glabrous; anthers connate, dithecal, opening by introrse longitudinal slits, purple or white, (0.6—)1-1.8(-2.2) cm long, (1.8—)3-5(-7.5) mm wide, the 3 dorsal ones longer than the 2 ventral ones, the latter with tufts of stiff white hairs at the apex, otherwise glabrous, sometimes pubescent along the sutures, rarely on the surfaces; pollen tricolporate or rarely dicolporate, prolate, ellipsoidal, 50-65 u long, 32-45 u in diameter. Ovary inferior, 2-carpellate, 2-loculed; placentae axile; style slender, terete, with a ring of stiff white hairs near apex; stigma
2-lobed, the lobes appressed and non-receptive as the style grows through the anther tube, pushing out pollen, after which the stigmas spread and become receptive. Fruit an orange or yellow berry, subglobose, obovoid, ellipsoid, or oblong, rarely obpyriform or obconic, (1.2)2-3.5(-4) cm long, (0.9-2-3.5(-4) cm in diameter, smooth, rarely muricate or with 10 longitudinal or ridges; pericarp thick, leathery; placentae juicy or spongy; apex truncate, crowned with a low circular rim and base of style. Seeds numerous, dark brown to black, minutely foveate-reticulate, shiny, 0.2-0.5 mm long. Chromosome number \( n = 14 \).

**Classification**

*Clermontia* is endemic to the six largest islands of the Hawaiian archipelago (Table 4): Kaua'i (one species), O'ahu (five species), Moloka'i (five species), Lana'i (four species), Maui (ten species), and Hawai'i (11 species). The species inhabit montane rain forests, cloud forests, montane bogs, and rarely subalpine forests at elevations of 150-2100 m. The genus is related to *Cyanea* Gaudich. sect. *Delisseoideae* (Hillebrand) Rock (see GENERIC RELATIONSHIPS), but differs by its distinctive profusely branched habit, subumbellate racemes of 2(-10) larger flowers with the corolla dorsally cleft to near the base, and larger orange or yellow berries.

*Clermontia* is divided into two sections: sect. *Clermontioideae*, seven species with calyx lobes less than 1/2 as long as the corolla, distinct or rarely connate basally, persistent, triangular or deltate,
Table 4. Geographic distribution of *Clermontia*. K = Kaua'i; O/W = O'ahu, Waianae Mts.; O/K = O'ahu, Ko'olau Mts.; Mo = Moloka'i; L = Lana'i; M/W = West Maui; M/E = East Maui; H/1 = Hawai'i, Kohala Mts.; H/2 = Hawai'i, Mauna Kea; H/3 = Hawai'i, windward Mauna Loa; H/4 = Hawai'i, leeward Mauna Loa and Hualalai; + = extant; x = presumed extinct

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<td>ssp. samuelii</td>
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<td>ssp. hanaensis</td>
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<td>C. hawaiensis</td>
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rarely oblong or ovate, firm, and green; and sect. Clermontia, 15 species with calyx lobes as long as the corolla or rarely as little as 2/3 as long, connate, deciduous, mimicking the corolla in shape, color, and texture. These two sections are maintained, but each is subdivided into series. The first section comprises three series: ser. Unilabiatae, two species characterized by a unilabiate corolla with downcurved lobes 1/4-1/5 as long as the arcuate tube; ser. Sarcanthae, two species characterized by a thick fleshy bilabiate corolla with the two dorsal lobes longer than the three ventral; and ser. Clermontioideae, five species characterized by a bilabiate corolla with erect or spreading lobes equalling or exceeding the suberect or curved tube in length. The autonymic section comprises three series: ser. Dupliciflorae, seven species with the perianth bilabiate, the lobes spreading, equalling or exceeding the suberect or curved tube in length; ser. Parviflorae four species with perianth rotate, the lobes recurved, equalling or exceeding the erect or suberect tube in length; and ser. Clermontia, four species with perianth tubular, the lobes suberect or slightly spreading, 1/5-1/2 as long as the curved or arcuate tube.

Typification

As originally described, Clermontia included three species: C. grandiflora, C. oblongifolia, and C. persicifolia. Although Swart (1979) indicated that no type had been designated, Rock (1919) clearly chose Clermontia oblongifolia as the lectotype of the genus. As such,
St. John's (1969) subsequent choice of the same species is superfluous. In addition to typifying the genus, Rock (1919) also designated lectotypes for new taxa of Clermontia published by Hillebrand (1888). These taxa were based upon specimens in Hillebrand's personal herbarium. Following Hillebrand's death in 1886, this collection went to the Botanisches Museum in Berlin. Unfortunately, the Berlin authorities did not retain Hillebrand's collection intact (Rock 1919). Numerous specimens presumed to be duplicates were distributed to herbaria throughout the world. Worse, Hillebrand's original labels were discarded and their information transcribed (often incompletely) onto standard Botanisches Museum labels. Rock studied the specimens remaining at Berlin and designated what he termed (Rock 1919: 6) "lectotypes".

Tragically, over three million specimens deposited in the Botanisches Museum, including nearly all of Hillebrand's personal herbarium, were destroyed during the night of 1-2 March 1943 as the result of an incendiary bombardment by the Royal Air Force (Hiepko 1987, Lack 1987). However, Felix Widder (in litt. to Otto Degener, 8 Jan 1949) quoted K. H. Rechinger of the Naturhistorisches Museum at Wien as stating that the Lobelioideae were at that institution, on loan to Wimmer (see TAXONOMIC HISTORY), and so survived the attack. Similarly, Hiepko (1987) and Lack (1987) indicated that the Lobelioideae were among the few major groups to survive the war.

Nonetheless, when I visited the Botanisches Museum in 1987, I could locate only a handful of pre-1943 specimens of Clermontia. James
L. Luteyn (pers. comm.) had previously noted a similar scarcity of pre-1943 specimens of Burmeistera Triana, another genus of tribe Delisseeae. A thorough search disclosed very few pre-1943 specimens of any genus of Delisseeae. Nearly all pre-1943 specimens seen were members of tribe Lobelieae. Apparently, Wimmer borrowed and returned the Delisseeae prior to 1943, as these genera were treated in the first volume of his monograph (Wimmer 1943). The genera of Lobelieae were treated in the second volume (Wimmer 1953) and presumably were the specimens on loan to him during the war. Thus, it is necessary once again to designate lectotypes for Hillebrand's novelties.

In designating new lectotypes, the first choice should be a duplicate of Rock's original choice, i.e., an isolectotype. However, as noted by Rock (1919), it is very difficult to ascertain which of Hillebrand's specimens are duplicates in the conventional sense. Most are unnumbered, undated, and bear only sketchy locality data. For purposes of typification, I am assuming that any Hillebrand specimen with the same label information as Rock's original choice is an isolectotype, unless it conflicts with the protologue. If no isolectotypes could not be located, one of the original syntypes is designated as the lectotype. In either case, preference is given to specimens that were not distributed by Berlin. These still bear Hillebrand's original labels, and so can be equated more readily with the protologue. I know of three such sets: (1) a set sent by Hillebrand (cf. Hillebrand 1888: ix) to the Royal Botanical Gardens at Kew in July 1865; (2) a set at the British Museum (Natural History)
received in December 1872; and (3) a set at the Gray Herbarium presumably brought there when Hillebrand visited Asa Gray in 1871 (cf. St. John 1942). Specimens distributed by Berlin were used only if no appropriate specimen could be located in one of these sets.

Specimen citations

The grouping of specimens cited under each species followings the convention used by Carr (1985a). Specimens are grouped first by island, from oldest to youngest (i.e., from northwest to southeast). East Maui and West Maui, though connected by a low dry isthmus, are regarded here as separate islands. Within each of the larger islands, secondary grouping of specimens is based on districts (arranged clockwise from the north), except on O'ahu, where mountain ranges (oldest to youngest) provide a more useful subdivision. The small islands of Moloka'i and Lana'i are not subdivided. Thus, the complete sequence for a hypothetical ubiquitous species would be as follows: Kaua'i (Hanalei, Kawaihau, Lihue, Koloa, and Waimea Districts), O'ahu (Wai'anae Mountains, Ko'olau Mountains), Moloka'i, Lana'i, West Maui (Lahaina and Wailuku Districts), East Maui (Makawao and Hana Districts), and Hawai'i (North Kohala, South Kohala, Hamakua, North Hilo, South Hilo, Puna, Ka'ū, South Kona, and North Kona Districts).

Several Hawaiian words commonly used in the specimen citations require brief definition. An ahupua'a (abbreviated "Ahu.") is a subdivision of a district. A kipuka is a vegetated area of relatively old lava surrounded by much younger barren lava. Such formations occur
only on the youngest island, Hawai'i. Makai indicates a direction
toward the shore of an island, while the contrasting term mauka
indicates a direction toward the summit, as in the expression "mauka of
Hilo", i.e., on the mountain slopes above Hilo. Commonly encountered
words for physiographic features include mauna (mountain), pali (cliff
or precipice), and pu'u (hill). In citing specimens collected in
forest reserves administered by the Hawai'i Department of Land and
Natural Resources, the words Forest Reserve are abbreviated F. R.,
e.g., "Hilo F. R." Abbreviations for herbaria follow Index Herbariorum
(Holmgren, Keuken & Schofield 1981).

KEY TO THE SECTIONS, SERIES, AND SPECIES OF CLERMONTIA

1. Calyx lobes less than 1/2 as long as corolla, persistent, distinct
or rarely connate at base, triangular, rarely oblong or ovate,
green, firm.

   I. Sect. Clermontioideae.

2. Corolla bilabiate; tube suberect or curved, 1-3.6 cm long; lobes
erect or spreading, (1.7-)2-6.1 cm long, equalling or exceeding
tube in length.

3. Corolla lobes thin, firm, all spreading and of equal length;
peduncle as long as pedicels or longer; staminal column
exserted; anthers 3-5 mm wide; lamina chartaceous, upper
surface dull.
IA. Ser. Clermontioideae.

4. Corolla 3-4 cm long, dark purple at least on the lobes; tube 1.1-2 cm long; filaments 2.5-3 cm long; anthers 1-1.2 cm long.

3. C. waimeae.

4. Corolla 4-6 cm long, white, green, or purple; tube 2-2.7 cm long; filaments 3-4.8 cm long; anthers 1.3-1.8 cm long.

5. Peduncle spreading, equalling or slightly exceeding pedicels in length; filaments 3.7-4.8 cm long; anthers 1.4-1.8 cm long; lower surface of lamina glabrous or pubescent on veins; margin callose-crenulate; petiole terete; berries subglobose.

1. C. cleromonticoides.

5. Peduncle deflexed, 3-5 times longer than pedicels; filaments 3-3.6 cm long; anthers 1.3-1.4 cm long; petioles winged; lower surface of lamina pubescent; margin callose-serrulate; berries obovoid or obpyriform.

2. C. pyrularia.

3. Corolla lobes thick, fleshy, the 2 dorsal lobes erect or suberect and much longer than the 3 ventral lobes; peduncle less than 1/2 as long as pedicels; staminal column included; anthers 4.5-7.5 mm wide; lamina coriaceous, upper surface glossy.

IA. Ser. Sarcanthae.

6. Corolla, hypanthium, pedicels, peduncle, and petiole
glabrous or sparsely pubescent; corolla green, the ventral lobes 0.5-1.5 cm long.

4. *C. arborescens.*

6. Corolla, hypanthium, pedicels, peduncle, and petiole muricate; corolla dark rose, the ventral lobes 2-3 cm long.

5. *C. tuberculata.*

2. Corolla unilabiate; tube arcuate, 4-6 cm long; lobes downcurved, 1-2 cm long, 1/4-1/5 the length of the tube.

IC. Ser. Unilabiatae.

3. Corolla tube 8-13 mm wide, narrower at middle than at base; pedicels 3-4.5 cm long, 2-5 times longer than the peduncle; anthers 1.7-1.8 cm long.

6. *C. peleana.*

3. Corolla tube 5-8 mm wide, of equal width from base to middle; pedicels 0.5-3 cm long, approximately as long as the peduncle; anthers 1.4-1.5 cm long.

7. *C. fauriei.*

1. Calyx lobes as long as the corolla or rarely as little as 2/3 as long, deciduous, connate for 1/5-4/5 their length, similar to corolla in shape, color, and texture.

II. Sect. Clermontia.

8. Perianth bilabiate or rotate, tube erect, suberect, or curved, lobes equalling or exceeding tube in length.

12. Perianth bilabiate, 3.8-6.5 cm long; lobes spreading; staminal column included or slightly exserted.
IIA. Ser. Dupliciflorae.

13. Petioles 5-13.5 cm long, yellowish-white, translucent; lamina membranaceous, upper surface pale green.

11. C. pallida.

13. Petioles 1.5-7 cm long, green, opaque; lamina chartaceous or coriaceous, upper surface green or dark green.

14. Perianth white, cream-colored, or greenish-white within; staminal column white, cream-colored, greenish-white, or magenta.

15. Perianth white externally, sometimes tinged green or purple; hypanthium 6-8 mm wide; lamina 1.5-4 cm wide, upper surface glossy.

10. C. persicifolia.

15. Perianth green externally, sometimes tinged with purple; hypanthium 8-22 mm wide; lamina 3.5-9.8 cm wide, upper surface dull.

16. Perianth 4.5-5.5 cm long, glabrous or sparsely pubescent, lobes 1.9-2.8 cm long; hypanthium 0.8-1.4 cm long; lamina chartaceous; anthers purple or rarely white, 1.1-1.4 cm long.

8. C. kakeana.

16. Perianth 5.5-6.5 cm long, pubescent, lobes 2.6-3.8 cm long; hypanthium 1.2-2 cm long; lamina coriaceous; anthers white, 1.7-2 cm
9. *C. lindseyana.*

14. Perianth purple or dark purple within; staminal column purple or dark purple.

18. Peduncle deflexed, 5-12 cm long; perianth tube 1.5-2 cm wide, lobes 4-7 mm wide; anthers 5-6 mm wide.

14. *C. drepanomorpha.*

18. Peduncle spreading, 0.3-4.5 cm long; perianth tube 0.7-1.5 cm wide, lobes 3-4 mm wide; anthers 3-4 mm wide.

19. Perianth 5-6.5 cm long, tube 2-3.2 cm long, equalling the lobes; filaments 3.5-4 cm long; peduncle 1.5-4.5 cm long; pedicels 1.5-3.5 cm long.

12. *C. kohalae.*

19. Perianth 3.8-5 cm long, tube 0.8-1.6 cm long, half as long as lobes; filaments 2.6-3.4 cm long; peduncles 0.3-1.8 cm long; pedicels 0.3-1.8 cm long.

13. *C. montis-loa.*

12. Perianth rotate, 1.5-4.5 cm long; lobes recurved; staminal column strongly exserted.

IIIB. Ser. *Parviflorae.*

20. Perianth 3.5-4.5 cm long, tube 7-10 mm wide; hypanthium
10-17 mm long, 8-12 mm wide; anthers 10-13 mm long, 3-4 mm wide.

18. *C. calophylla.*

20. Perianth 1.5-3.2 cm long, tube 3-6 mm wide; hypanthium 5-8 mm long, 3-8 mm wide; anthers 6-8 mm long, 2-3 mm wide.

21. Inflorescences 7-10-flowered; hypanthium obconic, 7-8 mm wide; perianth tube 1.4-1.6 cm long, 5-6 mm wide; filaments 2.5-2.8 cm long.

15. *C. multiflora.*

21. Inflorescences 2-5(-10)-flowered; hypanthium obovoid or turbinate, 3-7 mm wide; perianth tube 0.5-1.3 cm long, 3-5 mm wide; filaments 1.7-2.5 cm long.

22. Perianth rose-colored, lobes 1-1.6 cm long; leaves coriaceous; peduncle 0.5-1 cm long; filaments 1.7-2 cm long.

16. *C. micrantha.*

22. Perianth purple, green, or white, lobes 1.8-2.3 cm long; leaves chartaceous; peduncle 1-1.7 cm long; filaments 2-2.5 cm long.

17. *C. parviflora.*

8. Perianth tubular, tube curved or arcuate, lobes 1/5-1/2 as long as the tube.

IIIC. Ser. Clermontia.

22. Lamina coriaceous, upper surface glossy; hypanthium
hemispheric or obconic; anthers 1.3–1.8 cm long, 3–5 mm wide.

23. Perianth tube arcuate, outer segments flat; hypanthium 0.8–1.8 cm long, smooth; berry subglobose, smooth or with 10 shallow longitudinal furrows.

19. C. oblongifolia.

23. Perianth tube curved, outer segments with a median longitudinal ridge; hypanthium 1.7–2.2 cm, with 10 longitudinal ridges, the uppermost one forming a definite keel; berry obconic, obovoid, or ellipsoid, with 10 longitudinal ridges.

20. C. hawaiensis.

22. Lamina chartaceous, upper surface dull; hypanthium turbinate or obovoid; anthers 1–1.4 cm long, 2.5–3.5 mm wide.

24. Inflorescences spreading, peduncle 0.4–1.8 cm long; hypanthium 0.5–1 cm wide; perianth 3.6–4.8 cm long, rose-colored, or, 4–5.5 cm long, white tinged green.

21. C. samuelii.

24. Inflorescences pendent, peduncle (1–)3–11 cm long; hypanthium 0.9–1.9 cm wide; perianth 5.1–8.5 cm long, green, maroon, purple, or rose-colored.

22. C. grandiflora.

Clermontioideae Hillebrand, Fl. Hawaiian Isl. 240. 1888. --

TYPE (designated by Rock 1919: 285): Clermontia gaudichaudii Hillebrand, nom. illegit. [= Clermontia clermontioides (Gaudichaud) A. Heller].

Shrubs or trees, 1-8 m tall, terrestrial or epiphytic. Lamina oblong, elliptic, or oblanceolate, (5-)8-20(-28) cm long, (1.5-)2-5.5(-7) cm wide, coriaceous or chartaceous, glabrous or pubescent, rarely muricate; margin callose-crenulate, rarely callose-serrulate; apex acute, acuminate, or cuspidate, rarely obtuse; base cuneate or attenuate, rarely obtuse or rounded. Petiole (1-)1.5-6(-8) cm long, terete or rarely winged, green, opaque.

Inflorescences 2(-5)-flowered or 1-flowered by abortion; peduncle spreading, rarely deflexed, (0.4-)0.8-3(-6) cm long; pedicels spreading, rarely ascending, (0.5-)1-4.5(-5.3) cm long. Hypanthium hemispheric or obconic, rarely obvoid or oblong, (0.8-) 1-1.8(-2.2) cm long, (0.6-)1-1.5(-2) cm wide, smooth or rarely muricate. Calyx lobes triangular or deltate, rarely oblong or ovate, 1-5(-40) mm long, 0.5-4(-10) mm wide, distinct or rarely connate at base, persistent, firm, green. Corolla unilabiate or bilabiate, (3-)4-7(-9) cm long, green, purple, or white; tube suberect, curved, or arcuate, 1-6 cm
long, 0.4-2 cm wide; lobes spreading, downcurved, or suberect, 1-4(-6.1) cm long, 2-4(-7) mm long. Staminal column included or exserted, suberect or curved; filaments purple, magenta, or white, (2.5-)3-6.4 cm long; anthers purple or white, (1-)1.3-1.8(-2.1) cm long, 3-5(-7.5) mm wide. Berries subglobose, rarely obovoid or obpyriform, (1.8-)2-3.5(-4) cm long, (1.5-)2-3.5(-4) cm in diameter, smooth or rarely muricate.

The species of sect. Clermontioideae differ from those of sect. Clermontia by their calyx lobes, which are similar to those found in most Lobelioideae: green, firm, and persistent on the fruit, triangular or rarely oblong or ovate, less than half the length of the corolla, distinct or rarely connate at base. For this reason, Gaudichaud (s.d.), Gray (1861), Mann (1867-68), and Wawra (1872-1873) assigned these species to either Delissea (species with calyx lobes shorter than hypanthium) or Cyanea (species with calyx lobes longer than hypanthium). Hillebrand (1888) expanded the circumscription of Clermontia to include all species with few-flowered subumbellate racemes and distinctive branched habit, regardless of the length of the calyx lobes. However, he did distinguish two infrageneric groups of unspecified rank on this basis. The species transferred from Cyanea and Delissea formed the "Clermontioideae", while those conforming to the original circumscription of the genus became "Clermontiae genuinae".
These two groups were formalized as sections by Rock (1919), who designated *Clermontia clermontioides* (Gaudich.) A. Heller (as its homotypic synonym, *C. gaudichaudii* Hillebrand, nom. illegit.) as the type of sect. *Clermontioideae*. St. John (1969) apparently overlooked this typification, and designated *Clermontia arborescens* as the type of the section. This choice is not only superfluous, but also contrary to Article 22.4 of the *International Code of Botanical Nomenclature* (Voss et al. 1983). On the basis of the results of the cladistic analyses, this section is divided into three series: *Clermontioideae*, *Sarcanthes*, and *Unilabiatae*. 

A seriebus aliis Clermontiae corolla bilabiata lobis patentibus tubum erectiusculum vel curvatum longitudine aequantibus vel superantibus paulo, lobis calycis usque ad dimidium longitudinis corollae, et staminibus connatis exsertis differt.

Shrubs or trees, 1.5-7 m tall, terrestrial or epiphytic. Lamina oblong, elliptic, or oblanceolate, (5-)10-20(-28) cm long, 2-5.5 cm wide, chartaceous; upper surface dull; margin callose-crenulate; apex obtuse, acute, acuminate, or cuspidate; base cuneate or attenuate. Petiole 1-5(-7) cm long, terete or winged, glabrous or rarely pubescent. Inflorescences 2(-5)-flowered; peduncle spreading or rarely deflexed, (0.8-)2-6 cm long; pedicels spreading or ascending, 0.5-4 cm long. Hypanthium hemispheric or obconic, rarely obovoid or oblong, 0.8-1.8 cm long, 0.6-1.5 cm wide, glabrous or pubescent. Calyx lobes triangular or narrowly triangular, 0.3-3.6 cm long, 0.5-10 mm wide; apex acute or acuminate. Corolla bilabiata, 3-6 cm long, green, purple, or white; tube suberect or curved, 1.1-2.7 cm long, 0.4-1.2 cm
wide; lobes spreading, 1.6-3.6 cm long, 2-4 mm wide, equalling or exceeding the tube in length. Staminal column exserted, suberect or curved; filaments purple, or white, 2.5-3.8 cm long; anthers purple or white 1-1.8 cm long, 3-5 mm wide. Berries subglobose, rarely obovoid or obpyriform, 1.8-3.6 cm long, 1.5-3.6 cm wide.

The most primitive species of sect. Clermontioideae (i.e., those most similar to species of Cyanea sect. Delisseoideae) are segregated here as ser. Clermontioideae. They are characterized by a bilabiate corolla with spreading lobes equalling or exceeding the suberect or curved tube in length, and an exserted staminal column. The name used for this series is not an autonym, because it does not include the type of the genus, but rather a new combination using the same epithet and type as the sectional name. Although the use of this epithet is not mandated in this situation, it is in keeping with the spirit of Recommendation 22A of the Code (Voss et al. 1983). A Latin diagnosis, though not required, is provided nonetheless.

Shrubs or trees, 1.5-6.5 m tall, terrestrial or epiphytic. Lamina oblong, elliptic, or oblanceolate, 7-25 cm long, 2-5 cm wide, chartaceous, dull; upper surface green, glabrous; lower surface light green, glabrous or pubescent along the veins; margin callose-crenulate; apex acuminate, acute, obtuse, or cuspidate; base cuneate or attenuate. Petiole 1-7 cm long, glabrous or pubescent. Inflorescences 2(-4)-flowered or sometimes 1-flowered by abortion, glabrous or pubescent; peduncle spreading, 1.8-5 cm long, bibracteate at apex; pedicels spreading, 1.5-4 cm long, bibracteolate at or below middle. Hypanthium hemispheric or obconic, 1-1.5 cm long, 1-1.5 cm wide, glabrous or pubescent. Calyx lobes narrowly triangular or triangular, 0.3-3.6 cm long, 0.5-10 mm wide, distinct or connate at base; apex acute or acuminate. Corolla bilabiate, 4-6 cm long, green, purple, or white, glabrous or pubescent; tube suberect or curved, 2-2.7 cm long, 0.6-1.2 cm wide; lobes spreading, 2-3.6 cm long, 2-4 mm wide. Staminal column exserted, suberect or gently curved; filaments white or light purple, 3.7-4.8 cm long; anthers white or light purple, 1.4-1.8 cm long, 3-5 mm wide, glabrous. Berries orange or yellow, subglobose, 2-3.6 cm long, 2-3.6 cm in diameter. Chromosome number n = 14.

The basionym of this species, Delissea clermontioides, was published by Gaudichaud (s.d.) on a plate in a folio atlas illustrating plants collected during his voyage aboard the Bonite. This plate was published sometime in 1842, but the accompanying text was never
prepared (Stafleu & Cowan 1976). This left the identity and provenance of the plant portrayed open to interpretation. Hillebrand (1888) equated the plate with a new species of Clermontia from Kaua'i. He named his novelty Clermontia gaudichaudii, but cited Delissea clermontioides as a synonym. Heller (1897), who also equated Gaudichaud's plate with the plant of Kaua'i, provided the correct combination, Clermontia clermontioides. All subsequent authors (e.g., Rock 1919, Wimmer 1943, St. John 1973) have applied this binomial or Hillebrand's superfluous synonym (cf. the obstinate comment of Skottsberg 1944) to the common species on Kaua'i.

Unfortunately, the type specimen of Delissea clermontioides does not match specimens from Kaua'i (Lammers 1988b), nor did Gaudichaud ever visit that island (Lasegue 1845). However, the Bonite did call at Kealakekua Bay, in Kona District, Hawai'i (Lasegue 1845). The type of Delissea clermontioides was undoubtedly collected there, as it is labelled "Owhyhei" (a variant spelling of Hawai'i) and is a perfect match for the common species of Clermontia in that region. That species has been called Clermontia coerulea Hillebrand for the past century but now must be called Clermontia clermontioides. The earliest available name for the plant of Kaua'i is Clermontia fauriei.

Gaudichaud's plate clearly shows a plant with very short dentiform calyx lobes. In Hillebrand's (1888) description of Clermontia coerulea, he noted that the length of the calyx lobes varied from 4-18 mm. Rock (1919) observed that this variation was geographically correlated. In Ka'u District, calyx lobes were small and tooth-like,
while in Kona District, they were much larger. Nonetheless, Rock accepted Hillebrand's circumscription of the species and did not recognize these variants formally. Skottsberg (1926) and Wimmer (1929) confirmed Rock's observations on geographically correlated variability but believed that this should be reflected in the classification (see discussion under each subspecies below). My studies also support the formal recognition of two morphologically distinguishable and geographically distinct clusters of populations: plants from the southern portion of the species' range, with short distinct calyx lobes; and plants from the northern portion, with long connate calyx lobes. The remaining varieties are treated here as synonyms of either Clermontia fauriei (C. clermontioides var. epiphytica and C. clermontioides var. hirsutiflora) or C. peleana subsp. singuliflora (C. clermontioides var. mauiensis, C. gaudichaudii var. barbata, and C. gaudichaudii var. singuliflora).

KEY TO THE SUBSPECIES OF CLERMONTIA CLERMONTIOIDES

1. Calyx lobes distinct, 0.2-1 cm long, 0.5-3 mm wide.
   1a. C. clermontioides subsp. clermontioides.

1. Calyx lobes connate at base, 1-3.6 cm long, 3-10 mm wide.
   1b. C. clermontioides subsp. rockiana.

1a. Clermontia clermontioides subsp. clermontioides.
**Clermontia coerulea** Hillebrand, Fl. Hawaiian Isl. 243. 1888. TYPE (designated by Rock 1919: 295): HAWAIIAN ISLANDS. Hawai'i: Kona, Hillebrand s.n. (lectotype: B!).


**Clermontia coerulea** var. **degeneri** Skottsberg, Acta Horti Gothob. 15: 495. 1944. -- TYPE: HAWAIIAN ISLANDS. Hawai'i: w. side of Mauna Loa, between Koa Mill & 'Ohi'a Mill, 16 Sep 1938, Skottsberg 3306 (holotype: GB!; isotypes: BISH! K! S!).


**Clermontia konaensis** H. St. John, Pacific Sci. 30: 37. 1976. --
TYPE: HAWAIIAN ISLANDS. [Hawai'i: western slopes of Mauna Loa above Kealakekua Bay, Jan 1779] Nelson s.n. (holotype: BM!).

Lamina 7-22 cm long, 2-5 cm wide. Petiole 1-6 cm long. Peduncle 2.5-5 cm long; pedicels 2-4 cm long. Calyx lobes 0.2-1 cm long, 0.5-3 mm wide, distinct. Corolla 4-5 cm long; tube 2-2.5 cm long, 0.6-1.1 cm wide; lobes 2-3 cm long.

Distribution. (Fig. 10). Endemic to Hawai'i. Montane rain forests, 670-1525 m, on leeward Mauna Loa and Hualalai, from Pahala to Pu'u Lehua.

SPECIMENS EXAMINED. HAWAI'I. KA'U: Wai'ohinu Ahu., Conant & Casey 674 (BISH); Kiolaka'a-Kea'a Homesteads Addition, Davis 333 (BISH); Kahuku, Forbes 1082.H (BISH, P, US, WELT); Manuka Ahu., Higashino & Croft 5816 (BISH); Kahuku Ahu., Jacobi 1106 (BISH), Jacobi 1108 (BISH); Na'alehu, Rock 10003 (A, BISH, CAS, GH, NSW, NY), Rock s.n. (US); Kalaiki, Rock 26019 (BISH), Rock s.n. (BISH, UC); Moaula, Ruse s.n. (BISH). -- SOUTH KONA: Bishop Estate Forest, Carlquist 591 (RSA), Carlquist 2072 (RSA); Honaunau F. R., Corn ESP-153 (BISH); Honaunau F. R., Cuddihy 264 (BISH); Honaunau F. R., Davis 269 (BISH); between 'Ohi'a & Koa Mills, Degener 7812 (BISH, CAS, GH, K, MO, NY), Degener 7813 (BISH, MASS, NY, US); Greenwell Ranch, Degener 19205 (W), Degener 19208 (W), Degener 19211 (NY), Degener 19212 (NY), Degener 19371 (NY), Degener 19372 (NY), Degener 19373 (W), Degener 19374 (NY), Degener 19913 (NY); Papaloa, Degener 20247 (MO, NY, W), Degener &
Fig. 10. Distribution of the taxa of ser. Clermontioideae: Clermontia clermontioides subsp. clermontioides (dots), C. clermontioides subsp. rockiana (open circles), C. pyrularia (triangles), C. waimeae (squares).
Murashige 20329 (NY, W); Hanekane, Forbes 178.H (BISH, UC); Old Koa Mill, Hatheway & Richards 435 (W); Honauanau F. R., Herbst 1693 (BISH); Kapua Ahu., Higashino & Croft 6137 (BISH, US), Higashino & Croft 6170 (BISH, GB, US); Pahoeheo 2 Ahu., Jacobi 1127 (BISH); Pawaina-Pauahi-Papaloa trail, Lamoureaux 465 (HAW); Pawaina-Pauahi-Papaloa trail, Ozaki 1348 (BISH); Kealakekua, Rock 10031 (BISH); McCandless Ranch, Rock 25638 (BISH), Rock 25639 (L), Rock 26024 (BISH), Rock 26025 (BISH); Honakua Ahu., Rock 25655 (A, BISH, UC); Honaunau, Rock 25710 (BISH), Rock 26006 (BISH); Greenwell Ranch, Rock 25727 (BISH, RSA); Rock 25736 (BISH, MICH); Ho'opuola, Rock 25745 (BISH), Kapua, Rock 25748 (BISH), Rock 25754 (BISH, BM); Bishop Estate, Rock 26014 (BISH); Koa Mill, St. John et al. 18554 (BISH), St. John et al. 22477 (BISH, NY, US), St. John et al. 22478 (BISH, P); 'Ohi'a Mill, St. John et al. 22469 (BISH, NY, P); Honauanau F. R., St. John et al. 22544 (BISH); between Koa Mill & 'Ohi'a Mill, Skottsberg 3305 (BISH, GB, S); Honokua Ahu., Warshauer & McEldowney 1936 (BISH); Kealia Ahu., Honaunau F. R., Warshauer & McEldowney 1955 (BISH); Honaunau Ahu., Warshauer & McEldowney 1970 (BISH). — NORTH KONA: Pu'u Lehua, Rock s.n. (A, BISH, K, L, UC); Keauhou 1 Ahu., Warshauer & McEldowney 1860 (BISH), Warshauer & McEldowney 1871 (BISH). — NO PRECISE LOCALITY: Garber 197 (BISH); Menzies s.n. (BM); Rock s.n. (CAS).

Because Gaudichaud's plate of Delissea clermontioides depicts a plant with short calyx lobes, such plants constitute the autonymic
subspecies. Although Hillebrand's (1888) original circumscription of Clermontia coerulea encompassed both long-lobed and short-lobed plants, Rock (1919) designated a specimen of the latter as the lectotype. This specimen somehow survived the wartime conflagration at Berlin and clearly bears small dentiform calyx lobes. Consequently, the segregation of short-lobed plants as var. brevidens by Skottsberg (1926) was in error, the comments of Skottsberg (1944) and St. John (1973) notwithstanding.

Clermontia clermontioides is rather variable in color of the corolla, size and shape of the leaves, shape of the hypanthium, and length of the peduncles and pedicels. Unlike the variation in calyx lobe morphology, none of this variation is correlated with geographic distribution. Thus, infraspecific taxa based on differences in these features cannot be maintained: Clermontia coerulea var. degeneri (named for naturalist Otto Degener, 1899-1988), C. coerulea f. flavescens, and C. coerulea var. parvifolia. The second name requires typification, as it was based upon four specimens collected by Greenwell and distributed by Degener as part of his series. Only one of these syntypes, Degener 19375, could be located in the herbarium at Wien, where Wimmer worked. As this sheet was annotated "orig." by Wimmer and matches the protologue, it is designated above as the lectotype. The type of Clermontia konaensis is a specimen of C. clermontioides subsp. clermontioides. The calyx lobes are somewhat longer than average, but distinct and within the range of variation of that subspecies. The collection data cited above in brackets was taken from St. John (1976a,
1b. Clermontia clermontioides subsp. rockiana (F. Wimmer) Lammers,
ISLANDS. Hawai‘i, Remy 308 (holotype: P!; isotype: P!).

Clermontia coerulea var. greenwelliana F. Wimmer in Engler,
Pflanzenr. IV.276b (107.Heft): 762. 1953. -- TYPE (designated
by Lammers 1988b: 499): HAWAIIAN ISLANDS. Hawai‘i: along
Heifer Paddock-Papaloa fence, Kealakekua Ranch, South Kona,
5300 ft, 18 Mar 1949, legit Greenwell, Degener 19625
(lectotype: W!; isolectotypes: B! NY!).

Clermontia loyana Rock, Occas. Pap. Bernice Pauahi Bishop Mus. 22:
36. 1957. -- TYPE: HAWAIIAN ISLANDS. Hawai‘i: South Kona, land
of Kealia, between Komakawai and Kaunene, 6000 ft, 14 Mar 1956,
Rock 25651 (holotype: BISH!; isotype: BISH! W!).

-- TYPE: HAWAIIAN ISLANDS. Hawai‘i: Kona District, summit road
up w. slope of Hualalai above Kailua, ca. 4000 ft, 31 Jan 1965,
G. W. Gillett 1704 (holotype: BISH!; isotypes: HAW! HLA!).

Lamina 7-25 cm long, 2-4.5 cm wide. Petiole 2-6.5 cm long.
Peduncle 1.8-4 cm long; pedicels 2.2-3.5 cm long. Calyx lobes 1-3.6 cm
long, 0.3-1 cm wide, connate at base. Corolla 4.5-6 cm long; tube
2-2.7 cm long, 0.8-1.2 cm wide; lobes 2-3.5 cm long. Chromosome number \( n = 14 \).

Distribution. (Fig. 10). Endemic to Hawai'i. Montane rain forests, 840-1825 m, on leeward Mauna Loa and Hualalai, from Kealia to Pu'u Wa'awa'a.

**SPECIMENS EXAMINED. HAWAI'I.** — SOUTH KONA: Bishop Estate Forest, Carlquist 2070 (BISH, DUKE, GH, L, MICH, RSA, Z), Carlquist 2088 (BISH, RSA); Honaunau F. R., Corn ESP-166 (BISH), Honaunau F. R., Cuddihy 263 (BISH); Greenwell Ranch, Degener 19206 (NY), Degener 19370 (NY); Kealakekua Ranch, Degener 19616 (W), Degener 19623 (W), Degener 19624 (W); Papaloa, Degener & Murashige 20336 (W); Honaunau F. R., Fredericks s.n. (BISH); Honaunau F. R., Herbst 1694 (BISH); Pahoehoe 2 Ahu., Jacobi 1124 (BISH); Pawaina-Pauahi-Papaloa trail, Lamoureux 466 (HAW); Kealakekua, Rock 10032 (BISH, GH, M, MAK); McCandless Ranch, Rock 25638 (L), Rock 25639 (NSW), Rock 25701 (BISH), Rock 25702 (BISH, RSA, US), Rock 26007 (BISH), Rock 26008 (BISH, G, K, NSW, UC), Rock 26009 (BISH, WIS), Rock 26010 (BISH), Rock 26013 (BISH), Rock 26023 (BISH), Rock 26026 (BISH), Rock & Weissich 27500 (L), Rock & Weissich 27502 (BISH, RSA), Rock & Weissich 27503 (BISH, NSW); Kealia 2 Ahu., Rock 25654 (BISH); Bishop Estate, Rock 26004 (BISH); Kahalu'u, Rock s.n. (BISH); Kapua, Skottsberg 1935 (GB, S); Kealia Ahu., Honaunau F. R., Warshauer & McEldowney 1943 (BISH), Warshauer & McEldowney 1954 (BISH). — NORTH KONA: Honokohau 1 Ahu., Banko s.n. (BISH, US); Keahou 1 Ahu., Christ s.n. (BISH); Hualalai, Gillett 1701 (BISH, HLA),
Gillett 1702 (BISH, HLA), Gillett 1703 (BISH, HLA); Huehue Ranch, Need G90A1P (HAW); Koloko mauka, Higashino & Larosa 9598 (BISH); Holualoa F. R., Kondo s.n. (BISH); Hualalai, Lammers 5440 (OS), Lammers 5444** (MO, OS), Lammers et al. 5792 (OS, US), Lammers et al. 5793 (OS), Lammers et al. 5794 (OS), Lammers 5795 (OS), Lammers 5796 (OS), Lammers 5798 (OS); Mo'onulahea, Rock 3737 (BISH), Rock 3738 (BISH); Hinakapau'ula, Rock 3762 (BISH); Pu'u Lehua, Rock 25726 (BISH); Pu'uwa'awa'a, St. John et al. 11402 (BH, BISH, F, L, M, MIN, NY, UC, US, W, WELT); Kahaluu F. R., St. John et al. 18513 (BISH, P); Hualalai, Skottsberg 642 (BISH, GB, S), Skottsberg 666 (GB); Kaumalumalu, Sohmer 6915 (BISH); Keauhou 2 Ahu., Pu'u La'ala'a', Warshauer & McEldowney 1899 (BISH), Warshauer & McEldowney 1900 (BISH), Warshauer & McEldowney 1905 (BISH), Warshauer & McEldowney 1909 (BISH), Warshauer & McEldowney 1912 (BISH). — NO PRECISE LOCALITY: Gillett 1726 (HLA); Gillett 1727 (HLA); Gillett 1730 (BISH, HLA).

Wimmer (1929) was the first to distinguish the long-lobed and short-lobed populations of Clermontia coerulaea in a manner consistent with Rock's (1919) typification of that species. The long-lobed plants were segregated as Clermontia rockiana, while C. coerulaea was emended to include only short-lobed plants. The overall similarity of the two groups suggests that recognition as conspecific subspecies is more appropriate. The former, which commemorates Joseph Francis Charles Rock (1884-1962), here is transferred to subspecific rank under the correct binomial for the species.
Inexplicably, Skottsberg (1944) and St. John (1973) accepted not only Clermontia rockiana but also considered the long-lobed populations to be typical C. coerulea (cf. Skottsberg 1926). Apparently, this confusion was shared by Wimmer (1953), who described a set of long-lobed plants collected by Amy B. H. Greenwell as Clermontia coerulea var. greenwelliana. In describing the calyx lobes, Wimmer (1953: 762) even comments "sic Clermontiae rockianae similis". These specimens differ in no discernible way from subsp. rockiana.

The type of Clermontia loyana is a specimen of subsp. rockiana with calyx lobes at the maximum length in their range of variation. Such plants occur as scattered individuals in populations of subsp. rockiana. For example, in 1985, I studied a population of Clermontia clermontioides on the western slope of Hualalai. Within an area of less than 1000 m², five individuals were encountered. One (Lammers et al. 5794) had calyx lobes 30-36 mm long, matching the type of Clermontia loyana. The remainder (Lammers et al. 5792, 5793, 5795, and 5796) bore calyx lobes 15-25 mm long, average for subsp. rockiana. In all other features, these five plants were indistinguishable.

Similarly, Rock (1957) noted that Clermontia loyana and C. rockiana co-occurred at the type locality of the former. Because specimens referable to Clermontia loyana occur sporadically within populations of C. clermontioides subsp. rockiana, the former cannot be maintained even as a subspecies. The name honors naturalist Loy (Mrs. A. Lester) Marks.

The description of Clermontia hualalaiensis was accompanied by an
illustration (St. John 1987: fig. 6) showing a flower with six corolla lobes and no calyx lobes. However, the type is a rather typical specimen of subsp. rockiana.

2. Clermontia pyrularia Hillebrand, Fl. Hawaiian Isl. 243. 1888. -- LECTOTYPE (here designated): HAWAIIAN ISLANDS. Hawai‘i:

Hamakua, Parker's, 6000 ft, Hillebrand 90 (lectotype: K!).


United States Exploring Expedition s.n. (holotype: US!).

Trees, 3-4 m tall, terrestrial. Lamina narrowly elliptic or rarely oblanceolate, 15-28 cm long, 2.5-5 cm wide, chartaceous, dull; upper surface green, dull, glabrous or sparsely pubescent; lower surface pale green, dull, pubescent; margin callose-serrulate; apex acute or acuminate; base attenuate. Petiole winged, 1.5-3.5 cm long, pubescent. Inflorescences 2(-5)-flowered, pubescent; peduncle deflexed, 2.8-6 cm long, bibracteate at apex; pedicels abruptly ascending, 0.8-2 cm long, bibracteolate at or near base. Hypanthium obconic or obovoid, 1-1.8 cm long, 0.8-1.2 cm wide, pubescent. Calyx lobes triangular, 3-5 mm long, 1-2 mm wide; apex acute or acuminate. Corolla bilabiate, 4-4.5 cm long, white sometimes tinged green, pubescent; tube curved, 2-2.6 cm long, 5-8 mm wide; lobes spreading, 1.7-2.4 cm long, 2-3 mm wide. Staminal column somewhat exerted,
subereect; filaments white, 3-3.6 cm long; anthers white, 1.3-1.4 cm long, 3-4 mm wide, glabrous. Berries orange, obovoid or obpyriform, 1.8-2.8 cm long, 1.5-2.4 cm in diameter.

Distribution. (Fig. 10). Endemic to Hawai'i. Subalpine forests, 1585-2130 m, on windward Mauna Kea and leeward Mauna Loa.

SPECIMENS EXAMINED. HAWAII. NORTH HILO: pit where David Douglas was murdered, Degener et al. 20356 (B, MO, NY, W); Pu'u Huluulu, Forbes 835. H (BISH); Mauna Kea, ne. slope, Hitchcock 14305 (BISH, US); Hinahina, Hosaka 2491 (BISH, DAV, K, US); Maulua, Rock s.n. (BISH); Mauna Kea, Rock s.n. (BISH); Parker Ranch, Maulua section, Stephens s.n. (BISH); Humu'ula Ahu., Douglas Monument, Warshauer 1268 (BISH), Warshauer 1678 (BISH). -- SOUTH KONA: Papaloa, Kealakekua Ranch, Degener 19615 (NY, W); Hiefer Paddock-Papaloa fence, Kealakekua, Degener 19626 (NY, W).

The specimen designated by Rock (1919: 300) as the lectotype of Clermontia pyrularia (Hillebrand s.n., B) was destroyed in 1943. The sheet here designated as the lectotype is apparently the only surviving syntype.

Delissea obtusa var. mollis was treated by Hillebrand (1888), Rock (1919), Wimmer (1943), and St. John (1973) as a synonym of Cyanea obtusa (A. Gray) Hillebrand, a species otherwise restricted to Maui. Apparently, none of these authors examined the type, as it is clearly a sterile specimen of Clermontia pyrularia.
   TYPE: HAWAIIAN ISLANDS. Hawai‘i: Waimea, 12 Jul 1909, Rock 4794

   512. 1913. -- TYPE: HAWAIIAN ISLANDS. Hawai‘i: Alakahi trail,
   Waimea, 12 Jul 1909, Rock 4793 (holotype: BISH; isotypes:
   BISH! GH! L!).

Clermontia waimeae var. obovata Rock, Occas. Pap. Bernice Pauahi
   Bishop Mus. 22: 41. 1957. -- TYPE: HAWAIIAN ISLANDS. Hawai‘i:
   Kohala Mts., Kawaihae, Pu‘u 'Ahia, 4800 ft, 2 Jan 1932, St.
   John & Hosaka 11500 (holotype: BISH; isotype: US!).

Clermontia waimeae var. longisepala Rock, Occas. Pap. Bernice Pauahi
   Bishop Mus. 22: 42. 1957. -- TYPE: HAWAIIAN ISLANDS.
   Hawai‘i: Waimea, Jul 1910, Rock 25671 (holotype: BISH!).

Clermontia waimeae var. longisepala f. lanceolata F. Wimmer in
   Engler, Pflanzenr. IV.276c (108.Heft): 831. 1968. -- TYPE:
   HAWAIIAN ISLANDS. Hawai‘i: Waimea, Jul 1910, Rock s.n.
   (holotype: K!).

   TYPE: HAWAIIAN ISLANDS. Hawai‘i: S. Kohala District, Kawaihae
   1 Ahu., Kohala Mts., southwest of Kehena Ditch, 1 km northwest
   of Pu‘u 'Ahia, ca. 4250 ft, 30 Jul 1979, Warshauer & McEldowney

TYPE: HAWAIIAN ISLANDS. Hawai'i: Kahua 2 Ahu., Pu'a Iki,

Stemmermann et al. 4000 (holotype: BISH!).

Shrubs or trees, 1-7 m tall, terrestrial or epiphytic. Lamina oblong, elliptic, or oblanceolate, 5-15 cm long, 2-5.5 cm wide, chartaceous, dull; upper surface green, glabrous; lower surface light green, glabrous or pubescent; margin callose-crenulate; apex obtuse, acute, acuminate, or rarely cuspidate; base cuneate. Petiole 1-5 cm long, glabrous or pubescent. Inflorescences 2(-5)-flowered, glabrous or pubescent; peduncle spreading, 0.8-3 cm long, bibracteate near apex; pedicels spreading, 0.5-1.8 cm long, bibracteolate at or below middle. Hypanthium hemispheric, obconic, or oblong, 0.8-1.2 mm long, 0.6-1 cm wide, glabrous or pubescent. Calyx lobes triangular to narrowly triangular, 0.3-2.5 cm long, 0.5-3 mm wide; apex acute to acuminate. Corolla bilabiate, 3-4 cm long, dark purple on the lobes, greenish on the tube, glabrous or sparsely pubescent; tube suberect, 1.1-2 cm long, 4-6 mm wide; lobes spreading, 1.6-2.4 cm long, 2-3 mm wide. Staminal column exserted, suberect; filaments purple, 2.5-3 cm long; anthers purple, 1-1.2 cm long, 3.4 mm wide, glabrous or sparsely pubescent. Berries orange, subglobose, 2-2.5 cm long, 2-2.5 cm in diameter.

Distribution. (Fig. 10). Endemic to Hawai'i. Montane bogs, rain forests, and cloud forests, 1070-1520 m, in the Kohala Mountains.
SPECIMENS EXAMINED. HAWAI'I. NORTH KOHALA: Kehena ditch, Carlquist 1867 (BISH, RSA); Pu'u Iki, Davis 722 (BISH); Pu'u La'ala'au, Hoe 1896.0 (HAW); Pu'u Kalalau, Rock 25733 (BISH, L); Kehena ditch, Rock 25734 (BISH, NSW). -- SOUTH KOHALA: Alakahi Bog, Carlquist 2083 (RSA); Alakahi summit, Gustafson 2425 (BISH); before 1st cabin, Iwamoto J29 (HAW); head of Alakahi Str., Lammers et al. 5752 (B, BISH, K, MO, OS), Lammers et al. 5758 (OS); Waimea, Rock 4743 (BISH), Rock 4794b (BISH, P), Rock 4794c (BISH), Rock 4794d (BISH, M), Rock 4894e (A); Rock s.n. (BISH, NY, S, UC); Alakahi, Rock 4795 (BISH); Kawainui ditch, Rock 4795 (GH), Rock 4796 (BISH); Kohala reservoir, Rock 8847 (BISH).

-- NO PRECISE LOCALITY: Rock 25735 (BISH, L); Rock s.n. (BISH, CAS, NY, RSA).

As is so common among Lobelioidae, calyx lobes in this species vary considerably in size and shape. However, this variation is not correlated with geography. A population studied in 1985 contained both short-lobed (Lammers et al. 5752) and long-lobed (Lammers et al. 5758) individuals, at a ratio of approximately 5:1. Thus, it is not possible to recognize Clermontia waimeae var. longisepala at subspecific rank.

Size and shape of leaves also vary considerably within a population. As such, it is impossible to recognize infraspecific taxa distinguished on these bases, i.e., Clermontia waimeae var. obovata and C. waimeae var. longisepala f. lanceolata. Similarly, Clermontia parviflora var. calycina, which supposedly resembles C. parviflora in "aspect" (Rock 1913b, 1957), is indistinguishable from C. waimeae, and
so placed in synonymy.

St. John (1987) recently described two new species of *Clermontia* sect. *Clermontioideae* from the Kohala Mountains, but provided no insights on their suspected affinities. Neither can be distinguished from *Clermontia waimeae*. The holotype of *Clermontia bicolorata* is an individual with long calyx lobes, while that of *C. kahuaensis* is an individual with short lobes.
IB. Clermontia series Sarcanthae Lammers, ser. nov. — TYPE:

*Clermontia arborescens* (H. Mann) Hillebrând.

A seriebus aliis *Clermontiae* corolla bilabiata lobis crassis carnosis erectis vel erectiusculis inaequalibus (duobus dorsalibus tribus ventralibus longioribus) et staminibus connatis inclusis differt.

Shrubs or trees, 1.5-8 m tall, terrestrial or epiphytic. Lamina oblong, elliptic, or oblanceolate, 9-23 cm long, 2-6.5 cm wide, coriaceous; upper surface glossy; apex obtuse, acute, acuminate or cuspidate; base cuneate or attenuate. Petiole 1-5(-8) cm long, glabrous, pubescent, or muricate. Inflorescences 2-flowered, often 1-flowered by abortion; peduncle spreading, 0.4-1.8 cm long; pedicels spreading, 1.2-5.3 cm long. Hypanthium hemoispheric or obconic, rarely obovoid, 1-2.2 cm long, 1-2 cm wide, glabrous, pubescent, or muricate. Calyx lobes deltate, shallowly triangular, or triangular, rarely oblong or ovate, 0.2-4 cm long, 0.3-1 cm wide; apex obtuse, rounded, emarginate, or rarely acute. Corolla bilabiata, 5-7(-9) cm long, green or dark rose-colored; tube erect or suberect, 1-3.6 cm long, 0.8-2 cm wide; lobes thick, fleshy, unequal in length, the dorsal two erect or suberect, 3-5.3(-6.1) cm long, longer than the tube, the ventral three slightly spreading, 0.5-4 cm long. Staminal column included, suberect or curved; filaments magenta, 4.1-6.4 cm long; anthers dark purple,
1.3-2.1 cm long, 4.5-7.5 mm wide. Berries subglobose or rarely obovoid, 2.5-4 cm long, 2.5-4 cm in diameter.

*Clermontia arborescens* and closely-related *C. tuberculata* resemble the species of ser. *Clermontioideae* in their bilabiate corollas. However, they differ from all other species in the genus by their thick fleshy corolla lobes of unequal lengths, i.e., with the dorsal two longer than the ventral three. For this reason, they are segregated here as a new series, *Sarcanthae*. The epithet is derived by Latinizing and compounding the Greek nouns **sarc** , flesh, and **anthos**, flower, and refers to the unique corolla.


Shrubs or trees, 1.5-8 m tall, terrestrial or epiphytic. Lamina oblong, elliptic, or oblanceolate, 10-23 cm long, 2-6.5 cm wide, coriaceous; upper surface dark green, glossy, glabrous; lower surface greenish-white, dull, glabrous or sparingly pubescent along the midvein; margin callose-crenulate; apex obtuse, acute, acuminate, or cuspidate; base cuneate or attenuate. Petiole 1.5-8 cm long, glabrous
or rarely pubescent. Inflorescences 2-flowered or commonly 1-flowered through abortion, glabrous or rarely pubescent; peduncle spreading, 0.4-1.8 cm long, bibracteate at middle or apex; pedicels spreading, 1.2-4.8(-5.3) cm long, bibracteolate at or near base. Hypanthium hemispheric or obconic, 1-2.2 cm long, 1-2 cm wide, glabrous or rarely pubescent. Calyx lobes triangular, deltate, shallowly triangular, oblong, or ovate, 0.2-4 cm long, 0.3-1 cm wide; apex acute, obtuse, rounded, or emarginate. Corolla bilabiate, 5.5-8(-9) cm long, green externally, greenish-white or magenta internally, glabrous or rarely pubescent; tube suberect to curved, 2.2-3.6 cm long, 0.8-2 cm wide; lobes thick, fleshy, the dorsal two erect or suberect 3-5.3(6.1) cm long, 3-7 mm wide, acuminate, acute, obtuse, or rounded at apex, the ventral three forming a downcurved trifid lip 2.4-4 cm long, 0.4-1.2 cm wide. Staminal column included, curved; filaments magenta, 4.2-6.4 cm long; anthers dark purple, 1.3-2.1 cm long, 4.5-7 mm wide, glabrous or pubescent along the sutures. Berries orange, subglobose to obovoid, 2.5-4 cm long, 2.5-4 cm diameter.

Mann (1867-68) described Cyanea arborescens (the basionym of Clermontia arborescens) on the basis of a specimen from southern West Maui with calyx lobes "pollicaribus vel sesquipollicaribus", i.e., 25-38 mm long. Wawra (1872-73) subsequently described Delissea waihiae on the basis of an otherwise similar specimen from northern West Maui with calyx lobes "tubo duplo-triplo brevioribus", i.e., 4-6 mm long, based on his description of the hypanthium (calyx tube) as
"semipollicaribus". Hillebrand (1888) realized that both plants were referable to Clermontia and that they represented a single widespread species that varied considerably in size and shape of the calyx lobes. The short-lobed plants were common on Moloka'i, Lana'i, and much of Maui, while those with long lobes were restricted to southern West Maui.

Hillebrand's conclusions were overlooked by subsequent workers. As interpreted by Rock (1919) and Wimmer (1943), Clermontia arborescens included only plants with calyx lobes ca. 5 mm long. Neither author made any mention of long-lobed individuals, despite the fact that such plants clearly constitute the type of the species. This oversight may be attributed to the rarity of long-lobed plants. After the type was collected, over 85 years passed with no subsequent collections. By the time Otto Degener rediscovered long-lobed plants in 1952, the erroneous concept of Clermontia arborescens as a short-lobed species was firmly established. As a result, Degener's specimens were described by Wimmer (in Degener and Degener 1956a) as a new species, Clermontia furcata. Similarly, when St. John (1983) came across a long-lobed specimen collected by Mann and Brigham, he described it as a new species, Clermontia mannii, in honor of Horace Mann, Jr. (1844-1868). In so doing, he not only overlooked the fact that this specimen was most likely original material of Cyanea arborescens (Lammers 1988b), he also overlooked Wimmer's description of identical plants from the same locality as Clermontia furcata.
Clermontia arborescens as circumscribed here includes both the short-lobed plants of Moloka'i, Lana'i, and most of Maui, and the long-lobed plants of southern West Maui. Reports that this species also occurs on Kaua'i (Wimmer 1943, 1968; Rock 1957) are based upon misidentified specimens (Degener 7856, NY; MacDaniels 706, BISH) of Clermontia fauriei A. Léveillé (Degener & Degener 1960a). This species differs from Clermontia arborescens by its unilabiate corolla with longer and narrower arcuate tube, strongly exserted greenish-white or cream-colored staminal column, and narrower anthers. Further, Clermontia arborescens differs from all other species in the genus by its thick fleshy corolla with dorsal lobes much longer than the ventral ones. The numerical phenetic analyses suggest that this species comprises three clusters of populations that are geographically discrete and morphologically distinguishable. These three clusters are recognized formally as subspecies, and may be distinguished by the following key.

KEY TO THE SUBSPECIES OF CLERMONTIA ARBORESCENS

1. Calyx lobes deltate or shallowly triangular, 0.2-1.2 cm long.
   2. Lobes of the corolla acute or acuminate at apex, the dorsal two
      3-4 mm wide; lip of the corolla 4-9 mm wide.
      4a. C. arborescens subsp. waikoluensis.
   2. Lobes of the corolla rounded or obtuse at apex, the dorsal two
(4.5-)5-7 mm wide; lip of the corolla (7-)8.5-12 mm wide.

4b. C. arborescens subsp. waihiae.

1. Calyx lobes oblong, ovate, or triangular, 1.8-4 cm long.

4c. C. arborescens subsp. arborescens.


Lamina 10-19 cm long, 3-5 cm wide; lower surface glabrous or sparingly pubescent along the midvein. Petiole 2-6 cm long, glabrous or rarely pubescent. Peduncle 0.5-1.2 cm long; pedicels 2.5-4(-5.3) cm long. Hypanthium 1.5-2.1 cm long, 1.2-1.9 cm wide, glabrous or rarely pubescent. Calyx lobes deltate or shallowly triangular, 2-5(-10) mm long; apex acute or obtuse. Corolla 5.8-8(-9) cm long, glabrous or pubescent; tube 2.5-3.6 cm long, 0.8-1.6(-1.8) cm wide; dorsal lobes 3-4.8(-5.5) cm long, 3-4 mm wide, acute or acuminate at apex; trifid lip 2.4-4 cm long, 4-9 mm wide. Filaments 4.2-6.4 cm long; anthers 1.4-2.1 cm long, 4.5-6 mm wide, glabrous or pubescent.
Distribution. (Fig. 11). Montane rain forests on Moloka'i (520-1280 m) and Lana'i (600-1000 m).

SPECIMENS EXAMINED. MOLOKA'I. Kawela Gulch, Bishop 36904 (HAW*); Wailau Ridge, Cranwell 3429 (GB); Kaunuhaua, Davis et al. 796 (BISH*); Pu'u o Waha'ula, Degener 7825 (NY); 'Ohi'alele, Degener 7835 (A, MO, NY); between Waikolu Valley & Pu'u Ali'i, Degener 7844 (A, MO, NY); s. of Kualahuki, Degener 7845 (A, MO, NY); Kainalu, Degener & Murashige 20163 (LD, NY); head of Waikolu Valley, Degener & Tousley 22138 (B, BISH, MASS, NY, W); Pelekunu pali, Fagerlind & Skottsberg 6345 (GB*, UPS*); Kamalo, Faurie 589 (P); mts. above Pu'u Kolekole, Forbes 211.Mo (BISH), Forbes 224.Mo (BISH, L); Waikolu Lookout, Gillett 1680 (HLA); Wailau pali, Hillebrand s.n. (LE); Puko'o, Mr. Conradt's place, Hitchcock 15074 (US); Kalua'aha Ahu., Mauna'olu'olu Ridge, Jacobi & Higashino 1515 (BISH*), Jacobi & Higashino 1517 (BISH); Halawa Ahu., Kahawaiki Gulch, Jacobi & Higashino 1556 (BISH); Halawa Ahu., Moa'ula Gulch, Jacobi & Higashino 1559 (BISH); West Fork Kawela Gulch, Lammers et al. 5702 (OS); Pelekunu, Rock 6109 (A, BISH, GH, K, NY); Manuahui, Rock 6137 (BISH); Kawela Gulch, Rock 6163 (BISH, W), Rock 6176 (BISH, GH, UC); heights of Pelekunu, Rock 7032 (BISH); Pelekunu, Rock s.n. (NSW); Waikolu-Pelekunu, Rock s.n. (BISH); between Hanalilolilo & Pepeopae, St. John et al. 12587 (BISH); Kukuinui Ridge, St. John et al. 13285 (BISH, UC, US); Hanalilolilo, St. John et al. 23387 (A, BISH*); Mapulehu ridge, St. John et al. 23547 (BISH*, K*, P); Mapulehu Valley, St. John & Fosberg 12902 (BH, BISH, MIN, W); Pu'u Ali'i, St. John &
Fig. 11. Distribution of the subspecies of *Clermontia arborescens*: subsp. *arborescens* (open circles), subsp. *waihiae* (dots), and subsp. *waikoluensis* (triangles).
Williams 19927 (BISH, UC); Wawâ'ia Ahu., Kalapamo Ridge, Stemmerman & Montgomery 3956 (BISH), Stemmerman & Montgomery 3957 (BISH); Halawa Ahu., Hipuapua Str., Stemmerman & Montgomery 3957a (BISH). -- NO PRECISE LOCALITY: Hillebrand s.n. (B).

LANA'I: Munro Trail, Carlquist 2001 (BISH, RSA); Waialala Gulch, Degener 17780 (A, B, DS, MASS, MO, NY); Munro Trail, Degener et al. 24351 (NY, W); between Hulopae Gulch & Lana'ihele, Degener & Degener 28522 (A, B, BH, BISH, DS, DUKE, E, G, L, LD, M, MASS, MICH, MSC, NY, W, WIS); Hulopae Gulch, Degener & Degener 28565 (DUKE, L); Kahinahina Ridge, Degener & Degener 28571 (BH, BISH, BR, C, CHR, DS, DUKE, E, G, LD, M, MASS, MEL, MIN, MO, NSW, TI, U, UC, UPS, W, WELT, WIS, Z); Hauola Trail, Flynn 207 (BISH, PTBG); Munro Trail, Flynn 242 (OS, PTBG); mts. near Ko'ele, Forbes 44.L (BISH, MO); Lana'ihele, Krauss 963 (BISH); Munro Trail, Lammers et al. 5822 (OS), Lammers et al. 5827 (OS*), Lammers et al. 5830 (OS*); Kaibolena, Munro 21 (BISH*), Munro 132 (BISH*); Lana'ihele, Munro 210 (BISH*); Ha'alelepa'akai, Munro s.n. (BISH); Holopae-Kaibolena divide, Rogers s.n. (MICH, NY); Kaibolena-Ho'okio divide, Kaluku, St. John & Eames 18731 (BISH); Ho'okio Gulch, Spence 324 (BISH*, HLA*, L, US); Palawai, Stone 880 (BISH); Lana'ihele, Yondo s.n. (BISH, L, UC). -- NO PRECISE LOCALITY: Fagerlind & Skottsberg 6421 (S); Fagerlind & Skottsberg 6766 (S*, UPS*); Forbes 319.L (BH, BISH); Hitchcock 14648 (US); Munro s.n. (BISH).
makes no mention of the possible relationships of his novelty. The type, however, is indistinguishable from numerous specimens of *Clermontia arborescens* collected on Moloka'i and Lana'i. St. John's epithet, derived from the name of the type locality, is here transferred to subspecific rank in order to provide a name for the populations on these islands.

*Delissea fauriei* is included in synonymy with some hesitation. Previous workers (Rock 1919, Wimmer 1943, Chamberlain 1977) were unable to locate type material in any herbarium, nor have my searches been successful. The meagre diagnosis (cf. Rock 1914, Lauener & Green 1961, St. John 1980a) agrees better with *Clermontia arborescens* subsp. *waikoluensis* than with any other known lobelioid on Moloka'i. However, the possibility that the type is not even a member of Lobelioideae cannot be ruled out (Rock 1914, 1919).


**TYPE:** HAWAIIAN ISLANDS. "Kauai" [error for Waihe'e, West Maui], **Wawra 1956** (holotype: W!, photo: BISH!; isotype: W!).

Lamina 10-23 cm long, 2-6.5 cm wide; lower surface glabrous. Petiole 1.5-8 cm long, glabrous. Peduncle 0.4-1.4 cm long; pedicels 1.2-4.8 cm long. Hypanthium 1-2.2 cm long, 1-2 cm wide, glabrous. Calyx lobes deltate or shallowly triangular, 2-9(-11) mm long; apex acute, obtuse, or emarginate. Corolla 6.2-8(-8.8) cm long, glabrous;
tube 2.2-3.4 cm long, 1-2 cm wide; dorsal lobes 3.8-5.3(-6.1) cm long, (4-5-7 mm wide, obtuse or rounded at apex; trifid lip 2.5-4 cm long, (7-)8.5-12 mm wide. Filaments 4.4-5.7 cm long; anthers 1.3-2 cm long, 4.5-7 mm wide, pubescent or rarely glabrous.

Distribution. (Fig. 11). Endemic to Maui. Montane rain forests and cloud forests, from Waihe'e and Ka'anapali south to Pu'u Kukui (610-1525 m) and on the windward slopes of Haleakala (850-1825 m).

SPECIMENS EXAMINED. WEST MAUI. LAHAINA: Haela'au Cabin, Carlquist H21 (BISH, K, UC*), Carlquist 565 (RSA), Carlquist 1845 (BISH, MICH, RSA); trail to Nakalalua, Cranwell et al. 2685 (BISH, GB); Honokahua-Amalu ridge, Cranwell et al. 3925 (S), Cranwell et al. 3926 (GB); Pu'u Kukui, Crosby & Anderson 1871 (DUKE*); Haela'au, Degener et al. 25021 (BM, LE, MEL, NSW, U, W), Degener et al. 25028 (W); Hanakao'o, Forbes 45.M (BISH, CAS); Honokahau drainage basin, Forbes 449.M (BISH, P, US); Maunaho'oma, Forbes & Cook 23.M (A, BISH, DS); Pu'u Kukui trail, Harrison s.n. (BISH); Ka'anapali, Hillebrand s.n. (B); Pu'u Kukui, Hitchcock 14754 (US), Hitchcock 14794 (US); Pu'u Kukui, Munro 431 (BISH); trail to Violet Lake, Lammers & Hobdy 5688 (OS*), Lammers & Hobdy 5694 (OS*); Honokowai, Rock 8202 (BISH*, GH, MICH, NSW*, NY, P, US); Ka'anapali, Rock s.n. (W); Haela'au, St. John 10202 (BISH, F, L, M, MIN, NY, W, WELT); Pu'u Kukui, Wilbur & Webster 869 (DUKE, MICH). -- WAILUKU: Waihe'e Valley, Hillebrand s.n. (B); Lanilili, Lammers 5846 (OS*), Lammers & Sylva 5617 (OS), Lammers & Sylva 5618 (OS*), Lammers & Sylva 5623 (OS*). -- NO PRECISE LOCALITY:
Hillebrand s.n. (MEL).

EAST MAUI. MAKAWAO: ditch trail, 2 mi. from Pogue's, Bergman s.n. (BISH); Heed's Trail, Bonsey et al. H-512 (BISH, LE, U, WIS); Olinda Flume, Crosby & Anderson 1765 (BISH, DUKE*, GH, MICH, UC*); Olinda pipeline trail, Degener 7945 (BISH, CAS, CU, K, GH, MO, NY, W), Degener 7946 (BISH, MASS, NY); Waikamoi, Degener & Degener 27729 (B, BISH, BM, DUKE, G, L, MASS, NY, TI, W); Ukulele, Forbes 197.M (NSW), Forbes 928.M (BISH); Papa'aea, Forbes 2525.M (BISH, K, NY, UC); Olinda pipeline trail, Gillett 1698 (HAW, HLA); road to Waikamoi Flume, Gustafson 1104 (BISH); Waikamoi Str., Heed J27A1D (HAW); 2 mi. e. of Olinda, Henrickson 3737 (BISH, RSA, UC); Olinda pipeline, Hitchcock 14923 (US); Ukulele Camp to Waikamoi Str., Lammers 5581 (BISH, DUKE, K, OS*, PH), Lammers 5583 (OS*), Lammers 5584 (NY, OS*), Lammers 5588 (OS*); Ukulele Camp to Pu'u o Kakae, Lammers 5595 (OS, US), Lammers 5596 (OS), Lammers 5597 (OS), Lammers 5599 (OS), Lammers 5599 (OS), Lammers 5601 (B, OS*), Lammers 5602 (OS*), Lammers 5603 (OS*); road to Waikamoi Flume, Lammers & Hobdy 5629 (OS*), Lammers & Hobdy 5630 (OS*); Waikamoi Flume, Lammers & Hobdy 5648 (OS*), Lammers & Hobdy 5649 (OS*), Lammers et al. 5837 (MO, OS*, W), Lammers et al. 5839 (OS*, RSA), Lammers et al. 5840 (OS*); Waikamoi Str., Lammers & Kepler 5661 (OS*); Olinda pipeline, Lamoureux et al. 1998 (BISH); Makawao F. R., Little 31119 (NY); Olinda pipeline, Meebold 20706 (M); Makawao F. R., Montgomery & Mitchell s.n. (BISH); Kula pipeline, Munro 733 (BISH); Haleakala Ranch pipeline, Munro 734 (BISH); Waikamoi, Nagata 972 (HLA); Waikamoi, Neal & Hartt s.n. (W); Heed Trail, Ochikubo s.n. (HAW); Waikamoi, Rock 8515 (BISH,
CAS, GH, NSW, NY, W); Ke'anae trail, Rock s.n (BISH, CAS); Hamakua, Rock s.n. (NSW); Kula flume line, St. John 10325 (BISH); Kula pipeline, Skottsberg 884 (BISH, GB, S); lower Kula flume, Sohmer 6568 (BISH, NY); Ha'iku Ahu., 'Opana Gulch, Warshauer & McEldowney 2739 (BISH); Olinnda pipeline, Webster et al. 13953 (BISH, DAV, GH, MICH); Olinnda pipeline, Woolford 138 (BISH). -- HANA: Ke'anae Valley, Degener 7948 (BISH, NY); Kipahulu, Forbes 1689.M (BISH); Kaumakani Ridge, Funk 98 (HAW); Ha'iku Ahu., W. Wailuanui Str., Higashino & Holt 9054 (BISH); Ke'anae Ahu., W. Wailuanui Str., Higashino & Holt 9085 (BISH); Nahiku Ahu., Kukiwa Str., Higashino & Holt 9154 (BISH), Higashino & Holt 9165a (BISH*); between Pu'u Ahulili & Kaupo Gap, Higashino & Mizuno 2906 (BISH), Higashino & Mizuno 3012 (BISH); Kipahului F. R., Nuanualoa Str., Higashino & Mizuno 3066 (BISH), Higashino & Mizuno 3088 (BISH); Kipahulu Valley, Lamoureux & DeWreede 4046 (HAW); Kipahulu Ahu., Warshauer & McEldowney 2559 (BISH*). -- NO PRECISE LOCALITY: Meebold 28115 (M).

Delissea waihiae was named for the type locality, the village of Waihe'e (Wawra 1872-73). Wawra's statement that this locality was on Kaua'i was an error, as the only village by that name in the entire archipelago is located in northern West Maui (Rock 1919, Degener & Degener 1960a). He made an identical mistake involving another specimen collected at Waihe'e, Wawra 1955, the type of Delissea filigera (see discussion under Clermontia grandiflora subsp. grandiflora).
4c. Clermontia arborescens subsp. arborescens.


Lamina 14-20 cm long, 4-6.5 cm wide; lower surface glabrous or sparingly pubescent on the midvein. Petiole 3-6 cm long, glabrous. Peduncle 0.6-1.4 cm long; pedicels 2-4 cm long. Hypanthium 1.3-1.8 cm long, 1-1.8 cm wide, glabrous. Calyx lobes triangular, oblong, or ovate, 1.8-4 cm long; apex acute, obtuse, or rounded. Corolla 7-8 cm long, glabrous; tube 2.4-3 cm long, 1-1.5 cm wide; dorsal lobes 4-4.7 cm long, 5-7 mm wide; trifid lip 3-3.2 cm long, 0.9-1 cm wide. Filaments 5.2-5.7 cm long; anthers 1.8-2 cm long, 5-6 mm wide, glabrous or pubescent.

Distribution. (Fig. 11). Endemic to West Maui. Montane rain forests, 550-1325 m, from Iao Valley to Hana'ula.

SPECIMENS EXAMINED. WEST MAUI. LAHAINA: mauka of McGregor, Degener 22248 (B, W); Hana'ula, Hobdy 1254 (BISH*); Hana'ula, Lammers et al. 5564 (B, BISH, DUKE, NY, OS*, PH, US). -- WAILUKU: Kapilau Ridge, Bishop et al. 47110 (HAW); Iao Valley, Nakalaloa Str., Hobdy 864 (BISH*), Hobdy 914 (BISH); Waikapu Ahu., Pohakea Gulch, Warshauer & McEldowney 3154 (BISH).
The specimen used by St. John (1983) as the holotype of Clermontia mannii is the only known specimen upon which Mann (1867-68) might have based his description of Cyanea arborescens, the basionym of Clermontia arborescens. Consequently, it was designated the lectotype of Clermontia arborescens, making C. mannii its homotypic synonym (Lammers 1988b).


Shrubs or trees, 4-5 m tall, terrestrial. Lamina oblanceolate or oblong, 9-20 cm long, 2.5-5.5 cm wide, coriaceous; upper surface dark green, glabrous; lower surface pale green, glabrous or minutely muricate on the veins; margin callose-crenulate; apex obtuse; base cuneate or attenuate. Petiole 1-6 cm long, muricate. Inflorescences 2-flowered or often 1-flowered by abortion, muricate; peduncle spreading, 0.5-1 cm long, bracteate at apex; pedicels spreading, 3-5
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cm long, bibracteolate at base. Hypanthium obconic or obovoid, 1.4-1.9 cm long, 1.4-1.9 cm wide, muricate. Calyx lobes triangular, shallowly triangular, or deltate, 3-9 mm long, 3-5 mm wide, muricate; apex obtuse or acute. Corolla bilabiate, 5-7 cm long, dark rose-colored, muricate; tube suberect, 1-2 cm long, 1.2-1.8 cm wide; lobes thick, fleshy, suberect, the dorsal two 3.8-5.2 cm long, 3-5 mm wide, the ventral three 2-3 cm long, 3-5 cm wide. Staminal column exserted, suberect or curved; filaments magenta, 4.1-5.8 cm long; anthers dark purple, 1.5-2 cm long, 5.5-7.5 mm wide, glabrous or sparsely pubescent. Berries unknown, presumably muricate.

Distribution. (Fig. 12). Endemic to East Maui. Montane rain forests and cloud forests, 1650-1825 m, on the windward slopes of Haleakala.

SPECIMENS EXAMINED. EAST MAUI. MAKAWAO: Olinda pipeline, Degener 7950 (NY); Ukulele trail, Rock 12837 (BISH, L, US), Rock s.n. (BISH, CAS, GH, NSW, NY, US). -- HANA: Kaumakani Ridge, Funk 100 (HAW); Hana F. R., Harrison 256 (BISH), Harrison 426 (BISH); Hana F. R., Higashino & Holt 9301 (BISH); n. rim of Kipahulu, Harrison 288 (BISH), Harrison 413 (BISH); upper Hana F. R., Harrison 557 (BISH).

Clermontia tuberculata is closely related to C. arborescens subsp. waiaiae, differing primarily by the muricate flowers, longer ventral corolla lobes, and rose-colored corollas. The epidermal murications characteristic of this species are unique within the genus. Many
Fig. 12. Distribution of Clermontia tuberculata (triangles) and the subspecies of C. peleana: subsp. singuliflora (open circles) and subsp. peleana (dots).
species of the related genera *Cyanea* and *Rollandia* have muricate stems and leaves, but very few have muricate flowers (Carlquist 1962).

Perhaps not coincidentally, *Clermontia tuberculata* is wholly sympatric with one of these, *Cyanea aculeatiflora* Rock. The latter is closely related to *Cyanea macrostegia* Hillebr. subsp. *macrostegia*, differing primarily in characters similar to those separating *Clermontia arborescens* from *C. tuberculata*: muricate flowers and longer ventral corolla lobes. Because *Clermontia tuberculata* and *Cyanea aculeatiflora* are wholly sympatric and belong to radically different lineages, one might speculate that their muricate flowers represent parallel evolutionary responses to floral predation by some phytophagous insect endemic to windward Haleakala.

The specimens segregated by St. John (1978) as var. *subtuberculata* have fewer murications, but are otherwise identical to typical *Clermontia tuberculata*. For this reason, that name is treated as a synonym of *Clermontia tuberculata*. 
IC. Clermontia series Unilabiatae Lammers, ser. nov. -- TYPE:

Clermontia peleana Rock.

A seriebus aliis Clermontiae corolla unilabiata tubo arcuato 4-6 cm longo et lobis deflexis 4-5plio longiore, lobis calycis 1-4 mm longis, et staminibus connatis erectis vel erectiusculis exsertissimis differt.

Shrubs or trees, 1.5-7 m tall, terrestrial or epiphytic. Lamina oblong or elliptic, 5-20 cm long, 3-5 cm wide, coriaceous, glabrous; upper surface glossy; margins callose-crenulate; apex acute, acuminate, or cuspidate; base cuneate or obtuse, rarely rounded. Petiole (1.5-)3-8 cm long, terete, glabrous. Inflorescences 2-flowered or 1-flowered by abortion; peduncle spreading, 0.8-3 cm long; pedicels spreading, 0.5-4.5 cm long. Hypanthium hemispheric or obconic, 0.9-1.5 cm long, 1-1.5 cm wide, glabrous or rarely pubescent. Calyx lobes triangular, shallowly triangular, or deltate, 1-4 mm long, 0.5-4 mm wide; apex acute to acuminate. Corolla unilabiata, 5-7.2 cm long, green or purple; tube arcuate, 4-6 cm long, 0.5-1.3 cm wide; lobes curved downward, 1-2 cm long, 2-4 mm wide, 1/4-1/5 as long as the tube. Staminal column strongly exserted, erect or suberect; filaments purple or white, 4.8-6.3 cm long; anthers purple or white, 1.4-1.8 cm long, 3.5-4.5 cm wide. Berries subglobose, 2.5-3.5 cm long, 2.5-3.5 cm in diameter.
The two species of this series, Clermontia fauriei and C. peleana, differ from the other species of sect. Clermontioideae by their unilabiate corollas with downcurved lobes much shorter than the arcuate tube and strongly exserted erect or suberect staminal column. The name of the series is derived from the Latin adjective unilabiatus, one-lipped, in reference to the distinctive corolla.


Shrubs or trees, 1.5-6 m tall, epiphytic. Lamina oblong or elliptic, 8-20 cm long, 3-5 cm wide, coriaceous, glabrous; upper surface dark green, glossy; lower surface green sometimes suffused with purple, dull; margin callose-crenulate; apex acute, acuminate, or sometimes nearly cuspidate; base cuneate, obtuse, or almost rounded. Petiole 3-6 cm long, glabrous. Inflorescences 2-flowered or sometimes 1-flowered by abortion, glabrous; peduncle spreading, 0.8-1.7 cm long, bibracteate at middle or apex; pedicels spreading, 3-4.5 cm long, 2-5 times longer than peduncle, bibracteolate near base. Hypanthium hemispheric or obconic, 1-1.5 cm long, 1-1.5 cm wide, glabrous. Calyx lobes triangular, 1-2 mm long, 0.5-1 mm wide; apex acute or acuminate.
Corolla unilabiate, 5-7.2 cm long, dark purple and glossy or rarely greenish white and dull, glabrous; tube arcuate, 4-6 cm long, 0.8-1.3 cm wide, narrower at middle than at base; lobes downcurved, 1-2 cm long, 2-4 mm wide. Staminal column strongly exserted, erect or suberect; filaments dark purple or rarely greenish white, 4.8-6.3 cm long; anthers dark purple or rarely greenish white, 1.7-1.8 mm long, 3.5-4.5 mm wide, glabrous or sparsely pubescent along sutures and near apex. Berries orange, subglobose, 2.5-3 cm long, 2.5-3 cm in diameter.

This species commemorates Pele, the volcano goddess of Hawaiian mythology. As originally circumscribed, it comprised only plants of the windward slopes of Mauna Loa in Puna District with dark purple pigmentation in the corollas and leaves. *Clermontia singuliflora*, found once on the windward slopes of Mauna Kea in Hamakua District, has green flowers but otherwise is almost identical. The two species were distinguished by Rock (1919) on the basis of differences in peduncle and pedicel lengths, leaf size, and corolla color. Study of additional specimens not available to Rock, including purple-flowered plants from the windward slopes of Mauna Kea in Hilo District, indicates that the only consistent differences separating the two are the pigmentation of the corolla and leaves. Because the purple-flowered and green-flowered populations are allopatric, they are treated here as conspecific subspecies.
KEY TO THE SUBSPECIES OF CLERMONTIA PELEANA

1. Corolla green or greenish white, dull; lower surface of lamina green.
   6a. C. peleana subsp. singuliflora.

1. Corolla dark purple, glossy; lower surface of lamina suffused with purple, especially on the veins.
   6b. C. peleana subsp. peleana.


Lamina 10-14 cm long, 3.5-5 cm wide; lower surface green suffused with purple; apex acute to acuminate; base cuneate. Petiole 3-5 cm
long. Peduncle 0.8-1.2 cm long; pedicels 3-4 cm long. Corolla 5-5.5 cm long, greenish white, dull; tube 0.8-1.2 cm wide. Berries unknown.

Distribution. (Fig. 12). Montane rain forests, windward slopes of Haleakala on East Maui and Mauna Kea on Hawai‘i.


Clermontia singuliflora sensu Rock (1919) included only the type specimen collected on the windward slopes of Mauna Kea in Hamakua District, Hawai‘i. Virtually identical plants from windward Haleakala on East Maui were treated by St. John (1973) as Clermontia clermontioides var. barbata. These plants differ from populations of Clermontia fauriei (C. clermontioides, misapplied) by their broader (8-13 mm vs. 5-8 mm) corolla tube, wider at the base than at the middle; pedicels 2-5 times longer than (vs. about as long as) the peduncle; and longer (1.7-1.8 cm vs. 1.4-1.5 cm) anthers. In these features, however, they are identical to Clermontia peleana as here circumscribed. Because they lack the dark pigmentation characteristic of subsp. peleana, they are assigned to subsp. singuliflora.

The holotype of Clermontia gaudichaudii var. barbata, the basionym of C. clermontioides var. barbata, was destroyed in 1943. Because no duplicates are known, the name is typified here on the basis of Rock’s photograph of the holotype deposited at BISH. Both var. barbata and
the later Clermontia clermontioides var. maulensis (Hochreutiner 1934) were based explicitly on the unnamed C. gaudichaudii var. of Hillebrand (1888). Consequently, they are homotypic, and var. maulensis, as the later of the two, is superfluous and illegitimate.

This subspecies is presumed extinct. The only known specimen from Hawai'i was collected in 1909, and the most recent specimen from Maui was collected in 1920.

6b. Clermontia peleana subsp. peleana.

Lamina 13-20 mm long, 3-5 cm wide; lower surface green suffused with purple, especially on the veins; apex acuminate or nearly cuspidate; base cuneate, obtuse, or almost rounded. Petiole 4-6 cm long. Peduncle 1.4-1.7 mm long; pedicels 3-4.5 cm long. Corolla 5-7.2 cm long, dark purple, glossy; tube 0.9-1.3 cm wide. Berries subglobose, 2.5-3 cm long.

Distribution. (Fig. 12). Endemic to Hawai'i. Montane rain forests, 530-1150 m, on windward slopes of Mauna Kea and Mauna Loa. Epiphytic on Metrosideros polymorpha Gaudich. (Myrtaceae), Acacia koa A. Gray (Fabaceae), and other large trees.

SPECIMENS EXAMINED. HAWAI'I. NORTH HILO: Opea Ahu., Opea-Peleau Homesteads, Warshauer 1575 (BISH). -- SOUTH HILO: Saddle Rd., 14 mi. from Hilo, Carquist 611 (RSA); Hilo, Fairie 577 (A, BM, GO, P); Wailuku
R., *Flynn* 478 (PTBG); 'Ola'a Flume, *Forbes* 653.H (BISH, GB, M, NY, P); Halelouolu to Wailuku R., *Forbes* 720.H (BISH); Hilo, *Hillebrand* 91b (K); Wailuku R., 12 mi. w. of Hilo, *Lammers et al.* 5780 (K, MO, NY, OS); Saddle Rd., *Rock* s.n. (BISH, K); Saddle Rd., 14 mi. from Hilo *Shipman* s.n. (BISH); Wailuku R., *Wagner et al.* 4867 (BISH); Pi'ihonua Ahu., fork of Wailuku R. & Waipahoeahoe Gulch, *Warshauer* 1586 (BISH).

--- **PUNA:** Volcano Rd., 23 Miles, *Lindsey* s.n. (BISH, RSA); Glenwood, Rock 12846 (BISH, L), *Rock* s.n. (BISH, NY, US); Kilauea, *Rock* s.n. (A).

Rock (1919) stated that *Clermontia peleana* existed strictly as an epiphyte. All subsequent collections likewise have been made from epiphytic individuals. It is doubtful, however, that this species is an obligate epiphyte. More likely, this species formerly occurred terrestrially and epiphytically, as do most rain forest species of *Clermontia*. Terrestrial individuals may have been extirpated by naturalized herbivores, while the inaccessible epiphytes survived in their tree-top refugia. This subspecies is extremely rare and on the verge of extinction, with perhaps two extant populations known.


*Clermontia clermontioides* var. *epiphytica* Hochreutiner, *Candollea*
Shrubs or trees, 2-7 m tall, terrestrial or epiphytic. Lamina oblong or elliptic, 5-17 cm long, 1.5-7 cm wide, coriaceous, glabrous; upper surface dark green, glossy; lower surface pale green, dull; margin callose-crenulate; apex acute, acuminate, or cuspidate; base cuneate or obtuse. Petiole 1.5-8 cm long, glabrous. Inflorescences 2-flowered or commonly 1-flowered by abortion, glabrous or rarely pubescent; peduncle spreading, 0.8-3 cm long, bibracteate at apex; pedicels ascending, 0.5-3 cm long, equalling the peduncle, bibracteolate at or near base. Hypanthium hemispheric or obconic, 0.9-1.5 cm long, 1-1.1 cm wide, glabrous or rarely pubescent. Calyx lobes deltate or shallowly triangular, 2-4 mm long, 2-4 mm wide, distinct; apex acute or acuminate. Corolla unilabiate, 6-7 cm long, green sometimes suffused with purple externally, pale greenish-white or cream-colored within, glabrous or pubescent; tube arcuate, 4.2-5.8 cm long, 5-8 mm wide, of equal width from base to middle; lobes downcurved, 1.2-1.8 cm long, 2-4 mm wide. Staminal column strongly exserted, erect or suberect; filaments greenish-white or cream-colored,
4.8-5.5 cm long; anthers cream-colored, 1.4-1.5 cm long, 3.5-4.5 mm wide, glabrous or minutely pubescent. Berries orange or yellow, subglobose, 2.5-3.5 cm long, 2.5-3.5 cm wide.

Distribution. (Fig. 13). Montane rain forests, 365-1400 m, Kaua'i and O'ahu.

SPECIMENS EXAMINED. KAUA'I. HANALEI: Powerline Rd., Darwin 1136 (PTBG, US), Darwin 1145 (GH, K, PTBG, US); Hanalei Valley, Fagerlind & Skottsberg 6542 (S), Fagerlind & Skottsberg 6543 (GB, S, UPS); powerline trail, Fay & Perlman 215 (F); Waioli Valley, Forbes 121.K (BISH, BM, MICH, RSA); Pole Line trail, Herbst & Bishop 2466 (BISH); Wai'ale'a', Hitchcock 15482 (US); powerline trail, MacDaniels 706 (BISH); Wai'ale'a', Rock 5062 (BISH). -- KOLOA: Wahiawa Bog, Crosby & Anderson 1501 (BISH, DUKE, GH, MICH); n. of Wahiawa, Degener 7854 (A); between Alexander Dam & Wahiawa Bog, Fagerlind & Skottsberg 6482 (S, UPS); Wahiawa Bog, Flynn et al. 22 (PTBG); Kahili, Flynn 274 (PTBG); Wahiawa Mts., Forbes 298.K (BISH); Wahiawa Bog, Gillett & Stauffer 1537 (HLA); between Hanapepe & Wahiawa Rivers, Heller 2704 (F, UC, US); trail to Kahili, Lammers et al. 5865 (OS); Wahiawa Str., Lamouseroux 1506 (HAW); Wahiawa Ahu., Long et al. 1632 (HAW), Long et al. 1634 (HAW); Kalaheo Ahu., sw. of Kahili, Nagata 2098 (HLA), Nagata 2100 (HLA), Nagata 2101 (HLA); Kahili, Rock s.n. (BISH, RSA); trail to Kahili bog, St. John & Fosberg 13575 (BISH, W); Wahiawa Str., Stauffer et al. 5871 (A, BISH, DUKE, G, HAW, K, L, RSA, UC, US); Wahiawa Bog, Stern & Carlquist 1330 (BISH, RSA, US), Stern & Herbst 2941A (PTBG, RSA);
Fig. 13. Distribution of Clermontia fauriei.
Wahiawa Bog, Stone 782 (BISH, US), Stone 1651 (BISH). -- WAIHEA:
Alaka'i Swamp, Balgooy 4200 (BISH, OS); Alaka'i Swamp, Baxter s.n. (MO); Pihea, Carlquist 509 (RSA); Alaka'i Swamp, Carlquist 1773 (RSA);
Kalalau, Carlson 3751 (CAS, F); Wai'ale'ale trail, Chock 990 (BISH);
Ka'awako'o, Chock & Cliff 1162 (PTBG); Lehumakanoe, Cranwell et al. 2904 (BISH, GB, S); trail to Kilohana, Croat 44957 (MO, PTBG, US);
Alaka'i Swamp trail, Crosby & Anderson 1477 (BISH, DUKE, GH, MICH, UC);
Waimea Swamp, Degener 7855 (A, NY); Koke'e, Degener 7856 (NY);
Lehumakanoe, Degener & Degener 27726 (BISH), Degener et al. 23948 (W);
Kalalau Lookout, Degener & Greenwell 21636 (B, BISH, W), Degener &
Hatheway 20455 (A, BISH, BM, NY, W); Mohihi, Degener & Greenwell 21636a (B, W), Degener & Greenwell s.n. (B); Alaka'i Swamp, Degener &
Greenwell 21727 (B, BISH, MASS, NY, W); between Koke'e & Kawaikoi Str.,
Fagerlind & Skottsberg 6590 (S); Pihea trail, Flynn 276 (PTBG), Flynn
704 (OS); Kaholuamanu, Forbes 358.K (BISH, UC), Forbes 411.K (BISH,
US); Waimea drainage basin, Forbes 899.K (BISH), Forbes 1139.K (BISH);
Alaka'i Swamp trail, Gagne s.n. (UC); Kalalau Ridge, Gillett 1661
(HLA); Koai'e-Waialeaie trail, Heed J8A2P (HAW); Kalalau Lookout to
Alaka'i Swamp, Herat & Herat 295 (B, BISH); Kalalau Lookout, Herbst
1039 (BISH, HAW, HLA, L, US); Wainiha pali, Higashino & Crivellone 9648
(BISH), Higashino & Crivellone 9650 (BISH); Koai'e Str., Higashino &
Crivellone 9677 (BISH); Kaholuamanu, Hitchcock 15428 (US);
Koai'e-Waialeaie trail, Kaneshiro G83B1P (HAW); Halemanu to Kaholuamano,
Kusche 47 (A, CAS); Pihea to Kilohana, Lammers et al. 5369 (OS);
Kaholuamanu, Lydgate s.n. (BISH); Koke'e, Meebold 26373 (BISH, M);
Koke'e-Alaka'i Swamp, Richardson & Bowles 46 (HAW); Kaholuamanu, Rock 2428 (BISH), Rock 2499 (BISH), Rock 5954 (BISH, GH), Rock 12793 (BISH); Alaka'i Swamp, Rock s.n. (BM, RSA); Waiakealoha, Rock s.n. (NSW); Waimea, Rock s.n. (BISH, CAS, NY); Pihea, St. John 26745 (BISH); Alaka'i Swamp trail, Sleumer 4523 (L); Kawaikoi Str., Stone 3372 (BISH, L); Lehuamakanoe, Takeuchi Alaka'i-143a (BISH); trail to Kawaikoi Str., Takeuchi Alaka'i-165b (BISH); Kaluapuhi trail, Wichman & Chock s.n. (BISH). -- NO PRECISE LOCALITY: Forbes s.n. (NY); Knudsen s.n. (BISH); Rock s.n. (W); Wawra 2043 (LE, W); Wawra 2189 (W).

O'AHU. WAI'ANAE MTS.: ridge e. of central Makaleha Valley, Ozaki 1568 (BISH), Ozaki 1569 (BISH), Ozaki 1570 (BISH). -- KO'OLAU MTS.: head of Koloa Gulch, near Laie, Degener 20397 (B, BISH, BM, NY, W).

For many years, the sole species of Clermontia on Kaua'i was called C. clermontioides (Gaudich.) A. Heller or its illegitimate synonym, C. gaudichaudii Hillebrand. Both names are based on Delissea clermontioides Gaudich. However, the type of the basionym was not collected on Kaua'i, nor does it match plants growing on Kaua'i. Rather, it was collected in the Kona District of Hawai'i and represents the plant that has been called Clermontia coerulea Hillebrand for the past century (Lammers 1988b). The Kona plant must take the name Clermontia clermontioides, while the next available name for the species on Kaua'i is Clermontia fauriei. The latter commemorates Pere Urbain Jean Faurie (1847-1915), a Catholic missionary who collected in the Hawaiian Islands in 1909-10 (Rock 1914, Lauener 1980).
Hochreutiner (1934) examined Gaudichaud's specimens of Delissea clermontioides, but failed to realize that they were not collected on Kaua'i. Because Gaudichaud's material differed significantly from his own specimen collected on Kaua'i, he described the latter as a new variety, Clermontia clermontioides var. epiphytica. Although it is indeed quite different from true Clermontia clermontioides of Hawai'i, it differs in no significant way from the plants of Kaua'i (cf. Skottsberg 1944). Consequently, it is treated as a synonym of Clermontia fauriei.

Clermontia clermontioides var. hirsutiflora also is placed in synonymy. Rock (1957) distinguished it by the densely pubescent corolla. Although this character is very distinctive, it varies within populations, making it impossible to recognize meaningful subspecies on this basis.

Two additional varieties have been described from the easternmost islands of the archipelago: Clermontia gaudichaudii var. barbata Rock (including its illegitimate homotypic synonym, C. clermontioides var. mauiensis Hochr.) from Maui, and C. gaudichaudii var. singuliflora Rock from Hawai'i. Both are characterized by having a broader corolla tube, longer pedicels, and longer anthers than the Kaua'i plants. In these features, however, they are identical to Clermontia peleana of Hawai'i. The latter name is transferred to subspecific rank under Clermontia peleana, and the former is treated as its heterotypic synonym.

With the exclusion of these varieties from Maui and Hawai'i, the published distribution of Clermontia fauriei is restricted to Kaua'i
(Rock 1919, St. John 1973). However, in 1950, Otto Degener discovered a population on O'ahu, in the western portion of the Ko'olau Mountains. Six years later, Earl Ozaki made a second collection on O'ahu, this time in the western portion of the Wai'anae Mountains. The species has not been collected on O'ahu since that time. This is the first published report of these specimens, which are morphologically indistinguishable from plants on Kaua'i.
II. Clermontia sectio Clermontia — TYPE: Clermontia oblongifolia Gaudich.

Shrubs or trees, (0.4-)1-9 m tall, terrestrial or epiphytic. Lamina oblong, elliptic, or oblanceolate, (4-)10-20(-26) cm long, (1.5-)2-5.5(-9.8) cm wide, coriaceous, chartaceous, or rarely membranaceous, glabrous or pubescent; upper surface glossy or dull; margin callose-crenulate; apex acute, acuminate, or obtuse, rarely rounded or cuspidate; base cuneate or attenuate, rarely obtuse. Petiole (0.2-)2-7(-13.5) cm long, terete, green and opaque or rarely yellowish-white and translucent. Inflorescences 2(-10)-flowered; peduncle spreading, rarely deflexed or pendent; (0.3-)1-5(-12) cm long; pedicels spreading, rarely ascending or pendent, (0.3-)1-3(-7) cm long. Hypanthium hemispheric, obconic, obovoid, or turbinate, rarely oblong, (0.5-)0.7-1.5(-2.2) cm long, (0.3-)0.5-1.5(-2.2) cm wide. Perianth bilabiate, rotate, or tubular, (1.5-)3.5-6.5(-8.5) cm long, purple, green, white, rarely magenta or rose-colored, with calyx lobes mimicking the corolla in size, shape, connation, color, and texture; tube erect, suberect, curved, or arcuate, (0.5-)1-4.6(-5.7) cm long, (0.3-)0.8-1.5(-2) cm wide; lobes suberect, spreading, or recurved, (1-)1.9-3.2(-4.2) cm long, (0.9-)2-5(-7) mm wide. Staminal column included or exserted, erect, suberect, curved, or arcuate; filaments purple, magenta, white, or rarely rose-colored, (1.7-)2.5-5.5(-8.4) cm
long; anthers purple or white, (0.6-1-1.5(-2) cm long, 
(1.8-)3-4.5(-5.5) mm wide. Berries subglobose, rarely ellipsoid, 
oblance, obovoid, or obconic, (1.2-)2-3(-4) cm long, (0.9-)2-3(-4) cm in 
diameter, smooth, or rarely with 10 longitudinal ridges.

The remaining 15 species of the genus are distinguished from 
Clermontia sect. Clermontioideae (and all other Lobelioidae) by their 
"double-flowered" perianth, in which the calyx lobes are deciduous, as 
long as the corolla (rarely only 2/3 its length), connate for 1/5-4/5 
their length, and mimic the corolla in color, shape, and texture. 
Because such calyx lobes are unique in the family, Clermontia sect. 
Clermontia is regarded as a derived monophyletic lineage.

This section has been called "Clermontiae genuinae" (Hillebrand 
1888: 239), "section Clermontiae genuinae" (Rock 1919: 308), and 
"sectio Genuinae" (Wimmer 1943: 81). Because all three violate Article 
21.1 and/or 22.1 of the Code (Voss et al. 1983), they are not validly 
published (Article 32.1), are not names in the technical sense (Article 
6.6), and have no status under the Code (Article 12.1). The correct 
name for this section is the autonym, Clermontia sect. Clermontia, 
because it includes the type of the genus. This name was first used by 
Wimmer (1968), but was created automatically by Hillebrand's (1888) 
valid publication of "Clermontioideae" as an infrageneric group of 
unspecified rank.
IIA. Clermontia series Dupliciflorae Lammers, ser. nov. — TYPE:

Clermontia kakeana Meyen.

A seriebus aliis Clermontiae lobis calycis connatis deciduis aequantibus corollam longitudine et colore, perianthio bilabiato lobis patentibus aequantibus vel superantibus tubum erectiusculum vel curvatum longitudine, et staminibus connatis inclusis vel subexsertis differt.

Shrubs or trees, 1-7 m tall, terrestrial or epiphytic. Lamina oblong, elliptic, or oblanceolate, 7-26 cm long, 1.5-6.5 (-9.8) cm wide, coriaceous, chartaceous, or rarely membranaceous; upper surface dull or rarely glossy; apex acute, acuminate, obtuse, rarely rounded or cuspidate; base cuneate or attenuate. Petiole (1.5-)2—7(-13.5) cm long, glabrous or pubescent, green and opaque or rarely yellowish-white and translucent. Inflorescences 2(-7)-flowered, peduncles spreading or rarely deflexed (0.3-)1.2—5(-12) cm long; pedicels spreading or rarely ascending, (0.3-)1-3.5 cm long. Perianth bilabiate, 3.8-6.5 cm long, green, purple, or white; tube suberect or gently curved, 0.8-3.6 cm long; lobes spreading, 1.9-4.2 cm long, 2-7 mm wide, equalling or exceeding the tube in length. Staminal column included or slightly exserted, suberect or gently curved; filaments purple, magenta, or white, 2.5-5.2 cm long; anthers purple or white, 1-2 cm long, 2.5-5.5 cm wide. Berries subglobose, rarely ellipsoid or obovoid,
The name of this series is derived from the Latin words *duplex*, double, and *flos*, flower, in reference to both the distinctive "double-flowered" perianth and 2-flowered inflorescences. Though not restricted to these species, these two features are most obvious among *Dupliciflorae*. This series is distinguished by its bilabiate perianth with spreading lobes equalling or exceeding the tube in length and the included or slightly exserted staminal column. The series divides rather naturally into two subgroups: (1) species of O'ahu, Moloka'i, and Maui (one species extending to Hawai'i) with the perianth white, cream-colored, or pale green within (*Clermontia kakeana*, *C. lindseyana*, *C. pallida*, and *C. persicifolia*; and (2) plants of Hawai'i with the perianth dark purple within (*C. drepanomorpha*, *C. kohalae*, and *C. montis-loa*). Although these two groups could be recognized as subseries, I prefer not to base supraspecific taxa, even of relatively minor rank, on a single character. In any event, use of three infrageneric categories in a genus of just 22 species seems excessive.

8. *Clermontia kakeana* Meyen, Reise 2: 139. 1835. *Lobelia kakeana*  
-- TYPE (here designated): HAWAIIAN ISLANDS. O'ahu: near the Tantalus/Pauoa Flats trail junction, 20 Jan 1984, Takeuchi Ko'olau-56b (neotype: BISH!#).

-- TYPE (here designated): HAWAIIAN ISLANDS. "Iles Sandwich" [O'ahu, Ko'olau Mountains above Honolulu, Oct 1836], Gaudichaud 144 (lectotype: PI; isolectotypes: P[4]!).


Clermontia macrocarpa var. cymosa Hillebrand, Fl. Hawaiian Isl. 241. 1888. -- TYPE: HAWAIIAN ISLANDS. O'ahu: slopes of Ka'ala, Hillebrand s.n. (holotype: B, destroyed!, photo: BISH!).


Clermontia montis-loa f. molokaiensis F. Wimmer in Engler,
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Shrubs or trees, 1-6 m tall, terrestrial or epiphytic. Lamina elliptic, oblanceolate, or broadly oblanceolate, 12-26 cm long, 3.5-9.8 cm wide, chartaceous, dull; upper surface green, glabrous; lower surface pale green, glabrous or pubescent; margin callose-crenulate; apex obtuse, acute, acuminate, or cuspidate; base cuneate or attenuate. Petiole 1.9-7 cm long, glabrous or pubescent. Inflorescences 2(-7)-flowered, glabrous or sparsely pubescent; peduncle spreading, 1.2-5.6 cm long, bibracteate at apex; pedicels spreading, 1-2.5 cm long, bibracteolate at or below middle. Hypanthium hemispheric or
obovoid, 0.8-1.4 cm long, 0.8-1.4 cm wide, glabrous or sparsely pubescent. Perianth bilabiate, 4.5-5.5 cm long, pale green or very rarely rose-colored externally, greenish-white, white, or cream-colored within, glabrous or sparsely pubescent; tube suberect or curved, 1.8-3.4 cm long, 0.8-1.4 cm wide; lobes spreading, 1.9-2.8 cm long, 2.5-4.2 mm wide. Staminal column included or slightly exserted, suberect or gently curved; filaments magenta or rarely white, 2.7-3.8 cm long; anthers dark purple or rarely white, 1.1-1.4 cm long, 3-4.5 mm long, glabrous. Berries orange, subglobose or oblong, 1.8-3.4 cm long, 1.5-3.4 cm in diameter. Chromosome number $n = 14$.

Distribution. (Fig. 14). Montane rain forests in the Wai'anae Mountains (365-1060 m) and Ko'olau Mountains (245-610 m), O'ahu; Moloka'i (565-1100 m); West Maui (610-1070 m); and on the windward slopes of Haleakala (120-1270 m), East Maui (120-1270 m).

SPECIMENS EXAMINED. O'AHU. WAI'ANAE MTS.: Wai'anae firebreak, Campsall A-4 (HAW); Pu'u Pane, Carr et al. 992 (HAW*); Pu'u Kanehoa & Kalua'a Gulch, Darwin 1042 (GH, PTBG, US); Schofield firebreak trail, Degener et al. 7884 (BISH, CAS, CU, GH, MO, NY, US); Hale'au'au Gulch, Degener & Caindec 20891 (A, B, BH, BISH, BM, G, K, M, MASS, MICH, MIN, NSW, NY, UC, US, W); Makaha Valley, Forbes s.n. (DS, WELT); Pu'u Hapapa, Lamoireux 1559 (HAW, L); Ka'ala, Selling 3546 (BISH, GB, S); Pu'u Kaua, Suehiro s.n. (BISH); Ka'ala, Suehiro s.n. (BISH); Pu'u Hapapa, Takeuchi & Shimabukuro 2775 (F); Ka'ala, Topping 2877 (NY, UC); Wai'anae'uka, Webster 1523 (MICH, NY, US); Wai'anae'uka, Wilbur 672
Fig. 14. Distribution of Clermontia kakeana.
(DUKE*, NY); Ka'ala, Yunker 3480 (F). — KO'OLOAU MTS.: Tantalus, Abbe et al. 10076 (A, L, NY); Wa'ahila Ridge, Anderson 66-27 (HLA); Waimano trail, Bailey s.n. (BH); Wa'ahila Ridge, Balgooy & Stuessy 4117 (OS*); Pupukea-Kahuku, Baxter s.n. (MO); Pacifique Hts., Bryan 380 (BISH); Wahiawa, Bryan s.n. (BISH); Kipapa Gulch, Bryan et al. s.n. (BISH*); Wa'ahila Ridge, Carlquist 1605 (BISH, DUKE, GH, K, L, MICH, RSA, UC, Z); Tantalus trail, Carlquist 1711 (BISH, GH, L, MICH, RSA); Kalihi Valley, Christophersen 1267 (BISH, WIS); Pu'u 'Ua'u, Christophersen s.n. (BISH); Kuli'ou'ou, Christophersen et al. s.n. (BISH); ridge to Konahuanui, Christophersen et al. 1731 (BISH); Kaunala-Waimea, Cowan 513 (BISH, G); Pu'ulu'u trail, Cowan 1022 (BH, F); Pauoa Flats to Konahuanui, Crosby & Anderson 1371 (BISH, DUKE*, GH, MICH*); Wa'ahila Ridge, Crosby & Anderson 1736 (DUKE); Manoa Cliff trail, Darwin 1090 (GH, K, PTBG, US); 'Opa' eula Gulch, Davis s.n. (IA); Manoa Valley, Degener H85 (MASS, NY); Tantalus, Degener 7831 (CU, K, MO, NY), Degener et al. 7890(1d) (GH, MASS, MICH, MO, NY, S, UC, US), Degener 7922 (NSW); Pauoa Flats, Degener 7849 (G); Pupukea-Kahuku, Degener 7883 (L), Degener 7926 (BISH, CAS, CU, K, MICH, MO, NY), Palolo Crater, Degener 7885 (MASS, NY, UC, US); Manoa Valley, Degener et al. 11380 (A, B, US); 'Aiea, Degener et al. 11536 (A, B, BISH, LE, MASS, MO, NY, US, W); Red Hill & Piko trail, Degener 17783 (BISH, DS, MASS, NY, PH, UC, US); Paumalu-Waimea ridge, Donaghho s.n. (BISH); Pauoa Valley, Eubank 106 (UC); Ka'au Crater, Eubank 162 (UC); Kalihi, Faurie 583 (A, BM, G, F); Pauoa Flats, Forbes 2 (BISH, US); Moanalua Valley, Forbes 1185 (BISH, W), Forbes s.n. (MO*); Hillebrand's Glen, Forbes 1285.0 (BISH); Nu'uanu
Valley, Forbes 1499.0 (BISH, W); Tantalus, Forbes 1665.0 (BISH, L, WELT); ridge e. of Kuli'ou'ou Iki, Forbes 2011.0 (A, BISH); Kalihi Valley, Forbes s.n. (BH, BISH*, M, P, UC, US); Wai'alae Iki, Forbes s.n. (NSW*); Waiolani, Forbes s.n. (BISH); Waimano Ridge, Forbes & Lake 1979.0 (BISH); Kalihi Valley, Forbes & Lobouchere 2296.0 (BISH);
Lanihuli trail, Forbes & Stokes s.n. (BISH); Kalihi Valley, Garber 115 (BISH, W); Tantalus, Garber 337 (BISH); Kuapa Pond, Gillespie 1091 (BISH, US); Kohana-Waikana divide, Gillett et al. 1331 (BISH, L);
Schofield-Waikane trail, Gillett 1465 (HLA); Tantalus, Gillett 1486 (HLA); Moanalua Ridge, Gosline 139 (HAW); Kipapa Gulch, Grant 7090 (BISH), Grant 7278 (BISH); Wa'ahila Ridge, Gupta 54 (HAW); Tantalus, Heller 2059 (A, AC, BISH, BM, CU, E, F, G, GH, K, L, LE, MICH, MIN, MO, MSC, NY, P, PH, UC, US, Z); Wa'ahila Ridge, Herat & Herat 338 (B, BISH, HAW); Ka'au Crater, Herbst & Bishop 951 (HAW*); Pauoa Valley, Hillebrand 78 (K); Manoa-Pauoa, Hillebrand s.n. (BM); Kipapa Gulch, Hosaka 146 (BISH*, CAS*, GH), Hosaka 529 (K, L, NSW); Kipapa Gulch, Hosaka 839 (BISH); Manoa Valley, Kerr s.n. (BISH); Kawai Iki trail, Kitamura s.n. (HAW); Pupukea-Kahuku trail, Krauss s.n. (BISH*);
Manoa-Palolo ridge, Krauss s.n. (BISH); Kahauiki-Kalihi ridge, Kuykendahl 86 (BISH); Manoa Cliffs trail, Lammers 5325 (OS*); Wai'alae Iki-Wai'ula ridge, Lamoureux 130 (HAW); 'Aiea trail, Lamoureux 159 (HAW); Tantalus, Lamoureux 1440 (HAW); Pupukea, Lamoureux 1490 (HAW);
Roundtop trail, Lee 10 (HAW); Konahuanui-Olympus trail, MacDaniels 142 (BISH); Palolo, MacDaniels 471 (BH); Kawai Iki ditch, MacMahon 6 (HAW); Tantalus, Nagata 52 (HLA); Wa'ahila Ridge, Nagata 77 (HLA); Ka'au
Crater, Newell 109 (CAS), Newell 112 (CAS); Waimea-Malaekahana, Ozaki 401 (BISH); Manoa, Meebold 20464 (M); Poamoho trail, Meebold 21225 (M); Punalu'u, Nakata 17 (BISH); Tantalus, Neal & Douglas 444 (CU); Pu'u Lanipo, Nishida s.n. (BISH); Konahuanui, Nishimoto s.n. (BISH); Tantalus, Octavio s.n. (BISH); Pauoa Valley, Rock 711 (BISH), Rock 713 (NSW), Rock 1047 (BISH), Rock s.n. (NSW, NY, US); Waianu Valley, Rock 1199 (BISH, GH, W); Halemano, Rock 8723 (BISH, GH, NSW*), Rock s.n. (NY, US); Wahiawa, Rock 8725 (BISH, GH, NSW), Rock s.n. (BISH, CAS, NY); Waikakalaua, Rock 12839 (BISH), Rock s.n. (BISH); 'Aihualama, Russell 110 (BISH); Kipapa Gulch, St. John 9977 (BISH); Pu'u Lanihuli, St. John 11200 (BISH); Ha'i ku Valley, St. John 12268 (BISH); Waimano trail, St. John 20199 (BISH); Waikakalaua Gulch, Shaw s.n. (BISH); Manoa Cliffs trail, Shigematsu & Char KS1 (HAW); Tantalus, Skottsberg 62 (BISH, GB, S); Manoa Valley, Skottsberg 243 (BISH, GB), Skottsberg 350 (GB, S); Manoa Cliffs trail, Sohmer 6109 (BISH); Manoa Cliffs, Steenis 20432 (L); Peahinaia Ridge, Stemmermann & Higashino 1259 (BISH*); Kahawainui Gulch, Stone 1236 (BISH); Pupukea, Stone 2814 (BISH), Stone 3657 (BISH, L); Ka'au Crater, Stone 3494 (BISH), Stone 3495 (BISH); Tantalus, Stone et al. 3517 (BISH); Pupukea, Suwanaijut s.n. (HAW); Tantalus/Pauoa Flats trail jct., Takeuchi Koolau-56a (GB); Tantalus, Tessene & Wagner 1734 (WIS*); Manoa Cliffs trail, Thorne 33369 (RSA); Olympus, Topping 3078 (UC); Manoa Cliffs trail, Topping 3093 (MO, UC); Upper Palolo, Topping 3178 (UC, US); Punalu'u, Webster 1587 (MIN); Kahawainui-'Ihi'ihi, Welch s.n. (BISH, W); Punalu'u trail, Wilbur 729 (DUKE*, W); Waimano Valley, Wong s.n. (BH); Wa'ahila Ridge,
Yamashita 63 (DUKE); Tantalus, Yoshihaga s.n. (BISH); Tantalus trail, Young 33 (HAW). -- NO PRECISE LOCALITY: Forbes s.n. (BISH); Gaudichaud 146 (P); Gaudichaud 149 (P); Hillebrand 75 (K); Hillebrand s.n. (GH, MEL, US); Hillebrand & Lydgate s.n. (BISH); Kelly 217 (CAS); Kelly s.n. (CAS); Macrae s.n. (GH); Mann & Brigham 232 (BISH, CU, G, GH, MASS, MO, NY, US); Mann & Brigham s.n. (BISH, CU); Rock 8724 (BISH); Rock 12838 (BISH); Rock s.n. (GH); Wawra 1658 (W); Wawra 2246 (G, LE, W).

MOLGA'AI. Kamoku Flats, Crosby & Anderson 1629 (BISH*, DUKE*, GH, MICH*); Maunahui, Degener 7826 (NY), Degener 7834 (B, BISH*, CAS, CU, DS, GH, MASS*, MICH, MO*, S*, US, WIS); Kainalu, Degener & Murashige 20162 (MO, NY, W); Kalae, Forbes 32.Mo (BISH, UC, US); Puko'o, Mr. Conradt's place, Hitchcock 15032 (US); Kahanui Ahu., Kikiakala, Jacobi 1418 (BISH); Puniu'ohua Ahu., Kahawai Iki Gulch, Jacobi et al. 1574 (BISH); Kalua'aha Ahu., Mauna'olu'olu Ridge, Jacobi & Higashino 1523 (BISH); Waialua Ahu., Moaula Gulch, Jacobi & Higashino 1572 (BISH); Waikolu Valley, Kondo s.n. (BISH); road to Hanalilolilo, Lammers et al. 5695 (B, OS*); Kahanui Ahu., Pu'u Kaeo, Lamoereux 1986 (HAW); Mapulehu, Rock 7038 (BISH, GH, NSW); N. Halawa-S. Halawa ridge, St. John 24700 (BISH); Honomuni, St. John 25191 (US); Mapulehu Valley, St. John & Fosberg 12869 (BISH, DS); Kalua'aha, Stemmerman et al. 826** (HAW); Wawa'ia Ahu., Kua Gulch, Stemmerman & Montgomery 3900 (BISH); Halawa Ahu., Kaunupahu, Stemmerman & Montgomery 3959 (BISH); Kaunakakai Ahu., road to Kamakou Preserve, Wagner et al. 4926 (BISH*); Kahanui Ahu., Waikolu Valley rim, Warshauer & MoEldowney 2361 (BISH); Pelekunu Ahu., Kolo Ridge, Warshauer & MoEldowney 3029 (BISH). -- NO PRECISE
LOCALITY: Stokes s.n. (BISH).

WEST MAUI. LAHAINA: Pu‘u Kukui, Bishop 47013 (HAW*); Haela‘au cabin, Carlquist 566 (RSA), Carlquist 1846 (RSA); Honokahua-Amalu ridge, Cranwell et al. 2769 (BISH*, GB, S); Haela‘au makai, Degener et al. 25027 (A, BM, C, G, LE, MICH, NSW, UPS, W); Honokohau Valley, Degener et al. 25029 (BM, G, LE, MEL, MICH, NSW, U, W); Paupau Ridge, Degener & Murashige 20022 (B, MO, NY, W); Haela‘au, Fagerlind & Skottsberg 6688 (UPS, S); Honokohau-Amalu ridge, Fagerlind & Skottsberg 6688b (S*); Honokahau drainage basin, Forbes 396.M (BISH, DS, M, US, WELT); Olowalu Valley, Forbes 2251.M (BISH); Maunaho‘oma, Forbes & Cook 34.M (A, BISH); Pu‘u Kukui, Hitchcock 14793 (US), Hitchcock 14795 (US); Pu‘u Kukui, Munro 420 (BISH); Pu‘u Kukui, Munro 616 (BISH, NY). --

WAILUKU: Kapilau Ridge, Bishop et al. 47102 (HAW*); 'Eke, Degener 7944 (AC, BISH, CAS, CU, DUKE, GH, MASS, MICH, MO, NY, US, W, WIS), Degener 7949 (BISH, GH, K, L, NY, US); Keahikauo, Degener 7953 (BISH); Iao Valley, Degener 17142 (A, NY, PH, UC); Makamaka'ole Str., Degener et al. 21138 (LE*, W); Iao Valley, Faurie 596 (P); Lanilili, Lammers 5845 (OS*), Lammers & Sylva 5614 (OS*, WIS), Lammers & Sylva 5621 (OS*). --

NO PRECISE LOCALITY: Curran s.n. (K, US); Wawra 1816 (W).

EAST MAUI. -- MAKAWAO: Kailua, Degener 17141 (A, CU, MICH, MO, PH, US); Kula pipeline, Forbes 1289.M (BISH, L, W); Olinda pipeline, Hitchcock 14928 (US); road to Waikamoi Str., Lammers & Hobdy 5627 (MO, OS*, RSA), Lammers et al. 5842 (B, OS*); Waikamoi Str., Lammers & Kepler 5651 (OS*); Olinda, Munro 478 (BISH), Munro 651 (BISH); Kula pipeline, Munro 735 (BISH); Honomanu ditch trail, Rock 8815 (BISH, GH);
Kailua, Rock s.n. (BISH); Kula Pipeline, Sohmer 5567 (BISH). -- HANA:
Pua'a Ka'a St. Pk, Crosby & Anderson 1800 (BISH, DUKE*, GH, MICH*, MO, RSA*, UC); 'O'opoua Str., Degener 7951 (BISH); Ke'anae Valley, Degener 7952 (BISH, MO); Kupau Valley, Degener 22082 (B, BISH, MASS, NY, W);
Hana Hwy., 30 mi. from Hana, Henrickson 3729 (BISH, NSW, RSA, UC); Hana Hwy., 16 mi. from Hana, Nagata 2666 (BISH, HLA); Hana Hwy., Herbst 859 (BISH, HAW, L), Herbst 1992 (PTBG); Pa'a kea Ahu., Hanawi Str., Higashino & Holt 9383 (BISH); Hana Hwy., 16 mi. from Hana, Ishikawa 169 (HLA); Pua'a Ka'a St. Pk., Lammers 5555 (NY, OS*, US, W), Lammers 5557 (OS*), Lammers 5558 (BISH, DUKE, K, OS*, PH), Lammers 5561 (OS*), Lammers et al. 5853 (OS*); Kipahulu Valley, Lamoureux & de Wreede 4047 (BISH); Hana Hwy., Nagata 2666 (BISH, HLA); Honomanu Ditch, Rock 8815 (L); Kaukauai Gulch, St. John & Catto 17806 (BISH); Ka'a lea Gulch, Webster et al. 13960 (BISH, DAV, GH). -- NO PRECISE LOCALITY:
Hillebrand s.n. (K).

Clermontia kakeana was named for the type locality, a small peak in the eastern Ko'olau Mountains of O'ahu called Pu'u Kakea (Meyen 1835, Degener & Degener 1958a). Rock (1919) was unable to locate original material, but Wimmer cited a specimen collected by Meyen and deposited at Berlin. This sheet was destroyed in 1943. Because no other original material has been located, a neotype must be designated. The specimen chosen was collected in the general vicinity of Pu'u Kakea, matches the brief diagnosis well, and is meticulously prepared.

The types of Clermontia macrocarpa var. cymosa and C. macrocarpa var. rosea also were destroyed during the war, and no duplicates are
known. Fortunately, Rock photographed these types prior to their destruction, and the prints deposited at BISH may stand as the types. The former was distinguished by its 5-7-flowered inflorescence. Such prolificous inflorescences appear to represent phenotypic rather than genotypic variation, as the number of flowers per inflorescence typically varies within an individual. The latter variety was distinguished by its pale rose perianth. Such plants occur sporadically (e.g., Stemmerman & Higashino 1259, BISH), but do not merit formal recognition.

Both Clermontia macrocarpa and C. macrophylla were based upon typical specimens of C. kakeana (Rock 1919, Wimmer 1943). They were published almost simultaneously by authors who were unaware of Meyen's earlier publication. Valid publication of the former was effected by a plate in the folio atlas illustrating plants collected during the voyage of the Bonite (Gaudichaud s.d.). No accompanying text was ever prepared (Stafleu & Cowan 1976). Several specimens of Clermontia kakeana collected by Gaudichaud on the voyage of the Bonite are deposited at P: five sheets labelled 144, two labelled 146, and a single sheet labelled 149. One of these must be designated as the lectotype. Gaudichaud 146 bears an unpublished manuscript name in Gaudichaud's handwriting. Gaudichaud 149 bears no identification; it was found in a folder of undetermined specimens. Two of the sheets of Gaudichaud 144 are labelled Clermontia macrocarpa in Gaudichaud's handwriting. Pencil sketches matching the plate in the atlas are attached to one of these. This sheet is designated here as the
lectotype. The other four sheets of that number are considered isolectotypes. All these specimens were presumably collected on O'ahu, in the Ko'olau Mountains above Honolulu. The Bonite's only other port-of-call in the Hawaiian archipelago (Lasegue 1845) was Kealakekua Bay, Hawai'i, where this species does not occur.

Leaf width and corolla pubescence vary considerably in Clermontia kakeana, with a general trend toward narrower leaves and more pubescent corollas on Moloka'i and Maui. Degener and Degener (1958a) distinguished plants of Moloka'i as Clermontia kakeana var. forbesii, named in honor of botanist Charles Noyes Forbes (1883-1920). This variety differed from the typical by its longer, narrower leaves. Wimmer (1968) segregated Clermontia kakeana f. gracilis of East Maui on the basis of its longer petioles, peduncles, and pedicels, and longer more slender corollas. St. John (1971) distinguished Clermontia kakeana var. orientalis, also of East Maui, by its pubescent perianth. However, the numerical phenetic analyses clearly showed that the patterns of variation in these and other features, both within and among populations, are such that it is not possible to recognize meaningful subspecies. Consequently, these three names are treated as synonyms. The numerical analyses also demonstrated that St. John's (1987) recently described novelties from East Maui, Clermontia glabra and C. mauliensis, as well as Wimmer's (1968) C. montis-loa f. molokaiensis also differ in no discernible way from Clermontia kakeana as circumscribed here.

During field studies on West Maui in July 1984, an unusual
Clermontia was encountered on the southwestern slopes of Lanilili, at 700 m, just above a small bog. Clermontia grandiflora subsp. grandiflora and C. micrantha grew in the bog, while C. arborescens subsp. waihiae and C. kakeana occurred in the surrounding forest. This unusual individual (Lammers & Sylva 5619, OS) bore only unopened buds, but in general resembled Clermontia micrantha in its low stature, rose-colored flowers, and leaves suffused with purple. However, the buds were already as large as or larger than fully expanded flowers on nearby individuals of Clermontia micrantha. A search of the area disclosed no additional plants of similar morphology. This individual was relocated in July 1985, at which time flowers were in full anthesis (Lammers 5847**, BISH, OS, US). Not only were they twice as large as those of Clermontia micrantha, the perianth was also more or less bilabiate with spreading lobes and the staminal column was less exserted. In typical Clermontia micrantha, the perianth is rotate with reflexed lobes and the staminal column is strongly exserted. This unique individual appears to be the product of hybridization between Clermontia kakeana and C. micrantha. Morphologically, it is intermediate between the putative parents and probably represents an F₁. Examination of fixed microsporocytes from this individual (Lammers 1988a) showed no meiotic abnormalities.

Occas. Pap. Bernice Pauahi Bishop Mus. 22: 43. 1957. -- TYPE:
HAWAIIAN ISLANDS. Hawai'i: 2 miles west of Pu'u 'O'o Ranch,
6000 ft, 5 Apr 1957, legit Stephens, Rock 25900 (holotype:
BISH!; isotype: BISH! W!).

Clermontia lindseyana var. livida Rock, Occas. Pap. Bernice Pauahi
Bishop Mus. 23: 69. 1962. -- TYPE: HAWAIIAN ISLANDS. Hawai'i:
Mauna Kea, Shipman Ranch, Pu'u 'Akala, east slope, 6000 ft, Jan
1958, legit Lindsey, Rock 26029 (holotype: BISH!; isotypes: A!
B[2]! BISH! K[2]! L[2]! NSW! W!).

TYPE: HAWAIIAN ISLANDS. Hawai'i: N. Hilo Distr., Laupahoehoe
Ahu., east slope of Mauna Kea, southwest of Ha'akoa Stream,
Hilo Forest Reserve, ca. 5510 ft, 9 Aug 1977, Warshauer et al.
1289 (holotype: BISH!).

TYPE: HAWAIIAN ISLANDS. Hawai'i: Makakupu, legit Conant,
Jacobi 630 (holotype: BISH!).

Shrubs or trees, 2.5-6 m tall, terrestrial. Lamina oblanceolate
or elliptic, 13-24 cm long, 3.8-6.5 cm wide, coriaceous, dull; upper
surface dark green, glabrous or sparsely pubescent along midrib; lower
surface light green sometimes suffused with purple, pubescent; margin
callose-crenulate; apex acuminate, acute, or obtuse; base attenuate.
Petiole 2.5-7 cm long, pubescent. Inflorescences 2-flowered,
pubescent; peduncle spreading, 2.5-4 cm long, bibracteate at or near
apex; pedicels spreading, 1-2.5 cm long, bibracteolate at apex or middle. Hypanthium hemispheric or obovoid, 1.2-2 cm long, 1-2.2 cm wide, pubescent. Perianth bilabiate, 5.5-6.5 cm long, green rarely tinged purple outside, white or cream-colored within, pubescent; tube gently curved, 2.2-3 cm long, 0.9-1.8 cm wide; lobes spreading, 2.6-3.8 cm long, 3-5 mm wide. Staminal column included or slightly exserted, suberect or gently curved; filaments white or cream-colored, 3-4.5 cm long; anthers white, 1.7-2 cm long, 3.5-4 mm wide, glabrous. Berries orange, subglobose, 2.5-4 cm long, 2.5-4 cm in diameter.

Distribution. (Fig. 15). Montane rain forests and subalpine forests, 1220-1825 m, windward Haleakala on East Maui, and windward Mauna Kea and windward and leeward Mauna Loa on Hawai'i.

SPECIMENS EXAMINED. EAST MAUI. HANA: above Pu'u Pani, Forbes 1888.M (BISH, CAS, P, UC, US); s. slopes, Haleakala, Rock 8688 (BISH, GH, NSW).

HAWAI'I. NORTH HILO: Pu'u '0'o, Rock s.n. (A, BISH). -- SOUTH HILO: Pu'u Akala, Carquist 2122 (RSA); makai of Kulani Prison, Degener & Greenwell 21837 (B, BISH, MASS, NY); above Hakalau, Lindsey 25758 (BISH); Pu'u 'Akala, Rock 26030 (BISH); Makahanaloa Ahu., Kapue Str., Warshauer 1464 (BISH). -- KA'U: Keauhou Ranch, Clarke 689 (BISH); Keauhou Ranch, Davis & Cuddihy 887 (BISH); Kilauea F. R., Herat et al. 1004 (HAW); Kahuku, road to Nene Cabin, St. John 26798 (BISH, L); Kilauea F. R., Spatz 439 (HAW). -- SOUTH KONA: Kapua mauka, Degener et al. 34736 (GB, MO, NY); Kukuiopae Ahu., Warshauer & McEldowney 2022
Fig. 15. Distribution of Clermontia drepanomorpha (triangles) and C. lindsayana (dots).
Clermontia lindseyana commemorates Thomas Lindsey, an amateur botanist who brought the species to Rock's attention. It is most similar morphologically to Clermontia kakeana, differing by its coriaceous leaves, larger flowers, and longer anthers. Rock (1957, 1962) also considered it to be similar to Clermontia hawaiensis, a species of ser. Clermontia with the lamina glossy on the upper surface; hypanthium glabrous, longitudinally-ridged; perianth tubular, glabrous, with longitudinally ridged lobes shorter than the tube; and berries obovoid or ellipsoid, longitudinally ridged.

Previously, this species was believed to be endemic to Hawai'i (Wimmer 1968, St. John 1973). The two specimens from East Maui cited above were identified by St. John (1971) as somewhat atypical representatives of Clermontia kakeana var. orientalis. However, on the basis of their coriaceous densely pubescent leaves, larger more densely pubescent flowers, and longer anthers, they are identified here as Clermontia lindseyana. The species is probably extirpated from East Maui, as the most recent specimen was collected in 1920.

Rock (1962) segregated plants with purple pigmentation on the lower surface of the lamina as Clermontia lindseyana var. livida. This character varies within populations, and so does not merit formal recognition. Two of St. John's (1987) recent novelties from Hawai'i, Clermontia albimontis and C. viridis, are indistinguishable from C. lindseyana. The latter of the two should not be confused with an
herbarium name used by Gaudichaud but never validly published (cf. Gray 1861, Rock 1919).

St. John (1973) inadvertently listed this species as "Cyanea lindseyana", a mistake copied by Fosberg and Herbst (1975). This combination was never validly published, as neither author made any reference to the basionym nor its place of publication. Clearly, this was simply a typographic error, and not an intentional transfer to another genus.


Shrubs or trees, 2-6 m tall, terrestrial or epiphytic. Lamina
elliptic or oblanceolate, 7-16 cm long, 1.5-4 cm wide, coriaceous, glabrous; upper surface dark green, glossy; lower surface pale green, dull; margin callose-crenulate, sometimes revolute; apex acute, obtuse, or rounded, rarely acuminate; base cuneate or attenuate. Petiole 2-7 cm long, glabrous. Inflorescences 2(-6)-flowered, glabrous; peduncle spreading, 0.6-3 cm long, bibracteate at or below middle; pedicels spreading, 1.2-3 cm long, bibracteolate at or near base. Hypanthium hemispheric, obconic, or oblong, 0.7-1.2 cm long, 6-8 mm wide, glabrous. Perianth bilabiate, 4.8-6 cm long, white sometimes tinged green or purple, glabrous; tube suberect or gently curved, 2.2-3.6 cm long, 5-8 mm wide; lobes spreading, 2-3.2 cm long, 2-3 mm wide. Staminal column somewhat exserted, suberect or gently curved; filaments white, 3.8-5.2 cm long; anthers white, 1-1.4 cm long, 2.5-4 mm wide, glabrous. Berries yellow or orange, subglobose, 1.7-3 cm long, 1.8-3 cm in diameter.

Distribution. (Fig. 16). Endemic to O'ahu. Montane rain forests in the Wai'anae Mountains (730-850 m) and Ko'olau Mountains (300-850 m). Reported from Lana'i by Rock (1919) and Wimmer (1943) on the basis of Hitchcock 14643 (US). Degener and Degener (1956b) suggested that this sheet was actually collected on O'ahu and was mislabelled. Instead, it is a correctly labelled but misidentified specimen of Clermontia grandiflora subsp. munroi.

SPECIMENS EXAMINED. O'AHU. WAI'ANAE MTS.: Mauna Kapu-Palikea trail, Beauchamp 1297 (RSA); Palikea, Cowan 666 (G); Ka'alal, Degener
Fig. 16. Distribution of *Clermontia persicifolia* (dots), *C. pallida* (open circles), *C. multiflora* (open triangles), and *C. micrantha* (closed triangles).
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12197 (W); Palehua-Palikea trail, Degener 19278 (NY); Pu'u Kaua, 
Degener & Obata 28080 (NY, US); Mokuleia, Forbes 1815.0 (A, BISH, K, 
NY, P, US); Pu'u Kalena, Grant 7377 (BISH); between Makaleha & Makaha 
Valleys, Hatheway 496 (W); Palikea trail, Herat & Herat 416 (BISH); 
Ka'ala, Hillebrand s.n. (K); Ka'ala & Wailua, Hillebrand & Lydgate s.n. 
(BISH); Palikea, Rogers s.n. (NY); Waianae'uka, Rogers s.n. (NY); 
Palawai Gulch, Russ s.n. (BISH); Ka'ala, Selling 3544 (GB, K, S); 
Palehua Iki, Skottsberg 296 (GB, S); Mokuleia trail, Wilbur 407 (BH, 
DUKE). -- KO'OLAU MTS.: Pupukea-Kahuku trail, Baxter s.n. (MO); 
Waikane trail, Carlquist 579 (RSA); Wiliwilinui Ridge, Carlquist 1754 
(BISH, RSA); Kipapa Gulch, Chang s.n. (BISH); N. Halawa Valley ridge, 
Char et al. s.n. (HAW); Pupukea-Kahuku trail, Christophersen 1379 
(BISH, L, NSW); Ewa F. R., Christophersen & Wilder 1614 (BISH); Ka'au 
Crater, Corn s.n. (BISH); Wiliwilinui Ridge, Cowan 592 (BISH); Halawa 
Ridge, Cowan 965 (F, NY); Wiliwilinui Ridge, Crosby & Anderson 1522 
(BISH, DUKE); Waialae Valley, Degener H84 (GH, MASS, NY); Waioili, 
Degener 4247 (L); Palolo Crater, Degener 7886 (A); Pupukea-Kahuku, 
Degener 7821 (A, B, NY), Degener 7887 (A, CAS, CU, GH, MASS, MICH, MO, 
NY, US, W, WIS), Degener & Hatheway 20719 (PH, W), Degener et al. 7918 
(K, MO, NY) Degener et al. 11925 (B, L, S, W), Degener et al. 24102 
(BM, C, LE, MEL, U, W); S. Halawa Gulch, Degener et al. 7901 (MICH, MO, 
NY); Middle Halawa Ridge, Degener et al. 11374 (NSW, W); Kipapa trail, 
Degener et al. 11375 (W); Pig-God trail, Punalu'u, Degener et al. 11376 
(W); Peahinaia trail, Degener et al. 12785 (B, DS, MO, NY, PH, UC); 
Wiliwilinui Ridge, Degener et al. 19712 (B, NY, W, WIS); Paumalu mauka,
Degener et al. 27978 (B, BM, C, G, L, M, MSC, TI, U, UC, W, WIS, Z); Black Jct., Degener & Carroll 20545 (BM); Poamoho trail, Degener & Degener 27438 (DUKE); 'O'io Str., Degener & Degener 30178 (B, L, MASS, MICH, NY, RSA, Z); Wilhelmina Rise Ridge, Degener & Park 7911 (GH, K, MASS, NY, US); Ka'au Crater, Rubank 167 (UC); Nu'uanu trail, Forbes & Janowsky 1941.0 (BISH); Waimanu Ridge, Forbes & Lake 1992.0 (A, BISH); Waiolani Ridge, Forbes s.n. (BISH); Halawa Ridge, Fosberg 13843 (BISH, F, PH); Castle Trail, Fosberg & Hosaka 13955 (BISH); Palolo Crater, Garber 282 (BISH), Garber 391 (BISH, NY); Kahuku F. R., Gerrish 7 (HAW); Kipapa Gulch, Grant 7075 (BISH); Wiliwilinui Ridge, Gupta 115 (HAW); Kipapa Gulch, Hasegawa s.n. (BISH, NSW); Pu'u Lanipo, Hatheway & Hess 91 (F); Waiolani, Heller 2391 (A, AC, BM, E, F, G, GH, K, L, MICH, MIN, MO, MSC, NY, P, PH, UC, Z); Ka'au Crater, Herbst & Bishop 950 (HAW); Wai'alepuepe, Hillebrand & Lydgate s.n. (BISH); Kau'ula-Pahipahialua divide, Hirayama s.n. (NY); Waikane, Hosaka 289 (BISH); Kipapa Gulch, Hosaka 517 (BISH), Hosaka 562 (BISH); Kawaiola F. R., Hosaka 2503 (BISH); head of Poamoho Gulch & Punaluu Gulch, Hosaka & Fosberg 1890 (BISH); Castle Trail, Hosaka & Fosberg 1902 (BISH, US); Kawaiinui Gulch, Hosaka & Fosberg 1909 (BISH); between Castle & Laie trails, Kerr 234 (BISH); Mau'umae Ridge, Lammers & Imada 5543 (OS, RSA, W, WIS), Lammers & Imada 5546 (DUKE, K, MO, OS, PH); Wai'alae Nui Ridge, Lammers & Kama 5485 (BISH, OS, US); Kalawao-Halawa ridge, Lamoureux 171 (HAW); Pupukea, Lamoureux 1487 (HAW), Lamoureux 1489 (HAW); Halawa trail, Lamoureux 1497 (HAW); Kipapa Gulch, Liu s.n. (BISH, K, L); Pupukea trail, Lyon et al. s.n. (BISH); Waipi'o-Waiawa ridge, MacDaniels 29
(BISH); Lanihuli, MacDaniels 157 (BISH); Poamoho trail, Meebold 21223
(M); Wainake trail, Meebold 21318 (M); Pupukea trail, Nakamoto 9 (HAW);
Kawailoa-Punalu'u trail, Neal & Hartt s.n. (BISH); Ka'au Crater, Newell
110 (CAS); Malaekahana Str., Ozaki 402 (BISH); Waikane-Schofield trail,
Ozaki 1143 (BISH); Waimea-Malaekahana, Ozaki 1396 (BISH); Punalu'u,
Rock 698 (BISH), Rock 700 (BISH); Palolo Valley, Rock 12791 (BISH, M),
Rock s.n. (CAS, GH); Wai'alae Iki-Wai'upea divide, Rogers s.n. (NY);
Waikakalaua Gulch, St. John 10468 (BISH, L); Paumalu, St. John 11100
(BISH, L, NY, US, WELT); Kahuku, St. John 11101 (BISH, UC); Pu'u
Peahinaia, St. John 11120 (BISH, K, L, NSW); Pu'u Lanihuli, St. John
11201 (BISH); Pu'u Kamana, St. John 11663 (BISH, UC); Kipapa Gulch,
Selling 2608 (GB); Wiliwilinui Ridge, Shinohara 247 (BISH); Palolo
Crater, Skottsberg 891 (BISH, GB); Pupukea, Stone 2813 (BISH), Stone
3654 (BISH); 'Opae'ula Ridge, Suehiro s.n. (BISH); Waikane-Schofield
trail, Suehiro s.n. (BISH); Black Jct., Swanholm s.n. (PH); Wai'alae
Nui Ridge, Takeuchi Koolau-184b (HAW); Mau'uma Ridge, Takeuchi
Koolau-198c (HAW), Takeuchi 2354 (BISH), Takeuchi 2362 (BISH); Paumalu
mauka, Takeuchi et al. 2167 (BISH); Laie, Takeuchi et al. 2204 (BISH, GB);
Wahiawa, Takeuchi et al. 2368 (BISH), Takeuchi et al. 2369 (BISH);
'Aiea, Takeuchi & Pyle 2268 (BISH); Lanipo trail, Topping 3157 (A, UC);
Kahana, Tsuji s.n. (BISH); Paumalu, Wong s.n. (DS). -- NO PRECISE
LOCALITY: Gaudichaud 148 (P); Gaudichaud s.n. (G); Hillebrand s.n.
(MEL); Remy 307 (P); Wawra 2206 (G, LE, W).
**Clermontia persicifolia** is morphologically most similar to *C. pallida*, but differs by its coriaceous lamina with upper surface dark green and glossy, opaque green petioles, white perianth with narrower lobes, and white staminal column. Its leaves are nearly indistinguishable from those of **Clermontia oblongifolia** subsp. **oblongifolia**, a member of ser. **Clermontia**. The latter differs by its broader hypanthium, tubular arcuate perianth with lobes much exceeding the wider tube, flower buds rounded or obtuse at apex, curved staminal column, and longer anthers.

Original material of **Clermontia persicifolia** could not be located by either myself or Rock (1919) or Wimmer (1943). The two Gaudichaud specimens cited above were collected in 1836, during the voyage of the Bonite, seven years after the publication of **Clermontia persicifolia**. Gaudichaud lost over half of his collections when the Uranie foundered near the Falkland Islands (St. John & Titcomb 1983). Possibly, this species was among those lost, and the description and plate were prepared from his notes and sketches. In any event, a neotype must be designated. The protologue contained no indication of the locality at which this species was collected. However, the Uranie's only port-of-call on O'ahu, where the species is endemic, was Honolulu (Lasegue 1845, St. John & Titcomb 1983). Presumably, Gaudichaud encountered it somewhere in the Ko'olau Mountains above the harbor. The specimen designated as the neotype was collected in this same general region, and is a tolerable match for Gaudichaud's plate and brief description. Furthermore, the specimen is complete and well
prepared, with several duplicates available for distribution to major herbaria.

In the protologue of Clermontia persicifolia, Gaudichaud (1826-30) listed "Lobelia cleromontiana" as a synonym. Under current provisions of the Code (Voss et al. 1983), names published only as synonyms are not validly published (Article 34.1), are not even names (Article 6.6), and simply do not exist (Article 12.1). Gaudichaud (1826-30) also published similar synonyms in Lobelia L. for Clermontia grandiflora and C. oblongifolia. However, these two combinations subsequently were validated by Endlicher (1836).

St. John (1939b) distinguished Clermontia epiphytica from its supposed closest relative, C. micrantha, by its narrowly oblanceolate leaves dark green above with green veins, petioles 4-6 cm long, 2-3-flowered peduncles 1-1.5 cm long, pedicels 1.5-2 cm long, perianth and staminal column white or greenish-white, and greenish or brownish berry 0.9-1.1 cm in diameter. It is indeed very different from Clermontia micrantha in these features, but virtually identical to C. persicifolia. As noted by Skottsberg (1944) and Degener and Degener (1956b), the type (cited above) and paratype (St. John 10468, BISH) are specimens of Clermontia persicifolia with immature fruit. This conclusion was subsequently accepted by St. John (1973), who reduced Clermontia epiphytica to synonymy.
TYPE (here designated): HAWAIIAN ISLANDS. Moloka'i, 1870,
Hillebrand s.n. (lectotype: K1; isolectotypes: GH! NSW! USI).
Lobelioid. 319. 1919. -- TYPE: HAWAIIAN ISLANDS. Moloka'i:
Wai'ale'ia and Waihanau, Rock 13116 (holotype: BISH!).
Clermontia oblongifolia f. glabra H. St. John, Nord. J. Bot. 3:
545. 1983. -- TYPE: HAWAIIAN ISLANDS. Moloka'i: Hanalilolilo,
head of Waikolu Valley, valley w. of tunnel on pipeline trail,
3900 ft, 19 Dec 1948, St. John et al. 23383 (holotype: BISH; isotypes: BISH[2]!).

Shrubs or trees, 2-5 m tall, terrestrial or epiphytic. Lamina
oblong, elliptic, or oblanceolate, 7-15 cm long, 2-4.5 cm wide,
membranous, dull, glabrous; upper surface pale green; lower surface
very pale green; margin callose-crenulate; apex acuminate or cuspidate;
base cuneate. Petiole yellowish-white, translucent, 5-13.5 cm long,
glabrous. Inflorescences 2(-7)-flowered, glabrous or pubescent;
peduncle spreading, 0.8-2.7(-5) cm long, bibracteate at or near apex;
pedicels spreading, 1.4-2.3(-3) cm long, bibracteolate at or near apex.
Hypanthium hemispheric, 0.7-1 cm long, 0.7-1 cm wide, glabrous.
Perianth bilabiate, 4.5-6 cm long, dark purple or dark magenta
externally, pale greenish-yellow within, glabrous; tube gently curved,
2.4-3.2 cm long, 0.7-1 cm wide; lobes spreading, 2-3.2 cm long, 3-4.5
cm wide. Staminal column included or slightly exserted, gently curved;
filaments dark purple, 3.8-5.2 cm long; anthers dark purple, 1.2-1.4 cm long, 3-4 mm wide, glabrous. Berries unknown.

Distribution. (Fig. 16). Endemic to Moloka'i. Montane rain forests, 915-1390 m.

SPECIMENS EXAMINED. MOLOKA'I. Hanalilolilo, Carlquist 2217 (BISH, BM, C, CHR, DUKE, E, F, G, GH, L, LE, MICH, RSA, UC, WIS, Z); Wailau Ridge, Cranwell 3430 (GB); Waikolu Valley, Cranwell et al. 2522 (BISH, GB, K, S); Hanalilolilo, Crosby & Anderson 1688 (BISH, DUKE); Waikolu Valley, Degener & Toussay 22134 (BISH); Pelekunu pali, Fagerlind & Skottsberg 6346 (UPS); Kamalo, Faurie 579 (A, BM, G, P); Pu'u Kolekole, Forbes 156.Mo (BISH); Puko'o, Forbes 277.Mo (BISH); Wailau pali, Forbes s.n. (BISH, K, W); Waikolu Lookout, Gillett & Carlquist 1960 (HLA); Kamalo, Hitchcock 15102 (US); Pu'u Kauwa trail, Ishikawa 133 (HLA); Hanalilolilo trail, Jacobi 1417 (BISH); Kawela Ahu., Pepeopae-Pelekunu trail, Jacobi & Higashino 1401 (BISH); Hanalilolilo, Nagata 2683 (HLA); Hanalilolilo, Lammers et al. 5696 (OS), Lammers et al. 5697 (K, MO, OS, US); Hanalilolilo, Lamoureux 44 (HAW); Kahanui Ahu., Pu'u Kaeo, Lamoureux 1984 (BISH); Wai'ale'a pali, Rock 14034 (A, BISH); Mapulehu, Rock s.n. (A); Hanalilolilo, St. John et al. 12378 (BISH); between Hanalilolilo & Pepeopae, St. John et al. 12602 (BISH, W); Wawa'ia Ahu., Kalapamo Ridge, Stemmerman & Montgomery 3870 (BISH); Honomuni Ahu., Kawaiuliuli, Stemmerman & Montgomery 3944 (BISH); between Hanalilolilo & Pepeopae, Wagner et al. 4936 (BISH); Wailau Ahu., Oloku'i, Warshauer & McEldowney 2955 (BISH); Wailau Ahu.,

This species differs from all other species of Clermontia by its membranaceous leaves and distinctive petioles. The latter are yellowish-white, almost chlorotic in appearance, and quite translucent, like the stems of Pilea pumila (L.) A. Gray (Urticaceae). Both character states are unique among Hawaiian Lobelioideae.

Because the specimen designated as the lectotype by Rock (1919: 319) was destroyed in 1943, one of the isolectotypes is here designated to replace it.

Stunted plants growing in exposed windswept situations were segregated by Rock (1919) as Clermontia pallida var. ramosissima. Because this variation appears to be environmentally induced, such plants do not warrant taxonomic recognition.

St. John (1983) distinguished Clermontia oblongifolia f. glabra from C. oblongifolia f. mauliensis by its oblanceolate leaves, shorter peduncles, and maroon and green perianth. However, the type of this novelty also differs from all other specimens of Clermontia oblongifolia by its translucent yellowish-white petioles and bilabiate perianth with suberect tube equalling the spreading lobes. In these features, however, it is a perfect match for Clermontia pallida.
   TYPE: HAWAIIAN ISLANDS. Hawai‘i: gulches back of Kohala, 1500
   ft, Jul 1910, Rock 8810 (holotype: BISH!, photos: BISH[2]!;

Clermontia kohalae var. robusta Rock, Coll. Hawaii Publ. Bull. 2:
   41. 1913. -- TYPE: HAWAIIAN ISLANDS. Hawai‘i: Kohala, Jul
   1910, Rock 8811 (holotype: BISH!; isotypes: BISH! GH!).

Clermontia leptoclada var. holopsila F. Wimmer in Engler,
   Pflanzenr. IV.276b (106. Heft): 82. 1943. -- TYPE: HAWAIIAN
   ISLANDS. Hawai‘i: Kohala, e. slopes of Pololu Valley, 11 Aug
   1926, Degener 2186 (holotype: BISH!; isotypes: A! BISH!
   NY[2]!).

Clermontia paradisia F. Wimmer in Engler, Pflanzenr. IV.276b (107.
   Heft): 761. 1953. -- TYPE (designated by Wimmer in Degener &
   Degener 1956c): HAWAIIAN ISLANDS. Hawai‘i: Kohala, ditch trail
   west of Kaukini Cabin, 18 Feb 1952, Degener 21880 (lectotype:
   WI; isoleptotypes: B! W!). = Hybrid between C. kohalae and C.
   parviflora.

Clermontia leptoclada var. urceolata Rock, Occas. Pap. Bernice
   Pauahi Bishop Mus. 22: 39. 1957. -- TYPE: HAWAIIAN ISLANDS.
   Hawai‘i: Kohala, Parker Ranch, Kehena Ditch, 915 m, 20 Mar
   1957, Rock 25737 (holotype: BISH!; isotypes: BISH[2]! K! W!).

Clermontia convallis F. Wimmer in Engler, Pflanzenr. IV.276c (108.
   Heft): 827. 1968. -- TYPE: HAWAIIAN ISLANDS. Hawai‘i: Kohala,
   e. slopes of Pololu Valley, 11 Aug 1926, Degener 2186
TYPE: HAWAIIAN ISLANDS. Hawai'i: Kohala Mts., above Middle Camp on trail to Kaukiini, Honokane Canyon, 28 Jun 1966, G. Gillett 1917 (holotype: BISH; isotypes: HLA! US!).

Trees, 2-6 m tall, terrestrial or epiphytic. Lamina narrowly elliptic or oblanceolate, 10-21 cm long, 2-5.5 cm wide, chartaceous, dull; upper surface green, glabrous; lower surface pale green, glabrous or sparsely pubescent; margin callose-crenulate; apex obtuse, acute, or acuminate; base attenuate. Petiole 2-6 cm long, glabrous. Inflorescences 2(-4)-flowered, glabrous or pubescent; peduncle spreading, 1.5-4.5 cm long, bibracteate at middle or apex; pedicels spreading, 1.5-3.5 cm long, bibracteolate at middle. Hypanthium obconic or obovoid, 1-1.5 cm long, 1-1.5 cm wide, glabrous. Perianth bilabiate, 5-6.5 cm long, dark purple, glabrous; tube suberect or gently curved, 2-3.2 cm long, 0.9-1.5 cm wide; lobes spreading, 2.7-3.8 cm long, 2-4 mm wide. Staminal column included or slightly exserted, suberect or gently curved; filaments dark purple, 3.5-4 cm long; anthers dark purple, 1.3-1.5 cm long, 3-4 mm wide, glabrous or sparsely pubescent. Berries orange, subglobose, 2-3.2 cm long, 2-3.2 cm in diameter.

Distribution. (Fig. 17). Endemic to Hawai'i. Montane rain forests, 370-1370 m, in the Kohala Mountains and windward Mauna Kea.
Fig. 17. Distribution of *Clermontia kohalae* (dots) and *C. montis-loa* (open circles).
SPECIMENS EXAMINED. HAWAI'I. NORTH KOHALA: Honokane Valley, Carlquist 1866 (RSA); Kalae Valley, Carlquist 1890 (BISH, MICH, RSA); Pololu Valley, Degener 7816 (A, MO, NY), Degener & Degener 31568 (A, B, BH, BISH, DUKE, E, G, MASS, MICH, NY, W), Degener & Greenwell 21900 (B, BISH, MASS, NY, W); Makapala mauka, Degener et al. 27725 (B, BISH, DUKE, G, NY, MSC, TI, W, Z); Pololu-Honokanenui, Degener & Greenwell 21878 (B, BISH, MASS, NY, W); Honokane, Gillett 1895 (BISH, HLA); Pololu Valley, Lammers et al. 5817 (B, OS), Lammers et al. 5818 (DUKE, NY, OS, US, WIS), Lammers et al. 5819 (OS), Lammers et al. 5820 (OS); Pololu Valley, Lamoureux & Tabrah 2755 (BISH); Parker Ranch, Kehena ditch, Rock 25738 (BISH, L); Makapala Ahu., Waipunalau Str., Stemmerman & Montgomery 4004 (BISH); Kehena Ahu., Pololu-Honokane, Warshauer & McEldowney 2493 (BISH); Pu'ukapu Ahu., Kehena ditch, Warshauer & McEldowney 2494 (BISH). — SOUTH KOHALA: Kohala ditch, Bishop 067038 (HAW); Kohala, Rock s.n. (BISH, CAS, NSW, NY, US). — HAMAKUA: Ahualoa, Degener et al. 31570 (A, BISH, BR, CHR, E, MASS, MO, NY, TI, UC, W, Z), Degener et al. 31570a (B); Hi'ilawe, Rock 4572 (BISH), Rock 4573 (BISH, GH); Puakalehua Gulch, Rock 4579 (BISH); Waipi'o Valley, Rock 4647 (BISH); Kalopa Gulch, Takeuchi s.n. (BISH, OS). — NORTH Hilo: Kaiwilahilahi Str., Clarke & Cuddihy 666 (BISH). — NO PRECISE LOCALITY: Munro 528 (BISH); Munro s.n. (BISH, GB, M).

**Clermontia kohalae**, which takes its name from the village and district of Kohala in the Kohala Mountains of northwestern Hawai'i, is closely related to *C. montis-loa*, but differs by its longer peduncles,
pedicels, and filaments, and its larger perianth with lobes equalling the tube. Stunted plants growing in exposed windswept situations were segregated by Rock (1913a) as Clermontia kohalae var. robusta. Such environmentally induced variation does not merit taxonomic recognition. The other variety, Clermontia kohalae var. hiloensis, is treated here as a synonym of C. hawaiiensis. 

Clermontia kohalae apparently hybridizes with C. parviflora, a species of ser. Parviflorae, producing plants that have been described as C. paradisia. These hybrids are discussed below. It also hybridizes with Clermontia drepanomorpha, producing plants that have been described as Clermontia leptoclada (see discussion under C. drepanomorpha). However, the two varieties, Clermontia leptoclada var. holopsila and C. leptoclada var. urceolata, are not referrable to this hybrid. Rather, their types are specimens of typical Clermontia kohalae. Similarly, the type specimens of Clermontia convallis and C. epilosa cannot be distinguished from C. kohalae, and these species also are placed in synonymy.

The peculiar nomenclatural relationship between Clermontia leptoclada var. holopsila and C. convallis requires some explanation. Wimmer (1943) described the former on the basis of "Herb. Degener n. 2186!". He subsequently (Wimmer 1968) described the latter on the basis of "Degener n. 2186! - NY". In so doing, he made no reference to the previously published name, but rather suggested that the new species was most closely related to Clermontia montis-loa. Clearly, Clermontia convallis was not simply a new name at specific rank for C.
leptoclada var. holopsila. This taxonomic faux pas resulted in the creation of two names based on different duplicates of a single collection, both of which are synonyms of another taxon.

I have examined five sheets of Degener 2186. None is deposited at W, where Wimmer worked. A sheet at NY was annotated "Clermontia convallis sp. nov. (orig.)" by Wimmer. A sheet at BISH, stamped "Herbarium Otto Degener", was annotated "Clermontia leptoclada Rock var. holopsila E. Wim. n.v. Totaliter glabra!". These sheets apparently are the specimens upon which Wimmer based the two names. Consequently, the holotype of one name is an isotype of the other, while the remaining duplicates are isotypes of both.

Wimmer (1953) described Clermontia paradisa as a new species allied to C. leptoclada, on the basis of four numbers collected by Degener. Although no holotype was specified in the protologue, his annotations indicate that he utilized a sheet of Degener 21880 at W as the holotype. This sheet was marked "orig.", while duplicates in other herbaria were labelled "Isotypus". Sheets of the other three numbers were labelled "Paratypus". Wimmer communicated this information to Degener, who subsequently (Degener & Degener 1956c) published it, effectively lectotypifying the name. This typification was overlooked by St. John (1980b), who designated a sheet of Degener & Greenwell 21879 at BISH as the lectotype. In so doing, he also overlooked Wimmer's annotation of this sheet as "Paratypus", and the fact that the specimen does not match the description well. The type and some of the other material studied by Wimmer (Degener & Greenwell 21879, B, W;
Degener 21881, B, BISH, MASS, W; and Degener & Greenwell 21882, B) are interpreted here as hybrids between Clermontia kohalae and C. parviflora. The remaining duplicates of these numbers (including St. John's superfluous lectotype) are typical Clermontia parviflora and are cited under that species. The supposed similarity of Clermontia paradisia to C. leptoclada is the due to the fact that both binomials are based upon hybrid derivatives of C. kohalae.

   -- TYPE: HAWAIIAN ISLANDS. Hawai'i: Na'alehu, 9 Jan 1912, Rock
   10002 (holotype: BISH!; isotypes: GH! S!).

Clermontia montis-loa f. globosa Rock, Monogr. Stud. Haw. Lobelioid. 337. 1919. -- TYPE: HAWAIIAN ISLANDS. Hawai'i:
   Kilauea near Kalanilehua, 30 Aug 1917, Rock 12835 (holotype:
   BISH!).

Shrubs or trees, 2-5 m tall, terrestrial or epiphytic. Lamina ob lanceolate, or oblong, 8-19 cm long, 2.2-4.5 cm wide, coriaceous, dull; upper surface dark green, glabrous; lower surface pale green sometimes suffused with purple, pubescent; margin callose-crenulate; apex acute, acuminate, or cuspidate; base attenuate. Petiole 1.5-6 cm long, glabrous or pubescent. Inflorescences 2(-3)-flowered, glabrous or pubescent; peduncle spreading, 0.3-1.8 cm long, bibracteate at middle or apex; pedicels spreading, 0.3-1.8 cm long, bibracteolate at
middle. Hypanthium obconic or obovoid, 1.1-1.6 cm long, 0.8-1.1 cm wide, glabrous. Perianth bilabiate, 3.8-5 cm long, green or dark purple outside, dark purple within, glabrous; tube suberect, 0.8-1.6 cm long, 0.7-1.1 cm wide; lobes spreading, 2.4-3.8 cm long, 3-4 mm wide. Staminal column included or slightly exserted, suberect; filaments dark purple, 2.6-3.4 cm long; anthers dark purple, 1.2-1.5 cm long, 3-4 mm wide, glabrous. Berries orange, subglobose or ellipsoid, 2.5-3 cm long, 1.5-3 cm in diameter. Chromosome number n = 14.

Distribution. (Fig. 17). Endemic to Hawai'i. Montane rain forests, 1070-1700 m, on windward Mauna Kea and Mauna Loa. A report by Skottsberg (1944) that it also occurs in the Kohala Mountains is based upon a misidentified specimen (Cranwell et al. 3115, GB, S) of Clermontia calophylla, while the report from Moloka'i (Wimmer 1968) is based upon a misidentified specimen (Degener 7347, A, NY) of Clermontia kakeana.

SPECIMENS EXAMINED. HAWAI'I. NORTH HILO: Laupahoehoe Ahu., Ha'akoa Str., Warshauer 1293 (BISH); Honohina Ahu., Painiu Str., Warshauer 1338 (BISH). -- SOUTH HILO: Kulani Prison Rd., Carlquist 606 (RSA), Carlquist 608d (RSA), Carlquist 608e (RSA), Carlquist 608f (RSA), Carlquist 608i (RSA), Carlquist 608j (RSA), Carlquist 2030 (BISH, L, MICH, RSA); Saddle Rd., 13 mi. from Hilo, Carlquist 2039 (RSA); Saddle Rd., 12 mi. from Hilo, Darwin 1175 (GH, K, PTBG, US); Saddle Rd., 16 mi. from Hilo, Degener et al. 20014 (B, K, LD, NY, W); makai of Kulani Prison, Degener & Greenwell 21838 (B, BISH, LE, MASS,
NY, W), Degener & Greenwell 21839 (B), Degener & Greenwell 21840 (B, BISH, MASS, NY, W), Degener & Greenwell 21840a (MEL, U, W); Kulani forest, Fagerlind & Skottsberg 6290** (GB, S, UPS), Fagerlind & Skottsberg 6290b (S); Pu'u Maka'ala, Gustafson 1682 (BISH); Kulani Prison Rd., Henrickson 4121 (BISH, NSW, RSA, UC, US); Saddle Rd., 19.8 mi. from Hilo, Herbst 900 (BISH, HAW, HLA, L, US); Hilo F. R., Wailuku R., Herbst & Ishikawa 5143 (BISH, HAW, HLA, L); Upper Waiakea F. R., Disappointment Rd., Lammers 5420** (NY, OS, US, W); Hilo F. R., Wailuku R., Lammers 5424 (MO, OS, RSA, WIS), Lammers 5425 (B, BISH, OS, PH); Stainback Hwy., Lammers et al. 5785 (OS); Kulani Prison, Lamoureux 366 (HAW), Lamoureux 390 (HAW); Kulani Rd., Lindsey s.n. (L); Kulani Rd., Long 4306 (HAW); s. of Hilo, MacDaniels 228 (BISH); Kulani forest, Rock 26000 (BISH, K, L), Rock 26001 (BISH); Saddle Rd. kipuka, Rock s.n. (BISH); Kulani Rd., St. John et al. 22332 (NY), St. John et al. 22344 (NY, US); Upper Waiakea F. R., Tree Planting Rd., Wakida ESP 347 (BISH); Pi'ihonua Ahu., Warshauer 1526 (BISH), Warshauer 1527 (BISH); fork of Wailuku R. & Waipahoeohoe Gulch, Warshauer 1587 (BISH), Warshauer 1638 (BISH); kipuka 17 mi. se. of Pohakuloa, Webster et al. 13968 (BISH, DAV, GH). -- PUNA: 'Ola'a F. R., Herat et al. 573 (BISH, HAW), Herat et al. 574 (BISH, HAW), Herat et al. 575 (BISH, HAW); 'Ola'a F. R., Disappointment Rd., Lammers et al. 5805 (DUKE, K, OS, PH), Lammers et al. 5806 (B, BISH, OS), Lammers et al. 5807** (OS); 'Ola'a forest, Lindsey s.n. (BISH); 'Ola'a Ahu., Pu'u Kulani, Warshauer 1259 (BISH). -- KA'U: Degener place, Andrews 301 (NY); Ka'ala'ala Ahu., Waihaka Gulch, Casey & Collins JDJ-627 (BISH), Casey & Collins
Clermontia montis-loa is closely related to C. kohalae, but differs by its coriaceous leaves and shorter peduncles, pedicels, perianth, and filaments. The species is named for the type locality, Mauna Loa, an active volcano and the second highest peak (4169 m) in the archipelago.

Mook (1919) distinguished Clermontia montis-loa f. globosa by its larger subglobose berries. Size and shape of fruits varies considerably within populations and are not sound bases for infraspecific taxa.

Two other infraspecific taxa of Clermontia montis-loa are treated here as synonyms of other species. Skottsberg (1926) distinguished Clermontia montis-loa var. tenuifolia by its wider chartaceous leaves. He subsequently (Skottsberg 1944) treated it as an unnamed forma of Clermontia parviflora. It differs from Clermontia montis-loa by its
rotate perianth with narrower recurved lobes and its strongly exserted staminal column; and from _C. parviflora_ by its larger darker flowers, larger hypanthium, and wider leaves. In all these features, however, it is indistinguishable from _Clermontia calophylla_. Wimmer (1968) distinguished _Clermontia montis-loa_ f. _molokaiensis_ by its larger leaves. However, it also differs by its chartaceous leaves and uniformly green perianth with a longer tube. In these characters, it is identical to _Clermontia kakeana_.

In areas of sympatry on leeward Hawai‘i, sporadic intermediates of _Clermontia montis-loa_ and _C. parviflora_ are found. These plants resemble a large-flowered _Clermontia parviflora_, but the perianth is somewhat bilabiate with less-recurved lobes and darker pigmentation, while the staminal column is less exserted. These intermediates are interpreted as hybrids. Examination of fixed microsporocytes from such plants revealed no meiotic abnormalities (Lammers 1988a). These hybrids have been collected in the vicinity of Stainback Hwy. (Carlquist 608b, RSA; Carlquist 608c, RSA; Carlquist 608g RSA; Carlquist 608h, RSA; Lammers et al. 5808**, B, K, OS; Lammers et al. 5809, BISH, OS) and along the Saddle Road (Lammers 5419, BISH, DUKE, MO, NY, OS, US; Lammers 5427, OS, PH, W).


Trees, 2-7 m tall, terrestrial or epiphytic. Lamina oblanceolate or elliptic, 8-22 cm long, 1.5-4.5 cm wide, chartaceous, dull; upper surface green, glabrous; lower surface pale green sometimes suffused with purple, glabrous or sparsely pubescent along midrib; margin callose-crenulate; apex acute, acuminate, or cuspidate; base attenuate. Petiole 2-5 cm long, glabrous. Inflorescences 2(-4)-flowered, glabrous; peduncle deflexed, 5-12 cm long, bibracteate in upper half or at apex; pedicels abruptly ascending, 2-3.5 cm long, bibracteolate at middle. Hypanthium hemispheric to obconic, 1.5-2 cm long, 1.5-2 cm wide, glabrous. Perianth bilabiate, 4-5.5 cm long, dark purple, glabrous; tube suberect or gently curved, 1-1.6 cm long, 1.5-2 cm wide; lobes spreading, 2.8-4.2 cm long, 4-7 mm wide. Staminal column included or slightly exserted, suberect or gently curved; filaments dark purple, 3.4-4.2 cm long; anthers dark purple, 1.2-1.6 cm long, 5-5.5 mm wide, glabrous or sparsely pubescent along sutures. Berries orange, subglobose, 2-3 cm long, 2-3 cm in diameter. Chromosome number n = 14.

Distribution. (Fig. 15). Endemic to Hawai'i. Montane bogs, rarely rain forests and cloud forests, 915-1460 m, in the Kohala
Mountains.

**SPECIMENS EXAMINED. HAWAI'I. SOUTH KOHALA: Alakahi bog, Carlquist 2082 (BISH, RSA); Koiawe-Alakahi, Cranwell 3146 (BISH, GB, K, S); Kawainui, Cranwell et al. 3146b (S); head of Alakahi Valley, Degener et al. 20160 (NY, W); head of Koiawe Valley, Fagerlind & Skottsberg 6159 (S); head of Alakahi Str., Gillett 1707 (HLA); Hamakua ditch, Heed G87A3P (HAW); Waimea, Hitchcock 14326 (US); above Waikoloa Reservoir, Lammers et al. 5749 (OS), Lammers et al. 5750 (OS); head of Alakahi Str., Lammers et al. 5753 (OS), Lammers et al. 5759 (MO, OS, WIS); Upper Hamakua ditch trail, MacDaniels 288 (L); Alakahi, Rock 4736 (BISH), Rock 4747 (BISH), Rock 4751 (BISH, K, W), Rock s.n. (CAS); Rock 8762 (S); above Awini, Rock 8807 A, BISH, GH, MAK, NY, RSA, UC, W), Rock 8808 (BISH, GH), Rock 8809 (BISH, GH); Rock s.n. (A, BH, BISH, CAS, L, M, NSW, NY, P, RSA, S, UC, US, W); Pu'u Ahia, St. John & Hosaka 11495 (BISH, BM, L, MICH, W); above Waimea, Skottsberg 1128 (GB, S); Hamakua ditch, Skottsberg 6803 (UPS); Skottsberg 6825 (S, UPS); Pu'ukapu Ahu., Pu'u Kaiholena, Stemmerman & Montgomery 3979 (BISH), Stemmerman & Montgomery 3989 (BISH); Pu'ukapu Ahu., Pu'i Iki, Stemmerman & Montgomery 3994 (BISH).

**Clermontia drepanomorpha** is most related to **C. kohalae**, differing by its longer deflexed peduncle, larger hypanthium, shorter perianth with wider tube and lobes, and wider anthers. It also hybridizes with that species, producing plants of intermediate morphology that have
been described as *Clermontia leptoclada*.

As suggested by Carlquist (1969), plants segregated as *Clermontia leptoclada* appear to be the result of hybridization between *Clermontia drepanomorpha* and *C. kohalae*. These plants resemble the latter in their general floral structure, but have the deflexed peduncle and pubescent staminal column of the former. According to Rock (1913b, 1919), the type of *Clermontia leptoclada* grew on the boggy summit of the Kohala Mountains in company with *C. drepanomorpha*; *C. kohalae* grows in adjacent rain forests. The following specimens from the type locality are also regarded as hybrids between these two species: Rock 4762 (BISH), Rock 4765 (BISH), Rock s.n. (BISH, CAS, NY, S, UC).
IIB. Clermontia series Parviflorae Lammers, ser. nov. -- TYPE:

*Clermontia parviflora* Gaudichaud ex A. Gray.

A seriebus aliis Clermontiae lobis calycis connatis deciduis aequantibus corollam longitudine et colore, perianthio rotato lobis recurvatis aequantibus vel superantibus longitudine tubum erectum vel erectiusculum, et staminibus connatis erectis vel erectiusculis exsertissimis differt.

Shrubs or rarely trees, 0.4-5 m tall, terrestrial or epiphytic. Lamina oblong, elliptic, or oblanceolate, 4-19 cm long, 1-7 cm wide, chartaceous or coriaceous, dull; apex acute or acuminate, rarely cuspidate or obtuse; base cuneate or attenuate. Petiole 1.5-7.5 cm long, glabrous or pubescent, green and opaque. Inflorescences 2-5(-10)-flowered; peduncle spreading, 0.5-1.8 cm long; pedicels spreading, 0.7-1.8 cm long. Perianth rotate, 1.5-4.5 cm long, purple, rose-colored, or white, rarely green; tube erect or suberect, 0.5-1.8 cm long; lobes recurved, 1-3.4 cm long, 0.9-3 mm wide, equalling or exceeding the tube in length. Staminal column strongly exserted, erect or suberect; filaments 1.7-3.3 cm long; anthers 0.6-1.3 cm long, 1.9-4 mm wide. Berries subglobose, oblong, ellipsoid, or obovoid, 1.2-3 cm long, 0.9-3 cm in diameter.
The name of this series is derived from the specific epithet of the type species, and also refers to the relatively small flowers characteristic of the series. The Parviflorae are further distinguished by their rotate perianth with recurved lobes equalling or exceeding the erect or suberect tube in length and by the strongly exserted erect or suberect staminal column. Also, on the average, the plants are shorter and more branched than those in other series, and tend to produce a greater number of proliferous inflorescences.

15. Clermontia multiflora Hillebrand, Fl. Hawaiian Isl. 242. 1888. --
TYPE (here designated): HAWAIIAN ISLANDS. West Maui: Waihe'e, 1870, Hillebrand s.n. (lectotype: K!; isolectotypes: GH! MEL!).

Shrubs, 2-4 m tall (fide Hillebrand). Lamina elliptic, 10-12.5 cm long, 2.5-3.2 cm wide, chartaceous, dull, glabrous; margin callose-crenulate; apex acuminate; base cuneate. Petiole 4-7.5 cm long, glabrous. Inflorescences 7-10-flowered, glabrous; peduncle spreading, 1-1.8 cm long, bibracteate at apex; pedicels spreading, 1-1.8 cm long, bibracteolate at base. Hypanthium obconic, 7-8 mm long, 7-8 mm wide, glabrous. Perianth 2.4-3.2 cm long, purple (fide Hillebrand), glabrous; tube suberect, 1.4-1.6 cm long, 5-6 mm wide; lobes 1.2-1.6 cm long, 2-3 mm wide. Staminal column exserted, suberect; filaments 2.5-2.8 cm long; anthers purple (fide Hillebrand), 7-8 mm long, 2.5-3 mm wide, glabrous. Berries unknown.
Clermontia multiflora is morphologically most similar to Clermontia micrantha, differing by the many-flowered inflorescences; larger leaves and flowers; longer petioles, peduncles, and filaments; and wider anthers. Although Rock (1919: 331) designated a lectotype, it was destroyed in 1943. An apparent isolectotype is here designated to replace it.

This intriguing species was last collected prior to 1871 and is presumed extinct. Without additional specimens, it is impossible to ascertain whether the 7-10-flowered inflorescences are constant, or merely sporadic proliferous inflorescences produced on the same individual as 2-flowered inflorescences. Even if the many-flowered inflorescence is not a constant character, the species is still sufficiently distinct in other features to merit recognition. The paucity of specimens also precludes determination of the structural type of the corolla, and consequently, a confident assessment of the species' taxonomic position. However, it is here assigned to ser. Parviflorae on the basis of its relatively small flowers and general similarity to Clermontia micrantha.
Lobeloid. 334. 1919. Clermontia multiflora var. micrantha
Hillebrand, Fl. Hawaiian Isl. 242. 1888. — TYPE (here
designated): HAWAIIAN ISLANDS. West Maui: Waihe'e and Lahaina,
1870, Hillebrand s.n. (lectotype: K; isolecototypes: GH! US!).

Clermontia multiflora var. micrantha f. montana Rock, Indig. Trees
Haw. Isl. 511. 1913. — TYPE: HAWAIIAN ISLANDS. West Maui:
slopes of Pu'u Kukui, Aug 1910, Rock 8179 (holotype: BISH;

Shrubs, 0.4-2 m tall, terrestrial. Lamina elliptic or oblong,
4-10 cm long, 1-2.5 cm wide, coriaceous, dull, glabrous; upper surface
green or dark green; lower surface light green often suffused with
magenta especially on veins; margin callose-crenulate; apex acute or
acuminate; base cuneate or attenuate. Petiole 1.5-4 cm long, glabrous.
Inflorescences 2(-5)-flowered, glabrous; peduncle spreading, 0.5-1 cm
long, bibracteate at apex; pedicels spreading, 0.7-1.4 cm long,
bibracteolate near base. Hypanthium obovoid or turbinate, 5-8 mm long,
3-7 mm wide, glabrous. Perianth rotate, 1.8-2.8 cm long, rose-colored,
glabrous; tube suberect, 0.7-1.3 cm long, 3-5 mm wide; lobes recurved,
1-1.6 cm long, 1-2.7 mm wide. Staminal column exserted, erect or
suberect; filaments rose-colored or purple, 1.7-2 cm long; anthers
purple, 6-8 mm long, 1.8-2.2 mm wide, glabrous or minutely pubescent.
Berries orange, obovoid or subglobose, 1.2-1.5 cm long, 0.9-1.5 cm in
diameter.
Distribution. (Fig. 16). Montane bogs, 670-1460 m, West Maui; montane rain forests, Lana'i.

SPECIMENS EXAMINED. LANA'I. Between Ho'okio & Kumoa, Munro 333 (BISH); Kumoa Valley, Munro 391 (BISH, L, M), Munro 930 (BISH, L).

WEST MAUI. LAHAINA: Haela'au-Pu'u Kukui trail, Carlquist H23 (BISH, UC); lookout to Honokowai falls, Carlquist 556 (RSA); Honokohau Valley, Carlquist 2143 (BISH, MICH, RSA); Pu'u Kukui trail, Char & Arakawa PKWM 91-76 (PTBG), Char & Arakawa 93-76 (HAW); trail to Nakalalua, Cranwell et al. 2683 (BISH, GB, K, S); 'Eke, Degener 18062 (A, B, DS, G, MO, NY, PH, S, US); Pu'u Kukui, Degener et al. 25024a (W); Haela'au-Pu'u Kukui trail, Ewart 118 (BISH, W); Honokahau drainage basin, Forbes 457.M (BISH); Hanakao'o, Forbes 661.M (BISH, MO, NSW); Maunaho'oma, Forbes & Cook 33.M (BISH); Pu'u Kukui, Gillett 1782 (BISH, HLA); Violet Lake, Gustafson 2039 (OS); Pu'u Kukui, Harrison s.n. (BISH); Pu'u Kukui, Herbst & Bishop 1306 (HAW); Pu'u Kukui, Hitchcock 14784 (BISH, US), Hitchcock 14821 (US), Hitchcock 14856 (US); 'Eke trail, Hobdy 718 (BISH); Violet Lake, Lammers & Hobdy 5662 (K, NY, OS), Lammers & Hobdy 5663 (MO, OS, W), Lammers & Hobdy 5681 (BISH, DUKE, OS), Lammers & Hobdy 5683 (RSA, OS, WIS); Pu'u Kukui, Munro 422 (BISH), Munro 618.M (BISH, NY); Pu'u Kukui, Neal s.n. (BISH); Ka'anapali, Rock s.n. (NSW, NY, US); Pu'u Kukui, Rock s.n. (W); Nakalalua, St. John 10241 (BISH, NY, US, W, WELT); Pu'u Kukui, Skottsberg 766 (BISH, GB, S); Pu'u Kukui, Suthers s.n. (MSC); Honokowai Ahu., Pu'u Kukui trail, Warshauer & McEldowney 3034 (BISH); Pu'u Kukui, Wilbur & Webster 832.
Clermontia micrantha is similar morphologically to C. parviflora, but differs by the rose-colored perianth; coriaceous leaves; and shorter peduncles, perianth lobes, and filaments. Because the lectotype chosen by Rock (1919: 330) was destroyed in 1943, an isolectotype is designated here to replace it. Although relatively common in the bogs of West Maui, it may be extirpated on Lana'i, as the only known specimens from that island were collected in 1928-29.

Rock (1913b) distinguished Clermontia multiflora var. micrantha f. montana from C. multiflora var. micrantha (the basionym of C. micrantha) on the basis of its 2-flowered inflorescences and obovoid berries. These features vary within populations, and Rock (1919) subsequently reduced the forma to synonymy. An apparent hybrid with Clermontia kakeana is discussed under that species.
242. 1888. -- TYPE (here designated): HAWAIIAN ISLANDS.
Hawai'i: Hilo, Hillebrand s.n. (lectotype: BISH; isoolectotypes: BISH, MEL, NSW).


_Clermontia parviflora_ var. _umbriaticola_ Skottsberg, Acta Horti Gothob. 2: 270. 1926. -- TYPE: HAWAIIAN ISLANDS. Hawai'i: Hilo, Hiulani forest, 500 m, 8 Sep 1922, Skottsberg 434 (holotype: GB; isotypes: BISH, SI).

Shrubs, 1-3.5 m tall, terrestrial or epiphytic. Lamina elliptic or oblanceolate, 6-18 cm long, 1.5-5.5 cm wide, chartaceous, dull; upper surface green, glabrous; lower surface pale green often suffused with purple especially on veins, glabrous or sparsely pubescent; margin callose-crenulate; apex acute, acuminate, or cuspidate; base cuneate or attenuate. Petiole 1.5-5 cm long, glabrous or pubescent.

Inflorescences 2-5(-10)-flowered, glabrous or pubescent; peduncle spreading, 1-1.5 cm long, bibracteate at middle or apex; pedicels spreading, 0.8-1 cm long, bibracteolate at middle or base. Hypanthium obovoid or turbinate, 5-8 mm long, 3-5 mm wide, glabrous or sparsely pubescent. Perianth rotate, 1.5-2.8 mm long, purple, green, or white externally, pale purple or white within; tube erect or suberect, 0.5-1.1 cm long, 3-5 mm wide; lobes recurved, 1.8-2.3 cm long, 0.9-2 mm
wide. Staminal column strongly exserted, erect or suberect; filaments white or pale purple, 2-2.5 cm long; anthers white or pale purple, 6-8 mm long, 1.7-2.4 mm wide, glabrous. Berries yellow or orange, oblong, ellipsoid, or subglobose, 1.2-2.5 cm long, 1-2 cm in diameter. Chromosome number $n = 14$.

Distribution. (Fig. 18). Endemic to Hawai‘i. Montane rain forests, in the Kohala Mountains (365-1070 m) and on the windward slopes of Mauna Kea and Mauna Loa (120-1460 m).

SPECIMENS EXAMINED. HAWAI‘I. NORTH KOHALA: Honokane Valley, Carlquist 1863 (RSA), Carlquist 1864 (BISH, RSA), Carlquist 1865 (BISH, DUKE, GH, L, MICH, RSA), Carlquist 1866 (RSA); Kaukini Cabin, Degener 21880 (BISH, MASS, NY, W), Degener 21880a (W), Degener 21881 (BISH); Pololu-Honokanenui, Degener & Greenwell 21879 (BISH, MASS, NY, W), Degener & Greenwell 21879a (BISH, NY), Degener & Greenwell 21879b (W), Degener & Greenwell 21879c (W), Degener & Greenwell 21879d (W); Makapala mauka, Degener et al. 27724 (BISH, BM, NY); Honokane Iki Str., Flynn & Bergau 1362 (OS); Honokane, Gillett 1896 (BISH), Gillett 1897 (BISH, HLA, US), Gillett 1898 (BISH, HLA); Kohala, Hillebrand 79 (K), Hillebrand s.n. (BM); Kohala, Lydgate s.n. (W). -- SOUTH KOHALA: Waimea, Forbes 477.H (BISH); head of Alakahi Str., Gillett 1708 (BISH); Pu‘u La‘ala‘au, Hoe 1902.0 (HAW); head of Koiawe Str., Lammers et al. 5761 (OS); above Kamuela, Matsunami s.n. (DUKE, MICH); Holokaiea Gulch, Rock 4362 (BISH), Rock 4363 (A, BISH, DS, GH, L, NY, W, WELT), Rock 4366 (BISH); Waimea, Rock s.n. (BISH, G, GH, NSW, UC, US). -- HAMAKUA:
Fig. 18. Distribution of *Clermontia calophylla* (open circles) and *C. parviflora* (dots).
above Hi'ilawe, Rock 4575 (BISH); Puakalehua Gulch, Rock 4578 (BISH);
Pa'auhau 3 Ahu., Rock 4353 (BISH), Rock 4354 (W), Rock 4356 (NSW), Rock
4358 (BISH), Rock 4360 (A, BISH, GH, MAK), Rock s.n. (CAS, NY);
Pa'auhau Ahu., Rock 4364 (A, BISH, GH, NY, P, UC, US, W, WIS); Waipi'o,
St. John & Hosaka 11455 (BISH), St. John & Hosaka 11471 (BISH, GB, US).
-- NORTH HILO: Hilo F. R., Ha'akoa Str., Davis 694 (BISH); Hilo F. R.,
Laupahoehoe sect., Sohmer 6267 (HAW, MO); Hilo F. R., Blair Rd., Wakida
ESP 348 (BISH). -- SOUTH HILO: Kulani Prison Rd., Carlquist 600 (RSA),
Carlquist 607 (RSA), Carlquist 2026 (BISH, GH, MICH, RSA); Saddle Rd.,
Carlquist 2038 (RSA), Saddle Rd., 15 mi. from Hilo, Degener 20332 (MO,
NY); Kulani Rd., Degener 20648 (BISH, NY, W); Pana'ewa Forest, Degener
20950 (W); Kulani Prison Rd., Degener 21791 (B, BISH, MASS, NY, W);
mauka of 'Akaka Falls, Degener & Degener 27720 (BISH, E, K, M, NY, UC,
W, WIS, Z); Saddle Rd., 9 mi. from Hilo, Degener & Degener 27721 (B,
BISH, NY); Kaumana, Degener & Degener 34878 (B, C, CHR, E, G, GB, ISC,
MICH, UC), Degener & Degener 34878a (K, LD, M, MPU, NY, OSH, U, W,
WELT, WIS); Saddle Rd., 7 mi. from Hilo, Degener et al. 20177 (NY, W);
Saddle Rd., mile 19, Flynn 481 (PTBG); between Kauama Cave & 'Ola'a
Flume, Forbes 605.H (BISH, P); 'Ola'a Flume, Forbes 642.H (BISH),
Forbes 646.H (BISH); 'Akaka Falls, Forbes & Thoanum 617.H (BISH),
Forbes & Thoanum 621.H (A, BH, BISH, W); Saddle Rd., 3 mi. above
Country Club Rd., Heed G69A5P (HAW); Saddle Rd., 9.4 mi. above Hilo,
Heed G92A1P (HAW); Stainback Hwy., Herbst 873 (BISH, HAW, HLA, L, US);
Upper Waiakea F. R., Stainback Hwy., Higashino 7414 (BISH); back of
Hilo, Hillebrand & Lydgate s.n. (W); Stainback Hwy., Ishikawa 226 (HLA);
Upper Waiakea F. R., Disappointment Rd., Lammers 5409 (OS), Lammers 5414** (OS), Lammers 5418** (MO, OS, RSA, WIS), Lammers et al. 5784** (K, OS); Hilo F. R., Wailuku Rd., Lammers 5426 (NY, OS, PH, US, W), Lammers et al. 5778 (B, DUKE, OS); Kulani Prison, Lamoureux 389 (HAW); Hilo, Lydgate s.n. (MEL); Wailuku Rd., MacDaniels 82 (BH), MacDaniels 83 (BH), MacDaniels 204 (A, BISH); Saddle Rd., Matsunami s.n. (DUKE, MICH); Kulani Prison Rd., Matsunami s.n. (DUKE); Wright Rd. farm lots, Matsunami s.n. (DUKE, MICH); Saddle Rd., Mayr 255 (OS); Stainback Hwy., Nagata 1107 (HLA), Nagata 1875 (BISH, HLA), Nagata 2638 (HLA); Kulani Prison Rd., Newell 882 (BISH), Newell 883 (BISH), Newell 893 (BISH); Kulani Rd. & 15 3/4 Rd., St. John et al. 22367 (BISH, NY); 'Akaka Falls, Stone 3104 (BISH); Kulani Rd., Takeuchi 1729 (BISH); Upper Waiakea F. R., Disappointment Rd., Wagner et al. 4834 (BISH), Wagner et al. 4835 (BISH); Upper Waiakea F. R., Stainback Hwy., Webster et al. 14025 (BISH, DAV, GH, MICH, NSW); Punahoa 2, Woolford s.n. (BISH). --

PUNA: Degener's place, Andrews 406 (NY); 'Ola'a forest, Burton 517 (HAW), Burton 606 (HAW); Hwy. 11, Crosby & Anderson 1968 (DUKE); between Glenwood & Volcano House, Degener 2190 (BISH), Degener 2191 (BISH, NY); between Glenwood & 29 Miles, Degener 3713 (A, B, DS, MASS, MO, NY, PH, US), Degener 7879 (A, DS, MO, NY); 'Ola'a F. R., Degener 20960 (W), Degener & Degener 30795 (B, BH, BISH, M, MASS, MICH, NY), Degener & Degener 30797 (CHR), Degener & Degener 32413 (B, C, E, MICH, U); Makaopuhi Crater, Degener 7880 (NSW); Rte. 148A, Degener & Degener 27733 (BISH, BM, C, DS, G, M, MIN, MO, NSW, NY, U); 27 Miles, Degener & Degener 30794 (A, B, BISH, BR, C, DUKE, E, L, MASS, MICH, MIN, MSC, NY,
RSA, TI, U, UC, UPS, W, Z), Degener & Hitta 3967 (A, MICH, MO, NY);
Makaopuhi Crater, Fagerlind & Mitchell 578 (BISH); 20 Mile Rd., Funk
205 (BISH); Glenwood, Giffard 324 (BISH); Kalanilehua, Giffard s.n. (M);
'Ola'a F. R., Stainback Hwy., Herat et al. 602 (BISH, HAW), Herat
et al. 929 (BISH, HAW), Herat et al. 952 (BISH, HAW); Hwy. 11, 23 mi.
from Hilo, Herbst 949 (CANB, CAS, HAW, LD, UPS, US); Fern Estates
subdivision, Hoe 1122.0 (DUKE), Hoe 1124.0 (DUKE); Waikahekahe Ahu.,
Jacobi & Higashino 1304 (BISH), Jacobi & Higashino 1320 (BISH); Pu'u
Kamoamoa, Jacobi & Higashino 1339 (BISH); 'Ola'a F. R., Disappointment
Rd., Lammers et al. 5804 (OS), Lammers 5810 (BISH, OS); 'Ola'a F. R.,
Hwy 148, Lammas et al. 5813 (OS); Kahaualea Ahu., S. Glenwood Rd.,
Lammers et al. 5816 (OS); 'Ola'a, Lindsey s.n. (BISH); 29 Miles, Morley
130-H (BISH); Fern Estates Rd., Newell 620 (BISH), Newell 634 (BISH);
29 Miles, Rock 13122 (BISH), Rock s.n. (BISH, L); Pu'u Kauka,
Skottsberg 474 (BISH, GB, S); Funa Ahu., Eden Rock Estates, Stemmerman
& Jacobi 3800 (BISH). -- KA'U: Kilauea, Beardsley s.n. (BISH); Crater
Rim trail, Darwin 1159 (K, PTBG, US); Kilauea, Degener & Degener 27732
(B, BH, BISH, DUKE, G, L, MASS, MICH, MSC, NY, TI, W); Ka'alaiki,
Degener & Degener 34902 (A, BH, DS, LD, MO, NSW, TI, U, UPS, WELT, Z);
Bird Forest, Eastwood s.n. (CAS); Thurston Lava Tube to Kilauea Iki,
Eggler 8 (US); Kilauea Iki, Fagerlind & Mitchell 617 (BISH, L);
Kilauea, Mr. Horner's place, Fagerlind & Skottsberg 6246 (S, UPS);
Kapapala, Forbes 379.H (BISH); Kilauea, Forbes et al. s.n. (BISH, NY,
UC, US); Thurston Lava Tube, Gillett 1699 (BISH, HAW, HLA), Henrikson
& Johnson 4095 (BISH, NSW); Kilauea, Iltis et al. H-78 (WIS); Thurston
Several putative interspecific hybrids involving this species have been identified from throughout its range. In Puna District, sporadic hybrids with Clermontia hawaiiensis have been found. Plants of the Kohala Mountains described as Clermontia paradisia are hybrids with C. kohalae. On windward Mauna Kea and Mauna Loa, hybrids with Clermontia montis-loa are not uncommon. Each of these hybrids is discussed under the other parental species.

Hillebrand (1888) distinguished Clermontia parviflora var. pleiantha by its inflorescences of more numerous smaller flowers. As
noted previously, proliferous inflorescences occur sporadically in many
species of Clermontia, often on the same individual with typical
few-flowered inflorescences. An isoelectotype is here designated to
replace the lectotype selected by Rock (1919: 336), which was destroyed
in 1943.

Skottsberg (1926) distinguished Clermontia parviflora var.
umbraticola by its thinner long-acuminate leaves and glabrous peduncles
and calyx. These features are so variable within this species that the
variety cannot be maintained. Three other varieties previously
assigned to Clermontia parviflora are treated here as synonyms of other
species: C. parviflora var. grandis and C. parviflora var. intermedia
(C. calophylla); and C. parviflora var. calycina (C. waimea).

Cyanea blinii, apparently named for French botanist Constant Blin,
is based on a specimen of Clermontia parviflora (Rock 1914, Chamberlain
1977, St. John 1980a). Leveille's (1911) assignment of this specimen
to Cyanea is difficult to understand, as he clearly stated "calyx
corolla fere aequantibus".

Heft): 85. 1943. -- TYPE: HAWAIIAN ISLANDS. Hawai'i: Kohala
Mts., Kawaihale, Pu'u 'Ahia, 1600 m, 2 Jan 1932, St. John &
Hosaka 11503 (holotype: BISH!; isotype: W!).

Lobelioid. 339. 1919. -- TYPE: HAWAIIAN ISLANDS. Hawai'i:


*Clermontia parviflora* var. *intermedia* Skottsberg, Acta Horti Gothob. 15: 489. 1944. — TYPE (designated by Degener & Degener 1956c): HAWAIIAN ISLANDS. Hawai'i: Kohala Mts. above Kamuela, 29 Sep 1922, Skottsberg 1136 (lectotype: GB!).

Shrubs or trees, 1.5-5 m tall, terrestrial. Lamina broadly elliptic or elliptic, 12-19 cm long, 4-7 cm wide, chartaceous, dull; upper surface green, glabrous; lower surface light green, glabrous or pubescent; margins callose-crenulate; apex acuminate, acute, or obtuse; base cuneate. Petiole 3-7 cm long, pubescent. Inflorescences 2(-4)-flowered, pubescent; peduncle spreading, 1-1.7 cm long, bibracteate at middle or apex; pedicels spreading, 1-1.2 cm long, bibracteolate at middle. Hypanthium obovoid, turbinate, or hemispheric, 1-1.7 cm long, 0.8-1.2 cm wide, glabrous or pubescent. Perianth rotate, 3.5-4.5 cm long, greenish externally, purple or dark purple within, glabrous or pubescent; tube erect or suberect, 1-1.8 cm long, 0.7-1 cm wide; lobes recurved, 1.8-3.4 cm long, 1.2-2.5 mm wide. Staminal column exserted, erect or suberect; filaments purple or dark purple, 2.5-3.3 cm long; anthers dark purple, 1-1.3 cm long, 3-4 mm
wide, glabrous or sparsely pubescent. Berries orange, subglobose, 1.5-3 cm long, 1.5-3 cm in diameter. Chromosome number n = 14.

Distribution. (Figure 18). Endemic to Hawai`i. Montane rain forests, 885-1460 m, in the Kohala Mountains.

SPECIMENS EXAMINED. HAWAI'I. NORTH KOHALA: Kehena ditch, Carlquist 1857 (BISH, RSA). — SOUTH KOHALA: between Koiawe & Alakahi Valleys, Cranwell et al. 3115 (GB, S); Waimea, Hitchcock 14363 (US), Hitchcock 14408 (US); head of Koiawe Str., Lammers et al. 5763 (BISH, OS), Lammers et al. 5764** (OS), Lammers et al. 5765 (OS); Holokaiea Gulch, Rock 4363 (M); Waimea, Rock 4771 (BISH), Rock 4780 (A, BISH, GH, L, W), Rock 4781 (BISH), Rock 4814 (A, BISH, GH), Rock s.n. (BISH, CAS, NSW, NY, P, UC, W); Waipi'o, St. John & Hosaka 11456 (BISH, UC, US); Pu'u 'Ahia, St. John & Hosaka 11498 (BISH).

The populations recognized here as Clermontia calophylla previously were treated as infraspecific taxa of C. montis-loa (Skottsberg 1926) or C. parviflora (Rock 1919, Skottsberg 1944). Subsequent study shows that these populations form a well-defined species that differs from Clermontia montis-loa by its rotate perianth with narrower recurved lobes, strongly exerted staminal column, and wider elliptic leaves cuneate at base; and from C. parviflora by its larger darker flowers, larger hypanthium and fruit, and wider leaves. Wimmer (1943), who provided the name at specific rank, did not equate his novelty with these previously described varieties.
IIC. Clermontia series Clermontia, ser. nov. — TYPE: Clermontia oblongifolia Gaudichaud.

A seriebus aliis Clermontiae lobis calycis connatis deciduis aequantibus vel subequantibus corollam in longitudine et colore, perianthio tubulari tubo curvato vel arcurato lobis erectiusculis vel patentibus 1.2-4plo longiore, et staminibus connatis curvatis vel arcuratis inclusus vel paulo exsertis differt.

Shrubs or trees, 1-9 m tall, terrestrial or epiphytic. Lamina oblong, elliptic, or oblanceolate, (4-)6-20(-24) cm long, 1.5-5(-6.5) cm wide, chartaceous or coriaceous; upper surface glossy or dull; apex acute, acuminate, cuspidate, rounded, or obtuse; base cuneate, attenuate, or rarely obtuse. Petiole (0.2-)1-7(-11.5) cm long, glabrous or pubescent. Inflorescences 2(-5)-flowered; peduncles 0.4-5(-11) cm long; pedicels 1-4(-7) cm long. Perianth tubular, 3.6-6.5(-8.5) cm long; tube curved or arcurate, 2-5.7 cm long, 0.5-2 cm wide; lobes suberect or slightly spreading, 0.9-2.9 cm long, 2-7 mm wide, 1/5-1/2 as long as tube. Staminal column included or exserted slightly, curved or arcurate; filaments 3.5-7(-8.4) cm long; anthers 1-1.8 cm long, 2.5-5 mm wide. Berries subglobose, ellipsoid, obovoid, or obconic, 1.7-3.7 cm long, 1-3 cm in diameter, smooth or with 10 longitudinal ridges.
The remaining four species of Clermontia sect. Clermontia differ by their tubular perianth with suberect or slightly spreading lobes 1/5-1/2 as long as the curved or arcuate tube. Because this series includes the type of the genus, its name is an autonym, created automatically by the publication here of the other series.


Shrubs or trees, 2-7 m tall, terrestrial or epiphytic. Lamina oblong, elliptic, or oblanceolate, 6-20 cm long, 1.5-5.4 cm wide, coriaceous; upper surface dark green, glossy, glabrous; lower surface very pale green, dull, glabrous or pubescent; margin callose-crenulate; apex rounded, obtuse, acute, or acuminate; base cuneate or attenuate. Petiole 1.2-11.5 cm long, glabrous or pubescent. Inflorescences 2(-3)-flowered, glabrous or pubescent; peduncle spreading, 0.4-4.5 cm long, bibracteate at middle or apex; pedicels spreading, 1-4.5 cm long, bibracteate at or near base. Hypanthium hemispheric or obconic, 0.8-1.8 cm long, 0.9-1.4 cm wide, glabrous. Perianth tubular, 5-6.5 cm
long, green sometimes tinged purple externally, white or cream-colored within, glabrous or rarely pubescent; tube arcuate, 2.9-5.7 cm long, 0.9-1.6 cm wide; lobes suberect or slightly spreading, 1.2-2.5 cm long, 3-5 mm wide. Staminal column included or slightly exserted, curved or arcuate; filaments white or magenta, 3.7-6.6 cm long; anthers white or purple, 1.3-1.7 cm long, 3-5 mm wide, glabrous or sparsely pubescent.

Berries orange, subglobose, 1.7-3 cm long, 1.8-3 cm in diameter.

Chromosome number $n=14$; the count of $2n=22$ (Carlquist 1956) is aberrant (Lammers 1988a).

This is the most widely distributed species of Clermontia, with populations on four of the six islands that the genus inhabits. These populations may be grouped into three subspecies on the basis of geographically correlated differences in morphology. Each of these subspecies was recognized previously at the rank of forma (St. John 1973). Another forma recently described by St. John (1983), Clermontia oblongifolia f. glabra, is based upon a specimen of C. pallida, and is treated here as a synonym of that species.

Clermontia oblongifolia is morphologically similar to C. grandiflora, but differs by the spreading or ascending peduncles and pedicels, coriaceous lamina glossy on the upper surface, hemispheric or obconic hypanthium, and perianth white or cream-colored within. The mean lengths of several structures differ for the two species, although the overlap in their ranges vitiates using them in a dichotomous key. Nonetheless, these characters (Table 5) are useful for distinguishing
Table 5. Lengths of selected structures in *Clermontia grandiflora* and *C. oblongifolia*. For each structure, the mean length ± 1 S.D. is given, with the range in parentheses. All values are in cm, and were calculated from the raw data used in the numerical phenetic analyses.

<table>
<thead>
<tr>
<th>Structure</th>
<th><em>C. grandiflora</em></th>
<th><em>C. oblongifolia</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Lamina</td>
<td>8.4 ± 1.5 (4-15)</td>
<td>12.6 ± 2.9 (6-20)</td>
</tr>
<tr>
<td>Petiole</td>
<td>1.9 ± 0.7 (0.2-4)</td>
<td>4.4 ± 1.6 (1.2-11.5)</td>
</tr>
<tr>
<td>Peduncle</td>
<td>4.2 ± 1.7 (1-11)</td>
<td>1.5 ± 0.6 (0.4-4.5)</td>
</tr>
<tr>
<td>Pedicel</td>
<td>4.0 ± 1.2 (1.6-7)</td>
<td>2.1 ± 0.7 (1-4.5)</td>
</tr>
<tr>
<td>Anthers</td>
<td>1.1 ± 0.1 (1-1.4)</td>
<td>1.5 ± 0.1 (1.3-1.7)</td>
</tr>
</tbody>
</table>
most specimens of these two species.

KEY TO THE SUBSPECIES OF CLERMONTIA OBLONGIFOLIA

1. Lamina oblanceolate; petioles 1.2-3 cm long; peduncles 0.4-1 cm long.

17c. C. oblongifolia subsp. brevipes.

1. Lamina oblong or elliptic; petioles 3.6-11.5 cm long; peduncles 1-4.5 cm long.

2. Lamina rounded, obtuse, or acute at apex; hypanthium 0.8-1.4 cm long; flower buds rounded or obtuse at apex; filaments and anthers greenish-white or white.

17a. C. oblongifolia subsp. oblongifolia.

2. Lamina acuminate at apex; hypanthium 1.4-1.8 cm long; flower buds acuminate at apex; filaments magenta, anthers purple.

17b. C. oblongifolia subsp. mauiensis.

19a. Clermontia oblongifolia subsp. oblongifolia.


O'ahu: east ridge of Manoa Valley, 29 Mar 1936, Degener, Tam & Martinez s.n. (lectotype: W!).

Lamina oblong or elliptic, 8-20 cm long, 2.3-5.4 cm wide; apex rounded, obtuse, or acute; lower surface glabrous or pubescent. Petiole 3.6-11.5 cm long, glabrous. Inflorescence glabrous or pubescent; peduncle 1-4.5 cm long; pedicels 1.3-4.5 cm long. Hypanthium 0.8-1.4 cm long, 0.9-1.4 cm wide. Perianth 5.5-7 cm long, glabrous or rarely pubescent; tube 4-5.4 cm long, 1-1.3 cm wide; lobes 1.2-2 cm long, 3-5 mm wide; bud rounded or obtuse at apex. Filaments greenish-white or white, 4.8-6.6 cm long; anthers greenish-white or white, 1.3-1.5 cm long, 3.4-5 mm wide, glabrous or sparsely pubescent. Chromosome number \( n = 14 \).

Distribution. (Fig. 19). Endemic to O'ahu. Montane rain forests in the Wai'anae Mountains (790-1200 m) and Ko'olau Mountains (395-850 m).

SPECIMENS EXAMINED. O'AHU. WAI'ANAE MTS.: Mauna Kapu-Palikea trail, Beauchamp 1297 (DUKE); Ka'ala, Bergman s.n. (BISH); Mauna Kapu, Carr 888* (HAW*); Ka'ala, Christophersen & Hume 1745 (BISH); Ka'ala, Cowan 339 (BISH); Palikea, Cowan 666 (BISH); Palikea trail, Crosby & Anderson 1930 (BISH, DUKE); Ka'ala, Degener 7895 (A, DS*, NY), Degener 7905 (BISH), Degener 12196 (B, W), Degener 12197 (W); Palikea, Degener 19276 (NY, W), Degener & Silva 21043 (LE, W); Palehua-Palikea trail,
Fig. 19. Distribution of the subspecies of *Clermontia oblongifolia*: subsp. *oblongifolia* (dots), subsp. *mauiensis* (open circles), and subsp. *brevipes* (triangles).
Degener 19277 (NY); Pu'u Kaua, Degener & Obata 28080 (L); P'uu Kaua, Funk 16 (HAW); Mauna Kapu, Gillett 1868 (HLA); Palikea Valley, Heed G556AP (HAW); Palikea trail, Herat & Herat 416 (B, HAW); Ka'ala, Hitchcock 13393 (US); Wai'anaeuka, Hosaka 126 (BISH*, CAS); Schofield trail, Hume 545 (BISH); Pu'u Kaua, Lammers & Obata 5527 (BISH, NY, OS*, WIS); above Schofield Barracks, MacDaniels s.n. (BH); Ka'ala, Meebold 8592 (M); Wai'anaeuka, St. John 10048 (BISH, GB, US); Pu'u Kanehoa, St. John 14001 (BISH); Ka'ala, Selling 3601 (GB, K, S); Palikea trail, Spence 41 (BISH, HLA, L, US); Palikea, Webster 1408 (BISH); Wai'anaeuka, Webster 1524 (NY); Palikea, Wilbur 568 (DUKE*); Wai'anaeuka, Wilbur 668 (DUKE). — KO'OLAU MTS.: Kahana, Abbott 178 (NY), Abbott s.n. (DS*); between Kuli'ou'ou Valley & Ka'alaikei Valley, Allen 6 (HAW); Honolulu, Andersson s.n. (S); Pauoa Valley, anonymous 106 (BISH); Palolo Valley, Bergman s.n. (BISH); Konahuanui-Olympus trail, Bergman s.n. (BH, BISH); Palolo-Mt. Olympus trail, Carlquist H4** (UC); Castle Trail, Carlquist 1725 (RSA); Punalu'u Valley, Carlquist 2212a (RSA*); Moanalua Valley, Carlquist 2411 (BISH, MICH, RSA); N. Halawa Valley, Char et al. s.n. (HAW); Halawa, Chock 232 (BISH); Kuli'ou'ou, Christophersen et al. 1508 (BISH, L); Kalihi, Christophersen & Hume s.n. (BISH); Ka'au Crater, Corn s.n. (BISH); Halawa, Cowan 555 (F, K), Cowan 979 (G, MIN, W); Schofield-Waikane trail, Crosby & Anderson 1608 (DUKE); Wa'ahila Ridge, Crosby & Anderson 1737 (BISH*, DUKE, GH, MICH*, UC); Tantalus, Degener 7828 (CAS, CU, GH, MICH, MO, NY, POM, UC, US); Manoa Valley, Degener 7830 (CAS, CU, K, GH, MASS, MICH, MO, NY, S, US, W, WIS), Degener et al. 11372 (A, B, LE, W);
between Pauoa Flats & Konahuanui, Degener 7848 (GH, NSW, NY); S. Halawa Gulch, Degener 7904 (BISH, NY); Waikane, Degener s.n. (B); Pig-God trail, Punalu'u, Degener et al. 7917 (CAS, CU, DS, MO, NY, P, S), Degener et al. 11088 (BISH), Degener et al. 11140 (B, BISH, CAS, G, WIS); Middle Halawa Ridge, Degener et al. 11373 (NY, W); Honolulu pali, Faurie 587 (BM, P, G); Tantalus, Forbes 1230 (BISH), Forbes 1231.0 (A, BISH); Kalihi Valley, Forbes 1256.0 (BISH); Lanikuhani trail, Forbes 1468.0 (BISH, L, NY, UC, US, W, WELT), Forbes & Stokes s.n. (BISH); Pacific Hts. Ridge, Forbes s.n. (BISH); Moanalua Valley, Forbes s.n. (W); between Punalu'u & Kaipapa'u, Forbes & Thompson s.n. (BISH, K, NSW); Pauoa Valley, Garber 126 (BISH); Konahuanui, Garber 132 (BISH), Garber 135 (BISH); Olympus, Gosline 51 (HAW), Gosline 52 (HAW); Kipapa-Wai'ahu ridge, Grant 7239 (BISH); Wa'ahila Ridge, Gupta 59 (HAW); Konahuanui, Heller 2239 (A, AC, E*, F, G, GH, K, MO, MSC*, NY, UC, US, Z); Wilamino Hts. trail, Herat & Herat 496 (B, BISH, HAW); Ka'au Crater, Herbst & Bishop 952 (HAW); Nu'uanu, Hillebrand 73 (K); between Poamoho Gulch & Punalu'u Gulch, Hosaka & Fosberg 1888 (BISH); head of Castle Trail, Hosaka & Fosberg s.n. (BISH); Olympus trail, Kruckeberg 71 (DS*), Kruckeberg 73 (DS), Kruckeberg 218 (DS); Poamoho Ridge, Lammers & Kama 5505 (OS*); Wai'alae Iki-Wailupe ridge, Lamoureux 146 (HAW), Lamoureux 498 (HAW); Kalaumoku-Halawa ridge, Lamoureux 160 (HAW); 'Aiea, Lamoureux 160a (HAW); Pupukea, Lamoureux 1486 (HAW); Tantalus, Meebold 8285 (M); Manoa, Meebold 20465 (M); Wa'ahila Ridge, Nagata 79 (HLA); Ka'alakei Ridge, Nagata 952 (HLA); Halawa Ridge, Nagata 996 (HLA, L); Olympus, Newell 77 (CAS), Newell 78 (CAS); Ka'au Crater,
Degener (1937) distinguished *Clermontia oblongifolia* f. *kaalae* by the pubescent lower surface of the lamina. Although such plants are confined geographically to the Wai'anae Mountains, plants with glabrous leaves occur sympatrically, often in the same population. Consequently, the pubescent-leaved plants of the Wai'anae Mountains cannot be recognized as a fourth subspecies.
The type specimen of Clermontia aspera (cf. Wimmer 1968: fig. 12b) is a mixed collection consisting of a detached inflorescence of C. oblongifolia subsp. oblongifolia and a vegetative shoot of Rollandia lanceolata Gaudich. subsp. calycina (Cham.) Lammers. Incredibly, Wimmer (1968) commented that the leaves resembled those of a Cyanea or Rollandia, but that the detached inflorescence was similar to that of Clermontia oblongifolia! It apparently never occurred to him that such an unlikely combination of characters might result from a mixed collection. The application of the name is fixed here by designating the detached inflorescence as the lectotype. The effect of this action is to retain the name within Clermontia as a synonym. If the vegetative shoot were selected, the name would become a synonym in Rollandia, and be excluded from Clermontia.


Lamina elliptic, 12-20 cm long, 3-5.4 cm wide; apex acuminate. Petiole 3-5 cm long, glabrous or pubescent. Inflorescence glabrous or
pubescent; peduncle 1.6-2.8 cm long; pedicels 2.2-4.2 cm long.

Hypanthium 1.4-1.8 cm long, 1.2-1.4 cm wide. Perianth 5.4-6.4 cm long; tube 3.2-4.2 cm long, 0.9-1.6 cm wide; lobes 1.8-2.5 cm long, 4-5 mm wide; bud acuminate at apex. Filaments magenta, 3.7-5.5 cm long; anthers purple, 1.3-1.7 cm long, 3-4.5 mm wide, glabrous or pubescent.

Distribution. (Fig. 19). Montane rain forests on Lana'i (800-900 m) and Maui (900-990 m).

SPECIMENS EXAMINED. LANA'I. mts. near Ko'ele, Forbes 44.L (BISH); Kaiholena, Munro 55 (BISH); Mahana Valley, Rock 8014 (A, BISH*, M, NSW*, NY, W), Rock 8014a (BISH*, L), Rock s.n. (US); Kaiholena, Rock s.n. (CAS, NY).

WEST MAUI. LAHAINA: Pu'u Kukui trail, Arakawa & Char 12-76 (PTBG*); trail to Violet Lake, Lammers & Hobdy 5690 (OS*).


Clermontia oblongifolia subsp. mauliensis might be mistaken for C. grandiflora, a much commoner species with which it is sympatric. In addition to the characters delineated above that distinguish Clermontia oblongifolia as a whole, this subspecies also differs from C. grandiflora by its longer petioles.

Lamina oblanceolate, 6-11.8 cm long, 1.6-3.6 cm wide; apex rounded, obtuse, or acute; lower surface pubescent on veins. Petiole 1.2-3 cm long, pubescent. Inflorescences glabrous or pubescent; peduncle 0.5-1 cm long; pedicels 1-2 cm long. Hypanthium 1.1-1.4 cm long, 1-1.4 cm wide. Perianth 6-7.5 cm long, glabrous; tube 3.6-5.7 cm long, 1-1.4 cm wide; lobes 1.8-2.5 cm long, 4-4.5 mm wide; bud obtuse or rounded at apex. Filaments magenta, 5.4-6.6 cm long; anthers purple, 1.3-1.5 cm long, 3.5-5 mm wide, glabrous.

Distribution. (Fig. 19). Endemic to Moloka'i. Montane cloud forests, 1220-1280 m.

SPECIMENS EXAMINED. MOLOKA'I. Pelekunu, Cranwell 3427 (GB); Papa'ala pali, Degener 7824 (A, DS, MO*, NY); 'Ohi'a lele pali, Degener 7836 (A, B, DS, MASS, MO, PH, UC, US), Degener 7838 (A), Degener 7846 (A, MO*, NY, PH); Pepeopae Bog, Degener 7837 (A, MO); Kamalo, Faurie 586 (A, BM, G, P, W); Kamalo, Hitchcock 15080 (US); Papa'ala pali, Lamoureux 1990 (HAW*); Pelekunu trail, Rock s.n. (A*, BISH, M).
Clermontia oblongifolia subsp. brevipes might be confused with sympatric populations of C. grandiflora subsp. munroi, because of its relatively small short-petiolate oblanceolate leaves. In addition to the differences discussed above that distinguish Clermontia oblongifolia as a whole from C. grandiflora as a whole, these two subspecies also may be distinguished by the shorter peduncle and pedicels of the former.


Delissea filigera Wawra, Flora 56: 31. 1873. -- TYPE: HAWAIIAN ISLANDS. "Kauai" [error for Waihe'e, West Maui], Wawra 1955 (holotype: W!).

Shrubs or trees, 1-6 m tall, terrestrial or rarely epiphytic. Lamina elliptic or oblanceolate, 4-15 cm long, 1.5-4.5 cm wide, chartaceous, dull; upper surface green, glabrous; lower surface pale green, glabrous or pubescent along the veins; margin callose-crenulate; apex acute, acuminate, or cuspidate; base cuneate or attenuate.
Petiole 0.2-2.8(3.7) cm long, glabrous or rarely pubescent.
Inflorescences 2(-5)-flowered, glabrous or rarely pubescent; peduncle
pendent, (1-)3-11 cm long, bibracteate at or near apex; pedicels
pendent, 1.6-7 cm long, bibracteolate near base. Hypanthium turbinate
or obovoid, 0.7-1.8 cm long, 0.9-1.5(-1.9) cm wide, glabrous. Perianth
tubular, 5.1-8.5 cm long, green, purple, maroon, or rose-colored, often
longitudinally striped; calyx lobes rarely only 2/3 as long as the
corolla, glabrous; tube curved or arcuate, 2.8-5.5 cm long, 0.6-2 cm
wide; lobes suberect or slightly spreading, 0.9-2.9 cm long, 2-7 mm
wide. Staminal column included or slightly exserted, curved or
arcuate; filaments purple or magenta, 4.8-7(-8.4) mm long; anthers
purple, 1-1.4 cm long, 2.5-3.5 mm wide, glabrous. Berries orange,
obovoid or subglobose, 1.6-2.6 cm long, 1-2 cm in diameter. Chromosome
number n = 14.

Clermontia grandiflora var. brevifolia is illegitimate and a
homotypic synonym of C. grandiflora (Rock 1919, St. John 1939a). Gray
(1861) explicitly cited the latter as a synonym in the protologue. The
two other varieties recognized by Gray, Clermontia grandiflora var.
longifolia and C. grandiflora var. oblongifolia, are regarded here as
synonyms of Clermontia hawaiensis and C. oblongifolia, respectively.

Delissea filigera clearly is referable to Clermontia grandiflora
on the basis of its long pendent peduncle and pedicel (Rock 1919), but
it is not possible to identify the subspecies represented. The
holotype bears only mature fruit, while the subspecies are
distinguished by floral characters. Further, it is not possible to suggest a subspecific placement on the basis of its provenance. The type, although labelled "Kauai", was collected above Waihe'e on West Maui (Wawra 1872-73, Hillebrand 1888, Rock 1919; see also discussion under Clermontia arborescens subsp. waiiae), where both Clermontia grandiflora subsp. grandiflora and C. grandiflora subsp. munroi occur. Consequently, Delissea filigera is cited as a synonym of the species as a whole, rather than one of its component subspecies.

The numerical phenetic analyses suggested that previous classifications of this species by St. John (1939a) and Wimmer (1943) are untenable, and that only three morphologically and geographically distinguishable groups of populations could be delimited. These are recognized here as subspecies, and may be identified by the following key.

KEY TO THE SUBSPECIES OF CLERMONTIA GRANDIFLORA

1. Perianth 7.8-8.5 cm long; hypanthium 1.9-2 cm wide; filaments 8-8.6 cm long.
   18c. C. grandiflora subsp. maxima.

1. Perianth 5.1-7 cm long; hypanthium 0.9-1.5 cm wide; filaments 4.8-7 cm long.

2. Perianth tube arcuate, narrower at middle than at base; lobes 2-4 mm wide.
18a. *C. grandiflora* subsp. *munroi*.

2. Perianth tube curved, wider at middle than at base; lobes 4-7 mm wide.

18b. *C. grandiflora* subsp. *grandiflora*.


Lamina 5-11.5 cm long, 1.5-4 cm wide; lower surface glabrous or pubescent along veins. Petiole 0.2-4 cm long. Peduncle (1-)2.5-11 cm long; pedicels 2.2-6(-7) cm long. Hypanthium (0.7-)0.9-1.5 cm long,
Perianth 5.2-7 cm long; calyx lobes sometimes as little as 3/4 as long as corolla; tube arcuate, 3.2-4.9 cm long, 0.6-1.5 cm wide, narrower at middle than at base; lobes 1-2.9 cm long, 2-4 mm wide. Filaments 5-7 cm long; anthers 1-1.3 cm long, 2.5-3 mm wide. Chromosome number $n = 14$.

Distribution. (Fig. 20). Montane rain forests and cloud forests on Moloka'i (875-1385 m), Lana'i (525-850 m), West Maui (670-1100 m), and East Maui (900-1975 m).

SPECIMENS EXAMINED. **MOLOKA'I**. Kawela Str., Anderson 520 (BISH); Kamoku Flats to Pu'u Kolekole, Crosby & Anderson 1665 (BISH*, DUKE*, MICH*); Lalanui, Degener 7793 (B, BISH, CAS, CU, G, GH, LD, MASS, MICH, MO, NY, US, W, WIS); Kamolo, Faurie 585 (A, BM, G, P); Pu'u Kolekole, Forbes 254.Mo (BISH*, K, UC*, W); Wailau Ahu., Kapapa pali, Higashino & Holt 9434 (BISH); Kamalo, Hillebrand s.n. (W); Wailau pali, Hillebrand s.n. (S); Puko'o, Mr. Conradt's place, Hitchcock 15013 (US); Kamoku, Rock 6117 (BISH, GH); Mapulehu, Rock 7068 (BISH, NSW, NY, US), Rock s.n. (A, NSW, UC, US); Halawa Ahu., Kawaiui Str., Stemmerman & Montgomery 3970 (BISH); Kalua'aha Ahu., Manawai Gulch, Warshauer & McEldowney 2387 (BISH); Kahanui Ahu., Waihanau Str., Warshauer & McEldowney 2409 (BISH); Wailau Ahu., Kapapa pali, Warshauer & McEldowney 2985 (BISH). -- NO PRECISE LOCALITY: Hillebrand s.n. (GH, MEL); Remy 306 (GH, L, P).

**LANA'I**. Munro Trail, Carlquist 2002 (BISH, RSA); Kaiohlena Ridge, Degener & Degener 28647 (BISH); Ha'alelepa'akai Ridge, Flynn 192 (BISH,
Fig. 20. Distribution of the subspecies of Clermontia grandiflora: subsp. grandiflora (open circles), subsp. maxima (triangle), subsp. munroi (dots).
PTBG), **Flynn 193** (BISH, PTBG), **Flynn 194** (BISH, OS, PTBG); Hauola Trail, **Flynn 208** (BISH*, PTBG*); Ko'tele, **Forbes 41.L** (BISH, F, M, MO, US, W); Kaiholena Gulch, **Hobdy 2196** (BISH); Munro Trail, **Lammers et al. 5823** (OS), **Lammers et al. 5824** (B. BISH, OS*); Lana'ihale, **Munro 25** (BISH), **Munro 442** (BISH*, P, UC), **Munro s.n.** (BISH*, UC, W); Kaiholena, **Munro 138** (BISH*), **Munro 209** (BISH), **Munro 402** (BISH*), **Munro s.n.** (BISH*); Ha'alelepa'akai, **Munro 157** (BISH); Mahana, **Rock 8018** (A, BISH, GH, K, L, NSW, NY, UC, US, W, WELT), **Rock s.n.** (NSW*); Lana'ihale, **Rock s.n.** (CAS, NY); Lana'ihale, St. John & Cowan **22660** (NY); Kaiholena-Ho'okio divide, St. John & Eames **18723** (BISH, F, NY, WELT); Lana'ihale, **Spence 318** (BISH, HLA, L). -- NO PRECISE LOCALITY: Hitchcock **14643** (US), **Hitchcock 14677** (US); **Munro s.n.** (BISH).

WEST MAUI. LAHAINA: Haela'au-Pu'u Kukui trail, **Carlquist H22A** (BISH, UC); Haela'au cabin, **Carlquist 1847** (BISH*, RSA*); Haela'au, **Fagerlind & Skottsberg 6689** (UPS, S), **Fagerlind & Skottsberg 6697** (UPS); Honokahau drainage basin, **Forbes 497.M** (BISH*, P, UC*, US, WELT*); Olowalu Valley, **Forbes 2398.M** (BISH, L); Pu'u Kukui, **Herbst & Bishop 1395** (HAW*); Pu'u Kukui trail, **Yoshinaga 222** (BISH). -- WAILUKU: 'Eke, **Degener 7939** (A, DS, MASS, MO, NY); mauka of McGregor, **Degener et al. 22065b** (B, MASS, NY, W); Iao Valley, **Faurie 584** (P); 'Eke trail, **Hobdy 924** (BISH).

EAST MAUI. MAKAWAO: Olinda pipeline, **Degener 7941** (BISH), **Degener 7942** (BISH), **Degener 7943** (A, NY), **Degener 11379** (NY), **Degener & Topping 7940** (NY); Ukulele, **Forbes 156.M** (BISH*, K, L, UC, US), **Forbes 929.M** (A, BISH*), **Forbes 932.M** (BISH); Waikamoi-Olinda flume, **Gillett**
The numerical phenetic analyses of *Clermontia grandiflora* suggested that the segregate species proposed by St. John (1939a) were very similar to one another, but that it might be appropriate to distinguish them collectively as a subspecies of *Clermontia grandiflora*. Of the seven available epithets, that of *Clermontia munroi*, which honors naturalist George C. Munro, was chosen for transfer.

Wimmer (1943) published the name *Clermontia grandiflora* var. *vulgata* for what he considered to be the common facies of that species on Moloka'i, Lana'i, and Maui. Three species were cited as synonyms: *Clermontia molokaiensis*, *C. munroi*, and *C. reticulata*. He cited the holotypes of these three species as syntypes of the new variety. The holotype of *Clermontia reticulata* was chosen to be the lectotype of
Clermontia grandiflora var. vulgata by Lammers (1988b), making these names homotypic synonyms. Only the autonymic forma of Clermontia reticulata is included in C. grandiflora subsp. munroi. As noted by Wimmer (1943) and Skottsberg (1944), Clermontia reticulata f. pilifera is indistinguishable from typical C. grandiflora.

20b. Clermontia grandiflora subsp. grandiflora.


Lamina 4-12 cm long, 1.5-4.5 cm wide; lower surface glabrous or pubescent along the veins. Petiole 0.8-2.8 cm long. Peduncle 2.2-8.5 cm long; pedicels 1.6-7 cm long. Hypanthium 1.1-1.6 (-1.8) cm long, 1.1-1.4 cm wide. Perianth 5.1-7 cm long; calyx lobes sometimes as little as 2/3 as long as corolla; tube curved, 2.8-6.4 cm long, 0.9-1.4 cm wide, wider at middle than at base; lobes 0.9-1.7(-2.1) cm long, 4-7 mm wide. Filaments 4.8-6.4 cm long; anthers 1-1.4 cm long, 2.5-3.5 mm wide. Chromosome number \( n = 14 \).

Distribution. (Fig. 20). Endemic to West Maui. Montane bogs, 610-1750 m.

SPECIMENS EXAMINED. WEST MAUI. LAHAINA: Pu'u Kukui, Arakawa & Char PKWM 80-76 (HAW); Pu'u Kukui, Bishop & Theobald 1149 (HAW); Violet Lake, Bishop & Theobald 1155 (HAW); Violet Lake, Bonsey & Suthers s.n. (MSC); Pu'u Kukui, Bryan 683 (BISH); Haela'au cabin, Carlquist H22 (UC), Carlquist 564 (RSA*), Carlquist 567 (RSA); Pu'u Kukui, Carlquist 559 (RSA), Carlquist 2139 (BISH, RSA), Carlquist 2152 (BISH, RSA); Pu'u Kukui, Char & Arakawa PKWM 38-76 (HAW, PTBG), Char & Arakawa 83-76 (HAW); Nakalalua, Cranwell et al. 2687 (BISH, GB); between Pu'u Kukui & Nakalalua, Cranwell et al. 2707 (BISH, GB); Honokahua-Amalu ridge, Cranwell et al. 3923 (BISH, GB, S), Cranwell et al. 3924 (BISH*, GB*); Pu'u Kukui, Cranwell & Skottsberg 2641 (GB); Pu'u Kukui, Crosby & Anderson 1877 (BISH, DUKE); Pu'u Kukui, Degener et al. 25024 (BM, K, LE, NSW, W); Haela'au-Pu'u Kukui trail, Ewart & Munro 102 (BISH, W);
Pu'u Kukui, Gillett 1784 (BISH, HLA), Gillett & Hobdy 2428 (BISH*, HLA*); Pu'u Kukui, Hitchcock 14762 (US), Hitchcock 14788 (US); trail to Violet Lake, Lammers & Hobdy 5664 (NY, OS*, US), Lammers & Hobdy 5666 (OS*), Lammers & Hobdy 5667 (MO, NY, OS*, US), Lammers & Hobdy 5673 (BISH, OS*), Lammers & Hobdy 5678 (BISH, K, MO, NY, OS*, PH, RSA, US, W, WIS), Lammers & Hobdy 5684 (OS*), Lammers & Hobdy 5689 (B, OS*, WIS); Pu'u Kukui, Munro 432 (BISH), Munro 619 (BISH); Nakalalua, Nagata 1003 (HLA*); between Pu'u Kukui & Nakalaloa, Nagata 3562 (HLA); Pu'u Kukui, Neal s.n. (BISH, W), Neal & Hartt s.n. (W); Honokowai, Rock 8193 (A, BISH, CAS, GH, L, NSW, US), Rock 8205 (BISH, GH), Rock s.n. (NY, US); Pu'u Kukui, Skottsberg 747 (BISH, GB, S); Pu'u Kukui, Wilbur & Webster 800 (BISH, DUKE*, US), Wilbur & Webster 860 (DUKE, UC), Wilbur & Webster 900 (DUKE*, MICH*). -- WAILUKU: Lanilili, Lammers 5848 (DUKE, K, OS*), Lammers 5849** (OS*), Lammers & Sylva 5622 (MO, OS*, RSA, W).

The numerical phenetic analyses suggest that two formae described from the bogs of West Maui be treated as synonyms of Clermontia grandiflora subsp. grandiflora. Both Clermontia grandiflora f. hamata and C. reticulata f. pilifera are characterized by a perianth with a curved tube wider at middle than at base and relatively wide lobes, and hence are referable to this subspecies. However, the autonymic forma of the latter is treated here as a synonym of C. grandiflora subsp. munroi. Similarly, two recently described species are also referable here. St. John (1983) described Clermontia earina as a new
species related to *C. kohalae* of Hawai'i. As diagnostic characters, he cited the novelty's smaller leaves, shorter petioles and peduncles, longer pedicels, green perianth, and glabrous anthers. The holotype does indeed differ from *Clermontia kohalae* in these features, but in these and other features, it is a perfect match for *Clermontia grandiflora* subsp. *grandiflora*. Subsequently, St. John (1987) described *Clermontia spatulata* as new. Although he failed to speculate on its affinities, the holotype is an ordinary specimen of *Clermontia grandiflora* subsp. *grandiflora*.

18c. *Clermontia grandiflora* subsp. *maxima* Lammers, subsp. nov. —


A subspecies ceteris *Clermontiae grandiflorae* floribus maximis perianthio 78-85 mm longo, hypanthio 1.9-2 cm lato, et filamentis connatis 8-8.6 cm longis differt.

Lamina elliptic, 6.3-9.5 cm long, 2.8-3.8 mm wide; lower surface pubescent, especially along the midrib; apex acute; base cuneate. Petiole 1.8-2.5 cm long, glabrous. Inflorescences 2-flowered, glabrous; peduncle pendent, 4.4-4.6 cm long; pedicels pendent, 5.8-6.2 cm long. Hypanthium obovoid, 1.5-1.6 cm long, 1.9-2 cm wide, glabrous. Perianth 7.8-8.5 cm long; calyx lobes subequalling corolla; tube
arcuate, 4.6-5.5 cm long, 1.4-2 cm wide, narrower at middle than at base; lobes 2.2-3 cm long, 3-5.5 mm wide. Filaments 8-8.6 cm long; anthers 1.1-1.3 cm long, 3-4 mm wide. Berries unknown.

Distribution. (Fig. 20). Endemic to East Maui. Montane cloud forest, 1645 m, on the windward slopes of Haleakala.

_Gagne & Montgomery 386_ resembles _Clermontia grandiflora_ subsp. _munroii_ by its dull chartaceous elliptic leaves, pendent inflorescence, obovoid hypanthium, and arcuate perianth narrower at the middle than at the base and much longer than the lobes, but differs from all other known specimens of either subspecies by its enormous flowers. If one were to regard the perianth as a perfect cylinder and calculate its volume from the maximum length and width values, the flowers of this specimen are twice as large as those of the next largest specimen (24.5 cm$^3$ vs. 12.4 cm$^3$). Linear measurements of various floral structures similarly are substantially larger than the next largest known. The perianth is 11-21% longer; hypanthium, 27-33% wider; and filaments, 14-23% longer. These major gaps in the spectrum of variation are also evident in the Principal Components Analysis performed on this species. However, this specimen does not deviate from _Clermontia grandiflora_ in any qualitative floral characters, nor in any vegetative features. Consequently, it is described here as a new subspecies of _Clermontia grandiflora_, and christened with a most appropriate epithet.

Shrubs, 1.2-5 m tall, terrestrial. Lamina oblanceolate, elliptic, or broadly elliptic, 5-10 cm long, 1.8-4.5 cm wide, chartaceous, dull; upper surface dark green often tinged purple, glabrous or sparsely pubescent; lower surface pale green, sparsely or densely pubescent; margin salloose crenulate; apex acute, acuminate, or cuspidate; base attenuate, cuneate, or obtuse. Petiole 0.5-2.5 cm long, pubescent. Inflorescences 2(-5)-flowered, pubescent; peduncle spreading 0.4-1.8 cm long, bibracteate at or near apex; pedicels spreading, 1.2-2.8 cm long, bibracteolate at base. Hypanthium turbinate or obovoid, 0.8-1.4 cm long, 0.5-1 cm wide, glabrous or pubescent. Perianth tubular, 3.6-5.5 cm long, rose-colored or white tinged green, glabrous; tube curved or arcuate, 2-3.8 cm long, 0.5-1 cm wide; lobes slightly spreading, 1-2 cm long, 2-4 mm wide. Staminal column slightly exserted, curved or arcuate; filaments purple or magenta, 3.5-5.5 cm long; anthers purple, 1-1.3 cm long, 2.5-3 mm wide, glabrous. Berries unknown.

Clermontia samuelii resembles C. grandiflora, but differs by its shorter spreading inflorescence, more densely pubescent leaves, and smaller flowers. Forbes (1920) named it in honor of Samuel A. Baldwin.
of Makawao, Maui, who had accompanied him while collecting on Haleakala. As here circumscribed, this species comprises two subspecies, which may be distinguished by the characters given in the key below. These morphological differences are correlated with clear ecological differences. The autonymic subspecies grows in montane cloud forests at 1675-2100 m, while the other grows in montane cloud forests at 610-915 m. This species thus displays an interesting pattern of subspecific differentiation along an altitudinal gradient.

KEY TO THE SUBSPECIES OF CLERMONTIA SAMUELI

1. Lamina broadly elliptic, 5-7.5 cm long, lower surface sparsely pubescent; petiole 0.5-1.2 cm long; perianth white tinged green, 4-5.5 cm long; filaments 4.5-5.5 cm long.

   21b. C. samuelii subsp. hanaensis.

1. Lamina oblanceolate or elliptic, 8-11 cm long, lower surface densely pubescent; petiole 1.2-2.5 cm long; perianth rose-colored, 3.6-4.8 cm long; filaments 3.5-4.6 cm long.

   21a. C. samuelii subsp. samuelii.

Lamina broadly elliptic, 5-7.5 cm long, 2.7-4.5 cm wide; lower surface sparsely pubescent; apex acute, acuminate, or cuspidate; base cuneate to obtuse. Petiole 0.5-1.2 cm long. Peduncle 0.4-1 cm long; pedicels 1.2-2.8 cm long. Perianth 4-5.5 cm long, white tinged green; tube 3.2-3.8 cm long, 0.7-1 cm wide; lobes 1.5-2 cm long, 3-4 mm wide. Filaments 4.5-5.5 cm long.

Distribution. (Fig. 21). Endemic to East Maui. Montane rain forests, 610-915 m, on the windward slopes of Haleakala.

SPECIMENS EXAMINED. EAST MAUI. HANA: Nahiku Ahu., e. of Kukiwa Str., Higashino & Holt 9169 (BISH); Makapu'u Ahu., e. of Mokulehua Gulch, Higashino & Holt 9320 (BISH).

St. John (1939a) described Clermontia hanaensis as a new species most closely related to C. samuelii of higher elevations in the same region. The diagnostic characters used by St. John (1939) are indeed useful for distinguishing the two. However, in light of their great overall similarity (cf. Wimmer 1943, Degener & Degener 1960b), recognition as conspecific subspecies is judged more appropriate.

21b. Clermontia samuelii subsp. samuelii.

TYPE: HAWAIIAN ISLANDS. East Maui: Hana Distr., Kipahulu Ahu.,
northeast slope of Haleakala, 1.2 km east of Lake Wai'anapanapa,
Hana Forest Reserve, ca. 5960 ft, 28 Jun 1980, Higashino & Holt
9278 (holotype: BISH!).

Clermontia kipahuluensis H. St. John, Phytologia 63: 351. 1987.—
TYPE: HAWAIIAN ISLANDS. East Maui: Kipahulu, Warshauer et al.
2886 (holotype: BISH!).

Lamina oblanceolate or elliptic, 8-11 cm long, 2.8-3.5 cm wide;
lower surface densely pubescent; apex acute; base attenuate or cuneate.
Petiole 1.2-2.5 cm long. Peduncle 1.3-1.8 cm long; pedicels 1.5-2.8 cm
long. Perianth 3.6-4.8 cm long, rose-colored; tube 2-3.2 cm long, 5-8
mm wide; lobes 1-2 cm long, 2-3.5 mm wide. Filaments 3.5-4.6 cm long.

Distribution. (Fig. 21). Endemic to East Maui. Montane cloud
forests, 1675-2100 m, on the windward slopes of Haleakala.

SPECIMENS EXAMINED. EAST MAUI. HANA: near Wai'ele'ele, Cahill
520 (BISH); Haleakala, n. slope, Forbes 1215.M (BISH, NY, P, UC); n.
rim, Kipahulu Valley, Harrison 287 (BISH), Harrison 393 (BISH),
Harrison 428 (BISH).
Fig. 21. Distribution of *Clermontia hawaiensis* (dots) and the subspecies of *C. samuelii*: subsp. *hanaensis* (open triangles), subsp. *samuelii* (closed triangles).
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St. John (1971) described Clermontia rosacea as a new species that differed from its closest relative, C. montis-loa of Hawai'i, by its shorter, wider, chartaceous laminas; shorter petioles; longer pedicels; longer rose-colored corolla, and longer upper anthers. Although the holotype of this novelty is indeed quite different in these features from Clermontia montis-loa, it is indistinguishable on any basis from Clermontia samuelii subsp. samuelii. Although St. John (1987) did not indicate how his other two novelties from Hana District differ from one another or from previously described species, they, too, are indistinguishable from Clermontia samuelii subsp. samuelii.

HAWAIIAN ISLANDS. Hawai'i: Hilo & Kilauea, Hillebrand & Lydgate s.n. (lectotype: BISH!).

-- TYPE: HAWAIIAN ISLANDS. Hawai'i: Makaopuhi, Hoside & Kawaloa 2-5 (holotype: BISH!).

Trees or shrubs, 1.5-9 m tall, terrestrial or epiphytic. Lamina oblong or oblanceolate, 9-24 cm long, 2.5-6.5 cm wide, coriaceous; upper surface dark green, glossy, glabrous; lower surface very pale green, glabrous or pubescent on the veins; margin callose-crenulate; apex acuminate, acute, obtuse, or rounded; base attenuate. Petiole 2-7 cm long, glabrous. Inflorescences 2(-4)-flowered, glabrous or pubescent; peduncle spreading, 1.5-6 cm long, bibracteate at middle or apex; pedicels spreading, 1.5-4 cm long, bibracteolate at middle or base. Hypanthium obconic, 1.7-2.2 cm long, 1.1-1.8 cm wide, glabrous, with 10 longitudinal ridges, the uppermost one forming a definite keel. Perianth tubular, 5-6.5 cm long, greenish-white sometimes tinged purple or magenta, glabrous; tube curved, 3-4.6 cm long, 0.9-1.8 cm wide, narrower at middle than at base; lobes suberect or spreading slightly, 1.1-2.2 cm long, 3-7 mm wide, each outer one with a prominent median longitudinal ridge. Staminal column included or slightly exserted, curved; filaments magenta or rarely greenish-white, 4-5 cm long, glabrous; anthers purple or rarely greenish-white, 1.5-1.8 cm long, 4-5 mm wide, glabrous or sparsely pubescent. Berries orange, obconic, obovoid, or ellipsoid, 2.5-3.7 cm long, 1.5-3 cm in diameter, with 10 longitudinal ridges.
Distribution. (Fig. 21). Endemic to Hawai'i. Montane rain forests, 550-1760 m, on the windward slopes of Mauna Kea and Mauna Loa. The report from leeward Mauna Loa by Skottsberg (1936) was based upon a misidentified specimen (Skottsberg 1935; BISH, GB, S) of Clermontia clermontioides subsp. rockiana, as was his subsequent report (Skottsberg 1944) from Hualalai (Skottsberg 666, GB). The reports from Moloka'i by Degener and Degener (1958b) and Wimmer (1953, 1968) are based upon a misidentified specimen (Degener 7826, NY) of Clermontia kakeana Meyen.

SPECIMENS EXAMINED. HAWAI'I. SOUTH HILO: Hilo, Faurie 580 (A, G, P), Faurie 581 (BM, G, P), Faurie 582 (P); RR from Waiakea to 'Ola'a Mill, Forbes 641.H (BISH); s. of Hilo, MacDaniels 228 (NSW); above Hilo, Rock s.n. (GH); Ha'ena, Skottsberg 460 (BISH, GB); w. of Pahoa, Skottsberg 461 (BISH, GB). -- PUNA: road to Glenwood, Carlquist 599 (RSA); 24-mile mark, Hilo-Volcano hwy., Carlquist 2240 (BISH, C, DAV, DUKE, E, G, GH, K, L, LE, MICH, RSA, UC); Kapoho, Degener 7815 (A, MO, NY), Degener 7819 (MO, NY); 27 Miles, Degener & Degener 30798 (B, MASS, NY), Degener & Degener 32492 (C), Degener & Degener 33567 (LE), Degener & Degener 35060 (W, Z), Degener 35163 (WELT); Kea'au forest, Degener & Degener 30799 (A, L, MASS, W); 'Ola'a forest, Degener & Degener 30800 (E, K, M, MASS, MIN, MSC, NSW, TI, UPS, Z); makai of Makaopuhi Crater, Degener & Degener 31679 (W); se. of Belt Road, Degener & Degener 32410 (LD, MIN, NSW, P, S, U, UPS, WELT, WIS); beyond end of 20 Mile Rd., Funk 206 (BISH); 24 Miles, Giffard 337 (BISH, MAK); between Kapoho &
Pahoa, Giffard s.n. (BISH); Hwy. 11, 23 miles from Hilo, Herbst 947
(BISH, HAW, HLA, L, US); between 'Alae & Heake Craters, Hoe 1466.0
(HAW); Hwy. 11, between markers 25 & 26, Lammers 5448 (OS), Lammers
5449 (OS, PH, W), Lammers et al. 5811 (OS); Kea'au Ahu., S. Glenwood
Rd., Lammers et al. 5815 (OS); Chain-of-Craters Rd., van Loben Sels 614
(UC); Volcano Rd., MacDaniels 113 (BH); Chain-of-Craters Rd., Matsunami
s.n. (DUKE); 27 Miles, Morley 132-HJ (BISH); Napau Crater, Morley 187-H
(POM); Volcano Rd., Rock 8801 BISH, GH), Rock 12847 (BISH); Napau
trail, St. John et al. 11226 (BISH, W); between Kalapana & Pohoiki,
Setchell & Setchell s.n. (UC); Volcano Rd., Setchell & Setchell s.n.
(S, UC); Sulphur Banks, Shipman s.n. (BISH); Kahauale'a Ahu., Volcano
Hwy., Stemmerman & Montgomery 3808 (BISH); Kane Nui o Hamo, Stone 2988
(BISH, US); between Makaopuhi & 'Alae, Webster & Wilbur 1770 (DUKE).
-- KA'U: Bird Park, Degener 7820 (BISH, NY), Degener 18074 (A, NY);
Ka'alaikii, Degener & Degener 25150 (A, B, E, G, MTCH, NY, W); Bird
Forest, Eastwood s.n. (CAS); Kilauea Iki, Fagerlind & Mitchell 244
(BISH); Chain-of-Craters Rd., Fagerlind & Skottsberg 6263 (S);
Kapapala, Forbes 376.H (A, L, M); Palakea fence line, Forbes 1002.H
(BISH, WIS); above Ollie Shipman's, Forbes 1038.H (BISH, DS, NY, P, UC,
US); Kilauea, Forbes et al. s.n. (A, BISH); Crater Rd., Giffard 333
(BISH); Kalanilehua, Giffard 335 (BISH, K, NSW, P); Kilauea F. R.,
Herat et al. 1014 (BISH, HAW); trail to Thurston Lava Tube, Lammers
5393 (OS); Kipuka Puaulu, MacDaniels 98 (BH); Kilauea, Meebold 20973
(M); Kilauea, Rock 8762 (A, BISH, L), Rock 8771 (A, BH, BISH), Rock
8802 (BISH, GH), Rock 8803 (BISH, GH, K, L, P, S, UC, US, W), Rock s.n.
Clermontia hawaiiensis is morphologically similar to C. oblongifolia subsp. mauliensis, but differs by the larger 10-ridged hypanthium, 5-ridged perianth with curved tube, and obconic, obovoid, or ellipsoid 10-ridged berries. Rock (1913, 1919) called Rock 8803 the type of Clermontia hawaiiensis. However, he explicitly based this species upon Clermontia macrocarpa var. hawaiiensis, making the two names homotypic. The correct choice for the type would be a specimen collected by Hillebrand. Rock (1919) cited such a specimen deposited at B, and should have designated it as the lectotype. Unfortunately, this sheet was destroyed in 1943. The only other sheet collected by Hillebrand that is known to me is designated here as the lectotype.

The inclusion of Clermontia grandiflora var. longifolia as a synonym requires explanation. In the protologue, Gray (1861) cited no type specimen, only the synonyms "C. grandiflora, [sensu] Hook. & Arn. C. kakeana, Meyen ... C. macrophylla, Nutt. C. macrocarpa, Gaud. ..." and an unpublished herbarium name referable to C. kakeana. All these names refer to a single species, Clermontia kakeana, found on O'ahu, Moloka'i, and Maui. Consequently, subsequent authors have treated Gray's variety as a synonym of that species, tacitly assuming that Gray was simply proposing a new name at varietal rank for that species. In
this case, Gray's epithet would be homotypic with one of the synonyms, and a lectotype would have to be selected from among the types of these names. However, none of the type specimens of these names is a good match for Gray's brief diagnosis, and it is difficult to decide which would be the most appropriate choice for a lectotype.

However, one might alternatively interpret Gray's action as the description of a new variety based on a new type. The other species cited would then have been heterotypic synonyms in Gray's opinion. If this were the case, the type of Clermontia grandiflora var. longifolia would be some specimen studied and annotated by Gray. Only one such specimen has been located, a sheet at US collected by the United States Exploring Expedition and labelled by Gray as Clermontia grandiflora var. longifolia. This specimen matches the diagnosis well, and is here interpreted as the holotype. Unfortunately, this sheet was collected on Hawai'i, where Clermontia kakeana does not occur, and is a specimen of Clermontia hawaiensis. For this reason, Clermontia grandiflora var. longifolia is treated as a synonym of that species and not C. kakeana.

The large 10-ridged hypanthium and berry and 5-ridged perianth of Clermontia hawaiensis are very distinctive, and it is surprising that Wimmmer (1943) did not notice that the type of Clermontia kohalae var. hiloensis also exhibits these characters. This variety also differs from typical Clermontia kohalae by its glossy coriaceous leaves, and is treated here as a synonym of Clermontia hawaiensis. Similarly, St. John (1987) did not notice these features on the holotype of Clermontia
*subteralbulus*, which also is placed in synonymy under *C. hawaiensis*.
EXCLUDED NAMES

Clermontia carinifera A. Léveillé, Repert. Spec. Nov. Regni Veg. 12: 505. 1913. -- TYPE: HAWAIIAN ISLANDS. Kaua'i: Koloa, Dec 1909, Faurie 10 (holotype: not located). Léveillé's personal herbarium was purchased by E in 1919 (Stafleu & Cowan 1979), while duplicates of Faurie's Hawaiian collection are deposited at A, BISH, BM, and P (Lauener 1980). However, previous monographers of the Lobelioideae (Rock 1919, Wimmer 1943) and scholars studying the work of Léveillé (Chamberlain 1977, Lauener 1980) have been unable to locate type material for this name. My own attempts, involving over 50 herbaria (listed in the acknowledgments), were likewise unsuccessful. In the absence of a type, a positive identification is not possible. However, the meagre diagnosis (cf. Rock 1914, Lauener & Green 1961, St. John 1980a) and provenance of the specimen suggest that this name may be referable to Cyanea fissa (H. Mann) Hillebrand. It was not uncommon for Léveillé to mistakenly attribute his novelties to the wrong genus or family (Rock 1913c, 1914; Lauener & Green 1961).

However, subsequent workers (Wimmer 1943, Chamberlain 1977, Lauener 1980), including myself, have been unable to locate it in any herbarium. The brief diagnosis and the provenance of the type suggest that the name may be referable to *Cyanea sylvestris* A. Heller.


*Clermontia pluriflora* H. St. John, Phytologia 63: 351. 1987. — **TYPE:**


This specimen differs from other species of *Clermontia* by its 3-6-flowered inflorescences and corolla dorsally cleft only to the middle. These features are characteristic of *Cyanea*, and the type
is in fact an ordinary specimen of *Cyanea sylvestris* A. Heller.

**Moquinia** A. Sprengel, Tent. Suppl. Syst. Veg. 9. 1828, nom. rejic.; non

**Moquinia** DeCandolle, Prodr. 7: 22. 1838, nom. conserv. -- TYPE:

**Moquinia rubra** A. Sprengel, Tent. Suppl. Syst. Veg. 10. 1828. =

**Moquiniella** Balle, Bull. Seances Inst. Roy. Colon. Belg. 25: 1628. 1954. Bartling (1830) and Lindley (1836) listed this genus as a synonym of *Clermontia*, although its sole species was not formerly transferred. The genus clearly cannot be referred to *Clermontia* or any other genus of Lobelioidae, as its type is a species of Loranthaceae.
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Chapter II
EVOLUTION OF THE ENDEMIC HAWAIIAN GENUS
CLERMONTIA (CAMPANULACEAE: LOBELIOIDEAE)

INTRODUCTION

The Hawaiian Islands are the most isolated archipelago of significant size and physical diversity in the world (Wagner, Herbst & Yee 1985; Takhtajan 1986, Simon 1987). The nearest continent, North America, lies over 3800 km to the east, while the nearest other high islands, the Marquesas, are nearly as far to the south. The archipelago comprises eight major islands (from southeast to northwest): Hawai'i, Maui, Kaho'olawe, Lana'i, Moloka'i, O'ahu, Kaua'i, and Ni'ihau. Beyond these, the archipelago continues as a line of 124 islets, atolls, and reefs called the Leeward Islands. Beyond the last atoll, a line of guyots known as the Emperor Seamount Chain extends toward Kamchatka. Some of these apparently were once high islands comparable in size and elevation to the eight major islands (Jackson 1976, Sibley & Ahlquist 1982, McKenna 1983, Beverley & Wilson 1985).

Each island was created by volcanic eruptions from a melting anomaly or "hot-spot" in the asthenosphere (Wilson 1963, Morgan 1972, Jackson 1976, Rotondo et al. 1981). Over the last 70 million years (my), the Pacific Plate migrated northwestwardly over this relatively
stationary hotspot, displacing the islands away from the point source of magma. Vulcanism ceased and subaerial erosion progressed. As a result of this mode of origin, the archipelago is distinctly linear and its various elements are arranged in chronological sequence. The ages of the eight major islands range from 0.7 my (Hawai‘i) to 5.6 my (Kaua‘i), while ages between 7 my (Nihoa) and 70 my (Meiji Guyot) have been determined for the Leeward Islands and Emperor Seamount Chain (MacDonald and Abbott 1970; Jackson 1976; Jarrard & Clague 1977; Porter, Stuivert & Yang 1977). Older products of the mid-Pacific hotspot possibly have been subducted beneath the Eurasian Plate at the juncture of the Kurile Trench and Aleutian Trench.

Because of this de novo origin and extreme isolation, the indigenous flora is derived entirely from taxa capable of dispersal over enormous tracts of ocean via air flotation, oceanic drift, and birds. Carlquist (1967, 1974) estimated that only about 260 angiosperms accomplished this and established successfully in the archipelago. Of these, approximately one-third did not differentiate, i.e., Hawaiian populations are conspecific with extra-Hawaiian populations. In the remaining two-thirds, however, dispersal and establishment were followed by speciation. These 170 colonists gave rise to approximately 870 endemic species (Wagner, Herbst & Sohmer, in press). Stated another way, each species that successfully colonized the Hawaiian Islands and underwent differentiation has given rise to an average of five novel species each. Some colonists have given rise to much larger numbers of endemic species.
Carson (1985) has suggested that the term speciose be used to describe monophyletic lineages which have produced a relatively large number of species. Clearly, if one wishes to understand patterns and processes of evolution, speciose lineages offer excellent research opportunities. Unfortunately, the taxonomy of most of these groups is poorly understood (Fosberg 1948, Carlquist 1972), and modern revisions are needed before detailed evolutionary studies are possible (Wagner et al. 1985).

The most speciose lineage in the Hawaiian flora is a group of four genera of Lobelioideae (Campanulaceae) treated by Wimmer (1943) as subtribe Cyaneinae: Clermontia Gaudich. (22 spp.), Cyanea Gaudich. (51 spp.), Delissea Gaudich. (9 spp.), and Rollandia Gaudich. (8 spp.). These four genera are distinguished from all other lobelioid genera by their woody habit, axillary inflorescences, and baccate fruits. The monophyly of the group is supported by these unusual morphological features and their common chromosome number \( n = 14 \); Lammers 1988).

Previous authors have suggested that the Cyaneinae were derived from South American genera with baccate fruits (Hemsley 1885, Guppy 1906, Rock 1919, Carlquist 1974), or that they were of vague "austral" affinities (Skottsberg 1939, Fosberg 1948). However, recent studies (Lammers 1985; Lammers & Stein, in prep.) indicate that the Cyaneinae are derived from certain Indo-Malayan species of Pratia Gaudich. sect. Colensoa (J. D. Hook.) Hemsl. These species have baccate fruits, which makes it likely that they were dispersed to the Hawaiian Islands via frugivorous birds. Seeds may have been transported within the
gastro-intestinal tract or attached to facial feathers by the viscid remains of the pericarp (Carlquist 1966, 1974). From this initial colonist, 90 historically known species have evolved. Carlquist (1974), Ehrendorfer (1979), Simon (1987), and others have pointed out the critical need for evolutionary studies in this biologically fascinating group of endemics.

The recent completion of a taxonomic revision of one of these genera, Clermontia, affords the opportunity to undertake evolutionary studies among these plants. A monographer may lack expertise in the techniques of biosystematics, molecular biology, and population genetics; however, the intimate knowledge gained through detailed taxonomic study uniquely qualifies that person to generate hypotheses regarding various aspects of evolution in that group (Stuessy 1975). This is particularly true if the monograph is based upon field study, where the plants are viewed as living organisms in an integrated environment, and insights on species biology may be gained.

Clermontia includes 22 species and nine additional subspecies, found in wet forest and bog habitats on the six largest islands at elevations of 150-2100 m above sea level. The species are classified into two sections of three series each, on the basis of differences in floral morphology. This chapter will examine the origin and diversification of the genus, suggest modes of speciation that may have been operative, and discuss the possible role that pollinators may have played in the evolution of the genus.
ORIGIN AND DIVERSIFICATION

The Hawaiian archipelago affords a unique opportunity to discuss the chronistic dimension of evolution (cf. Stuessy 1983, 1987) with a reasonable degree of confidence, due to the known ages of the islands. Even without fossil evidence, one may infer the timing of various evolutionary events on the basis of phylogenetic patterns and island ages. The best example is provided by the so-called "picture-winged" species of Drosophila Fallen (Diptera: Drosophilidae). The evolution of this incredibly speciose lineage (106 species from a common ancestor) has been the subject of an intensive multidisciplinary study for over 20 years (Carson 1971, 1974, 1983, 1987; Carson & Kaneshiro 1976; Spieth 1982; Beverley & Wilson 1985). Their phylogeny has been reconstructed with a high degree of confidence, on the basis of chromosomal rearrangements and the geologic history of the archipelago. This in turn has made possible a detailed understanding of the patterns of inter-island dispersal and diversification. These patterns will be used for comparison with Clermontia in the following discussion, as they provide the best available information on this topic.

The derivation of Clermontia from species of Cyanea sect. Delisseoideae is well supported on the basis of comparative morphology. The cladistic analysis indicates that Clermontia cleromonticoides (Gaudich.) A. Heller is the most primitive species of the genus, i.e.,
the one least changed from the hypothetical ancestor (Fig. 10). This species is endemic to the very youngest island of the archipelago, Hawai'i, which is the product of seven separate volcanoes (MacDonald & Abbott 1970, Jackson 1976, Jarrard & Clague 1977). The first to appear above the sea was Kohala, approximately 700,000 years ago. About 200,000 years later and 100 km south, the outpourings of Ninole volcano created an island that eventually rose to a height of 2400 m. The island of Kohala increased in size through the incorporation of the subsequent Hualalai and Mauna Kea volcanoes. Ninole increased in size through the subsequent development of Kulani volcano, but remained separate from Kohala-Hualalai-Mauna Kea until connected by outpourings from Mauna Loa volcano.

Because the distribution of Clermontia clermontioides is restricted to southwestern Hawai'i, one might hypothesize that the genus originated on Ninole no more than 500,000 years ago. However, this raises several problems. First, this point of origin is at the maximum possible distance from the putatively ancestral species of Cyanea on Kaua'i. Although such a dispersal is not impossible, one would expect that dispersal would be commonest among adjacent islands. For example, among the picture-winged drosophilids, nearly 85% of the 45 inter-island dispersal events were between two adjacent islands (Carson 1983, 1987). In only one instance did a species "leap-frog" all the way from Kaua'i to Hawai'i. Second, an origin on Hawai'i would require a larger number of "back-migrations", i.e., dispersals from a younger island to an older one, and leave precious little time for
them. The biota of an older island is more stable, with fewer open niches, and thus more difficult to colonize (MacArthur & Wilson 1967, Carlquist 1974, Gorman 1979, Williamson 1981). Among the picture-wings, only 20% of the inter-island dispersal events were back-migrations (Carson 1983, 1987). Most importantly, in no instance was a species dispersed from Hawai'i to an older island. These general patterns suggest caution in accepting the hypothesis of an origin on Hawai'i in the last 500,000 years.

An independent estimate of when and where Clermontia diverged from Cyanea is provided by recent data on host-plant specificity among the picture-winged drosophilids. Numerous species utilize rotting tissue (stems, roots, leaves, flowers, fruits) of endemic Lobelioideae as ovipositing sites and larval substrates (Heed 1971, Montgomery 1975, Carson & Kaneshiro 1976). The species of Clermontia on O'ahu and Kaua'i are not utilized by picture-wings; lobelioid-feeders there use Cyanea only. Spieth (1982) interpreted this as evidence that, among lobelioid-feeders, utilization of Cyanea is a primitive trait, while use of Clermontia is derived. Apparently, Clermontia's unique repeatedly branched habit offered a superior array of niches (i.e., ovipositing sites) into which the picture-wings were able to radiate (Spieth 1982). This shift in host-plants is an example of association by descent (Mitter & Brooks 1983; Humphries, Cox & Nielsen 1986).

Picture-wings exploited Clermontia because they previously had exploited its ancestor. In essence, they "rode along" as the genus diverged from Cyanea and diversified.
On the basis of the phylogeny and behavioral ecology of the picture-wings and the geological history of the archipelago, Spieth (1982) concluded that Clermontia first became a nutritional resource for picture-wing larvae on Maui Nui approximately 1.8 my ago. Maui Nui is the name used for the ancient island formed from modern Moloka'i, Lana'i, and Maui by eustatic changes in sea level during the Pleistocene (MacDonald & Abbott 1970, Stearns 1978). This term is also used as a collective name for the three modern islands, particularly by biogeographers (Juvik & A string 1979, Olson & James 1982, Carson 1987).

Because Clermontia and picture-wings are associated by descent, Spieth's (1982) conclusion strongly suggests that Clermontia diverged from Cyanea on Maui Nui approximately 1.8 my ago. If Clermontia has been utilized by picture-wings for 1.8 my, it certainly could not have originated on Hawai'i, which is less than 700,000 years old. Similarly, it could not have arisen on Kaua'i or O'ahu 2.2-5.6 my ago; if it had, the species there should be utilized by picture-wings. From this we may infer that the species of Clermontia on O'ahu and Kaua'i are relatively recent immigrants from younger islands.

The only datum not concordant with the hypothesis that Clermontia originated on Maui Nui is the present lack of plesiomorphic species of sect. Clermontioideae on those islands. This absence might be attributable to extinction, either of populations of Clermontia clermontioides on Maui Nui, or of some more primitive species. Little is known about the nature and extent of prehistoric extinctions and
range reductions among the Hawaiian angiosperms. Among the birds, the only Hawaiian land animals with a significant fossil record (Olson & James 1982), extinction was certainly very common.

On the basis of all available data, it is hypothesized that Clermontia diverged from some species similar to Cyanea hirtella and C. sylvestris on Maui Nui not more than 1.8 my ago. The first product of divergence, either Clermontia clermontioides or an even more primitive species similar to it, subsequently was extirpated from Maui Nui. This hypothesis is concordant with the data from drosophilid host-plant specificity, requires the fewest back-migrations, and puts the geographic origin of the genus closer to the source area of the putatively ancestral species of Cyanea.

From this point of origin on Maui Nui approximately 1.8 my ago, the genus has spread throughout the the six largest islands of the archipelago. Frugivorous birds undoubtedly have served as agents of dispersal. A particularly likely candidate for a major role is Psittirostra psittacea (Gmelin) (Fringillidae: Drepanidinae), which formerly occurred in montane forests on the six largest islands. Unlike most drepanids, Psittirostra often wanders over great distances, typically in large flocks (Perkins 1903, Amadon 1950). Geographic races are not discernible, which suggests that gene flow within the archipelago (i.e., inter-island flights) have occurred frequently enough to forestall divergence (Amadon 1950, Grant 1980). This bird is known to have fed preferentially upon the berries of Clermontia (Perkins 1903, Munro 1944), and so may have been important in the
Comparison of the phylogeny of Clermontia (Fig. 10) with the geological history of the archipelago suggest the following biogeographic patterns. Following the divergence of the genus from Cyanea, a total of 14 dispersal events are believed to have occurred among the four major land masses of the archipelago (Fig. 22). All dispersals involved adjacent islands; the majority (79%) were from older islands to younger islands, specifically from O'ahu to Maui Nui (29%) and from Maui Nui to Hawai'i (50%). Only three (21%) proceeded in the opposite direction: two from Maui Nui to O'ahu, one from O'ahu to Kaua'i. This pattern is concordant with the view that colonization of older, biotically stable islands is more difficult than colonization of young islands with many open niches. Of the 22 known speciation events, eight (36%) were associated with inter-island dispersal; the remainder occurred autochthonously. Only six (43%) of the inter-island dispersals were not accompanied by speciation.

Very similar patterns were reported among the picture-wings by Carson (1983, 1987). The majority of dispersals (85%) were among adjacent islands, and (80%) from older to younger islands. Dispersals from Maui Nui to Hawaii were most common (33%); next in order were dispersals from O'ahu to Maui Nui (22%), and Kaua'i to Oa'hu (11%). The last pattern does not occur in Clermontia because that genus originated on young islands (< 2 my old) east of Kaua'i, while the picture-wings apparently diverged from their ancestors in the Leeward Islands west of Kaua'i 35 my ago (Beverley & Wilson 1985).
Fig. 22. Patterns of dispersal in Clermontia. Integers on islands indicate number of autochthonous speciation events; fractions on arrows indicate number of inter-island dispersal events not involving speciation (numerator) and number accompanied by speciation (denominator).
These general similarities suggest that using the biogeography of the picture-wings for comparison with Clermontia is justifiable.
Elucidation of the processes by which new species arise from existing species is best accomplished through synthesis of diverse data from biosystematic and molecular studies (Crawford et al. 1987, Sanders et al. 1987). As such data will not be available in Clermontia for some time, it is useful at present to at least infer possible modes of speciation on the basis of the available biogeographic, ecological, and geological data.

**Likely Modes**

Of the various modes of speciation described by Grant (1981), two types of primary speciation are likely to have been operative in Clermontia: quantum speciation and geographic speciation. The uniformity of chromosome numbers in the genus and all related genera (Lammers 1988) precludes the possibility of allopolyploid speciation. Despite the occurrence of sporadic hybridization on a homoploid level, none of the species show evidence of hybrid origin.

Quantum speciation involves the production of novel species from a random subset of the progenitor’s gene pool, through the intermediate stage of an allopatric (or possibly parapatric) peripheral population. Clearly, an archipelago is the ideal setting for the establishment of such populations via stochastic founder events (Carson 1971, 1983;
Williamson 1981). A combination of drift and selection drives divergence, as do the effects of inbreeding (Grant 1981). Inbreeding in peripheral isolates may result from the small initial population size characteristic of founder events, or from self-fertilization. Both patterns could occur in Clermontia, for at least one species, C. kakeana, is facultatively autogamous (Cory 1984).

On the basis of distributional patterns and inferred phylogeny, many taxa of Clermontia appear to be products of quantum speciation, or represent intermediate stages in that process. For example, Clermontia arborescens subsp. waihiae (Maui) and C. arborescens subsp. waikoluensis (Moloka'i and Lana'i) are vicarious subspecies that may represent the earliest stages of quantum speciation. The former is believed to have evolved from the latter via a founder event. The morphological differences separating the two are rather small, and were made apparent only through the use of multivariate statistics. Clermontia oblongifolia subsp. oblongifolia (O'ahu) has given rise to two vicarious subspecies on younger islands: C. oblongifolia subsp. mauliensis (Maui and Lana'i) and C. oblongifolia subsp. brevipes (Moloka'i). Again, these two derived subspecies probably are the result of founder events. However, the morphological differences among these three subspecies are much more striking, to the extent that recognition as distinct species might be defensible. In this case, a later stage of quantum speciation is suggested. Finally, the genus includes numerous pairs of closely related vicarious species that presumably represent a progenitor and a derivative produced by quantum
speciation. For example, *Clermontia persicifolia* (O'ahu) and *C. pellida* (Moloka'i) are sister taxa and presumably progenitor and derivative, respectively. Similarly, *Clermontia kohalae* (Kohala Mountains, Hawai'i) probably originated from a peripheral isolate of *Clermontia kakeana* (O'ahu, Moloka'i, and Maui).

Geographic speciation may also be operative in *Clermontia*. This mode is very similar to quantum speciation, but is more gradual and conservative, involving divergence of species from local races through the intermediate stage of geographic races. Grant (1981) illustrated five basic distributional patterns that result from geographic speciation. Examples may be cited in *Clermontia* that resemble these stages. Alternatively, these patterns could also result from quantum speciation within an island. It is not possible to distinguish these two modes from the available data. *Clermontia arborescens* subsp. *arborescens* and *C. arborescens* subsp. *waihiae*, found in northern and southern West Maui, respectively, may be regarded as contiguous geographic races. *Clermontia peleana* subsp. *singuliflora* and *C. peleana* subsp. *peleana*, found on the northern and eastern flanks of Mauna Kea, respectively, might be a pair of disjunct geographic races. *Clermontia kohalae* of the Kohala Mountains and windward Mauna Kea and *C. monta-loa* of windward Mauna Kea and Mauna Loa might be regarded as marginally sympatric semispecies. *Clermontia persicifolia* and *C. kakeana* on O'ahu are closely related but almost wholly sympatric. Possibly, they represent products of geographic speciation brought back into sympatry through erosion of the island (cf. Sanders et al. 1987).
It is notable that the examples for lower levels of divergence are on the younger islands, while the example of complete divergence and isolation is from an older island.

_Clermontia_ also includes a few examples that might be regarded as sympatric speciation from ecological races. _Clermontia kohalae_ and _C. drepanomorpha_ form a closely related pair of species endemic to the Kohala Mountains. The former grows in forested valleys, the latter in montane bogs near the summit. An earlier stage of such divergence may be illustrated by _Clermontia grandiflora_ subsp. _grandiflora_ and _C. grandiflora_ subsp. _munrol_ on West Maui. The former occurs in montane bogs and the latter in the surrounding rain forest.

**Adaptive Radiation**

In an isolated and physiographically diverse environment, speciation may involve adaptive radiation. This phenomenon is defined as the evolution from a single ancestral stock of a large number of species adapted in striking or unusual ways to a diverse array of niches (Bock 1970, Carlquist 1974, Gorman 1979, Cox & Moore 1985, Crawford et al. 1987). This definition embraces a genealogical, a morphological, and an ecological component, respectively. As such, it lies within the broad interface of evolution, taxonomy, and ecology. Only groups which satisfy all three criteria may properly be regarded as examples of adaptive radiation.

The flora of the Hawaiian Islands is commonly cited as one that is particularly rich in examples of adaptive radiation. An outstanding
example is provided by three endemic genera of Madiinae (Asteraceae: Heliantheae). The Hawaiian Madiinae form a monophyletic lineage of 28 species that occupy every conceivable terrestrial habitat from sea level to 3750 m, from barren lava flows receiving less than 30 cm of annual precipitation, to cloud forests and bogs receiving over 1300 cm annually, to alpine habitats above the clouds (Carr 1985a). The group encompasses an extraordinary array of habits, including matforming subshrubs, a cushion plant, mesophytic shrubs and trees, a liana, and semelparous and iteroparous rosette plants (Carr 1985b). This presumably adaptive morphological diversity is matched by equally diverse adaptations in vegetative anatomy (Carlquist 1959) and tissue osmotic potentials (Robichaux and Canfield 1985), and by repeated chromosomal repatterning (Carr & Kyhos 1986).

Are the 22 known species of Clermontia the product of adaptive radiation? The genus certainly fulfills the genealogical component of the definition: a single ancestor has given rise to numerous species, and in a very brief span of time. But are the other criteria met? If so, one would expect the various species to display (1) great ecological amplitude, and (2) exceptional diversity in morphology.

Ecological amplitude might be assessed in several ways. One estimate would be the number of vegetation zones (Ripperton & Hosaka 1942, Gagne & Mueller-Dombois 1985) in which the various species occurred. In Clermontia, little diversity is evident. Clermontia pyrularia is apparently the only species restricted to the cool tropical ecosystem (subalpine forest and scrub), although C. lindseyana
is sometimes found there. Clermontia drepanomorpha, C. grandiflora subsp. grandiflora, and C. micrantha occur in the montane bog ecosystem. The remainder are restricted to the pluviotropical ecosystem, particularly montane rain forest and upper montane rain or cloud forest. None occur in dryland sclerophyll forest, mixed mesophytic forest, mountain parkland, alpine scrub, beaches, recent lava flows, cliffs, or aquatic environments. Within the pluviotropical ecosystem, only minor microclimatic differences are noted. All species tend to occupy openings or margins within the forest. Some occur on exposed windswept sites (e.g., Clermontia oblongifolia subsp. brevipes), others in relatively sheltered spots (e.g., Clermontia kakeana). None are canopy or understory species. Clearly, when compared to many other speciose Hawaiian lineages, the range of habitats occupied by Clermontia is hardly remarkable.

Elevation above sea level offers another measure of ecological preferences. Although some differences are noted among the species of Clermontia, the general pattern is one of broad intraspecific ranges and little interspecific diversification into different altitudinal zones. Most species occur between 500 and 1500 m. A few descend to as low as 150 m on occasion; no species is restricted to sites below 500 m. Only three taxa (Clermontia pyrularia, C. samuelii subsp. hanaensis, and C. tuberculata) are restricted to elevations above 1575 m. Taxa that show very limited ranges (e.g., Clermontia oblongifolia subsp. maiensis, C. grandiflora subsp. maxima) are mostly rare taxa for which few data are available. Again, in comparison to other
Hawaiian endemics, Clermontia occupies a relatively narrow elevational range.

Clermontia also shows relatively little variation in habit and vegetative morphology. All species are repeatedly branched iteroparous shrubs and trees. There are no annual or perennial herbs, subshrubs, cushion plants, lianas, unbranched palm-like trees, or semelparous rosette plants. Epiphytism appears to be facultative in most species. This uniformity of habit is reflected in the interspecific homogeneity of the wood anatomy (Carlquist 1969). The foliage is remarkably similar from one species to the next, with only minor differences in size, outline, pubescence, and thickness.

Although Clermontia is a speciose monophyletic lineage, its lack of ecological amplitude and correlated morphological diversification marks it as a poor example of adaptive radiation. This situation appears to be unusual in the Hawaiian flora, and merits a consideration of possible causes. Perhaps genetic constraints or limitations are operative. If certain leaf configurations, enzyme systems, or tissue elastic properties (cf. Robichaux & Canfield 1985) are necessary to survive in a given niche, and a species is genetically incapable of producing the requisite feature, there is little chance it will ever exploit that niche. As a relatively recent product of a founder event, Clermontia may be genetically depauperate.
POLLINATION AND COEVOLUTION

Because the species of Clermontia are distinguished primarily on the basis of floral morphology, it is appropriate to evaluate the role that pollinators may have played in the evolution of the genus. Selective pressures generated by pollinating animals can affect the evolution of floral morphology (Paton 1982, Rathke 1983, Waser 1983). Differences in floral morphology may serve as a mechanism for reproductive isolation of species (Grant 1949, 1981). In this section, the possible influence of pollinators on the evolution of Clermontia will be examined.

Ornithophily

The available evidence regarding pollination in Clermontia has been summarized by Cory (1984) and Lammers and Freeman (1986). Facultative autogamy has been demonstrated in Clermontia kakeana (Cory 1984) and probably occurs in others (Rock 1919). On the basis of floral morphology, nectar-sugar compositions, and observations on the indigenous fauna, Lammers and Freeman (1986) concluded that outcrossing is effected by nectarivorous passerine birds (Passeriformes).

The historically known Hawaiian avifauna includes more than 20 passerine birds that derived at least minimal nourishment from floral nectar (Table 6). Although the Meliphagidae are represented by a few
Table 6. Distribution of endemic nectarivorous birds in the Hawaiian Islands. K = Kaua'i, O = O'ahu, Mo = Moloka'i, L = Lana'i, Ma = Maui, H = Hawai'i; c = common, r = rare, x = extinct in historical times, f = known only from fossils; * = reported to feed on nectar of Clermontia or other Lobelioideae. Data from Olson & James (1982), Lammers & Freeman (1986), and Pratt et al. (1987)

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<td>Chaetopelia sp. nov.</td>
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<td>*Drepanis funerea Newton</td>
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<td>*M. braccatus (Cassin)</td>
<td>r</td>
</tr>
<tr>
<td>*M. nobilis (Merrem)</td>
<td>x</td>
</tr>
<tr>
<td>*Palmeria dolei (Wilson)</td>
<td>x r</td>
</tr>
<tr>
<td>*Vestiaria coccinea (Forster)</td>
<td>c r r x c c</td>
</tr>
<tr>
<td>Considerable nectar:</td>
<td></td>
</tr>
<tr>
<td>*Hemignathus obscurus (Gmelin)</td>
<td>x x f x x x</td>
</tr>
<tr>
<td>*H. parvus (Stejneger)</td>
<td>c</td>
</tr>
<tr>
<td>H. sagittirostris (Rothschild</td>
<td>x</td>
</tr>
<tr>
<td>*H. virens (Gmelin)</td>
<td>r r x c c</td>
</tr>
<tr>
<td>Minimal nectar:</td>
<td></td>
</tr>
<tr>
<td>Hemignathus lucidus Lichtenstein</td>
<td>r x f r r</td>
</tr>
<tr>
<td>H. stejnegeri (Wilson)</td>
<td>c</td>
</tr>
<tr>
<td>Loxops coccineus (Gmelin)</td>
<td>x r r</td>
</tr>
<tr>
<td>L. caeruleirostris (Wilson)</td>
<td>r</td>
</tr>
<tr>
<td>Oreomystis bairdii (Stejneger)</td>
<td>r</td>
</tr>
<tr>
<td>O. mana (Wilson)</td>
<td>r</td>
</tr>
<tr>
<td>Pareomyza flaminea (Wilson)</td>
<td>x</td>
</tr>
<tr>
<td>P. maculata (Cabanis)</td>
<td>r</td>
</tr>
<tr>
<td>P. montana (Wilson)</td>
<td>x c</td>
</tr>
</tbody>
</table>
species, most belong to the Drepanidinae, an endemic subfamily of finches (Fringillidae) that includes 29 historically known species (Pratt, Bruner & Berrett 1987). An additional 18 species are known only from fossils (Olson & James 1982), while many of the historically known species are now extinct or in imminent danger of extinction (Greenway 1967, Berger 1981). The drepanids apparently diverged from continental species of Carduelinae (Fringillidae) in the Leeward Islands approximately 20 my ago (Sibley & Ahlquist 1982). The nectarivorous species undoubtedly evolved from insectivores who discovered nectar while foraging for insects among flowers (Amadon 1950, Bock 1970, Raikow 1977). The distinctive morphological adaptations for feeding on nectar, i.e., tubular tongues, nasal opercula, and slender bills of various lengths and curvatures, apparently arose autochthonously in the Hawaiian Islands (Raikow 1977, Pratt 1979).

This territoriality is enhanced by their capability for rapid associative learning, which allows them to form search images for particularly rewarding nectar sources (Stiles 1978, Carothers 1982, Feinsinger 1983).

Knowledge of pollinator visits to Clermontia is based almost entirely on observations made by ornithologists between 1890 and 1920. These reports have been summarized adequately elsewhere (Cory 1984; Lammers & Freeman 1986; Lammers, Weller & Sakai 1988) and are not repeated here. Only nine of the endemic nectarivores were ever observed visiting lobelioid flowers (Table 6). Six of these are now extinct or nearly so, which greatly hinders any sort of experimental studies of pollination biology.

The species of Clermontia are not the only plants believed to be pollinated by these birds. Ornithophily appears to be very well developed among the Hawaiian flora, with over 130 species (approximately 14% of the indigenous flora) believed to be pollinated by drepanids and meliphagids (Table 7). The closest extra-Hawaiian relatives of nearly all these species appear to be insect-pollinated taxa, which suggests that ornithophily has evolved autochthonously from entomophily in most cases (Lammers, unpublished). The importance of birds as pollen vectors is perhaps due in part to the paucity of insect pollinators. There are no nectarivorous Diptera in the archipelago, while the nectarivorous Hymenoptera are represented by 55 species of Nesoprosopis Perkins (Hylaeidae), an endemic genus of short-tongued bees (Zimmerman 1948). The Lepidoptera are represented by just a
Table 7. Ornithophilous angiosperms in the indigenous Hawaiian flora

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bidens cosmoides (A. Gray) Sherff</td>
<td>Ganders &amp; Nagata (1983)</td>
</tr>
<tr>
<td>Cyaneinae F. Wimmer (91 spp.)</td>
<td>Lammers &amp; Freeman (1986)</td>
</tr>
<tr>
<td>Erythrina sandwicensis Degener</td>
<td>Ehrendorfer (1979)</td>
</tr>
<tr>
<td>Geranium arboreum A. Gray</td>
<td>Medeiros &amp; St. John (1988)</td>
</tr>
<tr>
<td>Hibiscadelphus Rock (6 spp.)</td>
<td>Hobdy (1984)</td>
</tr>
<tr>
<td>Kokia Lewton (4 spp.)</td>
<td>Ehrendorfer (1979)</td>
</tr>
<tr>
<td>Lobelia L. (13 spp.)</td>
<td>Lammers &amp; Freeman (1986)</td>
</tr>
<tr>
<td>Metrosideros Banks ex Gaertn. (6 sp)</td>
<td>Baldwin (1953)</td>
</tr>
<tr>
<td>Sophora chrysophylla (Salisb.) Seem.</td>
<td>Baldwin (1953)</td>
</tr>
<tr>
<td>Stenogyne kameamehiae Wawra</td>
<td>S. G. Weller (pers. comm.)</td>
</tr>
<tr>
<td>Strongylopon ruber Vogel</td>
<td>Ehrendorfer (1979)</td>
</tr>
<tr>
<td>Trematolobelia A. Zahlbr. (4 spp.)</td>
<td>Lammers &amp; Freeman (1986)</td>
</tr>
<tr>
<td>Vaccinium calycinum Sm.</td>
<td>Carothers (1982)</td>
</tr>
<tr>
<td>Vicia menziesii Spreng.</td>
<td>Ralph et al. (1981)</td>
</tr>
</tbody>
</table>
handful of species (Zimmerman 1958): two butterflies (Lycaena blackburni Tuely, Lycaenidae; Vanessa tameamea Eschscholtz, Nymphalidae), three or four hawkmoths (Sphingidae), and several settling moths (Geometridae and Noctuidae). Further, in cold wet montane forests, the poikilothermic metabolism of these insects makes them much less efficient and reliable as pollinators than the endothermic passerines (Cruden 1977, Stiles 1978).

Ornithophily exacts a heavy cost in terms of plant resources. Nectarivorous birds, due to their large mass and internal thermoregulatory capabilities, have much higher energy requirements than anthophilous insects. This necessitates the production of large quantities of nectar, as well as structures to attract and accommodate pollinators and deter nectar-robbers and nectar-theives (Heinrich & Raven 1972; Carpenter & MacMillen 1976; Brown, Calder & Kodric-Brown 1978; Stiles 1978; Heinrich 1981; Feinsinger 1983). It is difficult to understand how such costs could be met unless doing so resulted in a substantial increase in fitness. For this reason, it is not likely that the floral diversity that characterizes Clermontia is the result of stochastic processes such as drift or non-adaptive radiation (Strid 1970, Gottlieb 1982, Gould 1984, Davis & Gilmartin 1985). Clearly, the size, structure, and color of the flowers have adaptive significance, and most probably have arisen due to selective pressures exerted by avian pollinators.
Coevolution of Drepanids and Lobelioids

It is clear from the preceding that Clermontia and its allies interact with drepanids and meliphagids: the flowers provide sustenance for the birds while the birds effect xenogamy. Some authors (Perkins 1903, Grant 1949, Spieth 1966, Ehrendorfer 1979, Faegri & van der Pijl 1979, Carlquist 1980, Cox & Moore 1985) have described these interactions between the drepanids and the lobelioids as an example of coevolution. The meliphagids are seldom mentioned by these authors, possibly because they are derived from nectarivorous ancestors and have undergone little diversification in the archipelago.

Coevolution has been defined as reciprocal evolutionary change in interacting non-interbreeding populations (Janzen 1980; Thompson 1982, 1986; Futuyma & Slatkin 1983). Classic examples of coevolution between plants and their pollinators are provided by Ficus L. (Moraceae) and Blastophaga Gravenhorst (Hymenoptera: Agaoinidae) (Wiebes 1979), and by Yucca L. (Agavaceae) and Tegeticula Zeller (Lepidoptera: Tineidae) (Powell & Mackie 1966). Authors who have suggested a coevolutionary relationship between lobelioids and drepanids imply that the numerous species in each group are a result of selective pressures exerted by the other. A coevolved relationship with pollinators might explain the fact that numerous species of Clermontia are distinguished primarily by floral morphology (Carlquist 1974). Coevolution is a very difficult phenomenon to demonstrate conclusively (Janzen 1980, Futuyma & Slatkin 1983, Mitter & Brooks 1983, Schemske 1983). Documentation requires integrated studies of population biology, systematics, and geographical
variation (Thompson 1986). Although no studies on the population biology of Clermontia have been undertaken, it is still desirable to evaluate, at least in a general way, the possibility of a coevolutionary relationship between the species of Clermontia and their pollinators, on the basis of the available systematic and biogeographic data.

Numerous ornithological observations and experiments have demonstrated in all Hawaiian nectarivores a strongly polytropic feeding behavior and lack of long-term flower-constancy (Perkins 1903, Amadon 1950, Carpenter & MacMillen 1976, Berger 1981, Carothers 1982, Pimm & Pimm 1982). This is also evident from a comparison of the number of species in each group. Ornithophilous plants outnumber nectarivores five-to-one; omitting birds that consume only minimal nectar increases the disparity. Himatione sanguinea affords an excellent example of polytropy (Amadon 1950). On the main islands of the archipelago, it feeds on the nectar of several species in Table 2, as well as that of introduced ornithophiles such as Fuchsia magellanica Lam. (Onagraceae) and Passiflora mollissima H. B. K. (Passifloraceae). On tiny arid Laysan in the Leeward Islands, a disjunct population (Himatione sanguinea freethii Rothschild) subsists on nectar from the inconspicuous and ostensibly entomophilous flowers of strand plants such as Tribulus cistoides L. (Zygophyllaceae), Portulaca lutea Soland. ex G. Forst. (Portulacaceae), and Sesuvium portulacastrum (L.) L. (Aizoaceae).
This polytropism makes it impossible for the drepanids to be involved in a classic "lock-step" species-specific pattern of coevolution with any members of the Hawaiian flora (Feinsinger 1983; Schemske 1983; Kiester, Lande & Schemske 1984). Nor should such an intimate relationship be expected among birds, whose average lifespans far exceed the average flowering periods of the plants (Stiles 1978, Strickler 1979, Law & Koptur 1986). Further, a naturalized nectarivorous passerine, Zosterops japonica Temminck & Schlegal (Zosteropidae), has recently been observed taking nectar from several endemic ornithophiles (Pimm & Pimm 1982, Cox 1983, Cory 1984), including Clermontia arborescens (Lammers et al. 1988). Cox (1983) has argued that the ease with which this bird has replaced endemic pollinators indicates the lack of a tightly coevolved system.

Nonetheless, interactions between the avifauna and flora of the Hawaiian Islands have involved some degree of mutual adaptation. The repeated evolution of ornithophily from entomophily in the indigenous flora, the autochthonous origin of nectarivory from insectivory in the avifauna, and a pronounced phylogenetic trend toward increasing dependence on nectar among the latter (Raikow 1977) support this hypothesis. Clearly, an adaptive shift from entomophily to ornithophily in plants can best be understood as a response to foraging behavior of birds. In the absence of other pollinators, the birds as a guild may have been able to generate strong selective pressures that led to the development of floral morphologies more compatible with bird visitation (Feinsinger 1983). The availability of guild of reliable
endothermic pollinators may have made it possible for these plants to reproduce in the cold rainswept mountains of the archipelago. The concomitant shift from insectivory to nectarivory among the birds can be understood as an outcome of the underexploitation of nectar-rich flowers, due to the paucity of anthophilous insects. In turn, the structural modifications of the tongue and bill might have arisen in response to the availability of this resource.

Mutual adaptation is also evident in a comparison of bill lengths of nectarivorous drepanids with the lengths of corolla tubes in Clermontia. Bills range from 1.9-7.2 cm long (Amadon 1950), while the lengths of corolla tubes in Clermontia range from 1.5-6 cm. Although such co-occurrence of characters alone is not strong evidence for mutual adaptation (Janzen 1980), it does indicate that birds with suitable bill lengths are available for the entire range of flower sizes in the genus. If variation in floral tube length and/or bill length were due to stochastic processes or correlated with other pollinators, one would expect to find flower tubes longer or shorter than the bills of the birds.

All this suggests that the ornithophilous flora and nectarivorous passerines in the Hawaiian Islands are an example of diffuse coevolution, in which two arrays of populations generate reciprocal selective pressures (Janzen 1980, Fox 1981, Wheelwright & Orians 1982, Feinsinger 1983, Schemske 1983). This pattern appears to be much more common than a strict one-on-one relationship, particularly in the case of mutualisms (Law & Koptur 1986).
In most ornithophilous systems, plant species significantly outnumber bird species (Stiles 1981, Wiens et al. 1981, Feinsinger 1983). The Hawaiian Islands are no exception (cf. Tables 6 & 7). Clearly, speciation among the plants has greatly exceeded speciation among the birds. As such, ornithophily in the Hawaiian Islands might conform to the recently proposed model for mixed-process coevolution (Thompson 1986). As Carson (1985) has commented, evolution results in both adaptation and speciation. In mixed-process coevolution, a pollinator adapts to a nectar source as a result of interactions between the two. However, the pollinator does not necessarily speciate, because the plant has little direct control over the bird's reproduction, only its survival. Speciation is much more likely to occur as a result of competitive interactions between the bird and other nectarivores (Feinsinger & Colwell 1978, Ford & Paton 1982, Rathke 1983). On the other hand, speciation is much more likely to occur in the plant because the pollinator exercises considerable control over fecundity. The plant is wholly dependent upon the bird for transfer of gametes. This model has wide applicability to pollinator/nectar source systems (Thompson 1986), and could account for the disproportionality in the numbers of ornithophilous plants and nectarivorous birds in the Hawaiian archipelago.

**Evolutionary Consequences in Clermontia**

Because the emphasis of this work is on the evolution of *Clermontia*, it is appropriate to examine the effects that drepanids and
meliphagids as a group may have had on the evolution of Clermontia,
within the context of a diffuse mixed-process coevolutionary
relationship. Specifically, has speciation resulted from interaction
with these birds?

Drepanid species are known to differ in foraging behavior,
primarily due to their territoriality (Carpenter & MacMillen 1976, Pimm
result in short-term floral constancy, which may be nearly as effective
as long-term constancy in minimizing improper pollinations (Rathke
1983). Further, it does not jeopardize the survival of the pollinator
through specialization to a single possibly unreliable resource.
Possibly, differences in foraging behavior among the birds due to
territoriality and short-term floral constancy could result in
morphological divergence in populations of Clermontia via character
displacement (Brown & Wilson 1956, Williams 1969, Rathke 1983,
Roughgarden 1983). These changes would reduce gene flow between the
divergent populations, effectively isolating them from one another.
This combination of morphological divergence with reproductive
isolation would result in speciation.

If this were the case, one would expect to find that sympatric
congeners are isolated by functional differences in floral morphology
(Grant 1949, 1981). These differences would serve to minimize improper
pollen transfers by partitioning resources (i.e., pollinators).
Species that waste resources on improper pollen transfers can
experience a marked decline in fitness (Waser 1978, Rathke 1983).
Thus, pollinators may have played a major role in the diversification of Clermontia by promoting reproductive isolation via external (i.e., ethological and mechanical) mechanisms (Grant 1949, 1981).

One type of adaptation for resource partitioning would involve major differences in gross floral structure. Variation in the proportional lengths of lobes and tube, the curvature and shape of the tube, the posture and position of the lobes could all affect the accessibility of the flowers to pollinators. For example, Hemignathus virens, a nectarivore with a rather short straight bill, obtains nectar in the correct way from relatively small open lobelioid flowers and presumably effects pollination. On large curved tubular flowers, it behaves as a nectar robber, piercing the base of the corolla tube (Perkins 1903). Long-billed species such as Drepanis spp., Vestiaria coccinea, and Moho spp., although capable of probing small open flowers, preferentially foraged at large curved tubular flowers (Perkins 1903, Munro 1944, Feinsinger 1983).

The six series that comprise Clermontia are distinguished by major structural differences in the flowers. These structural differences might provide important visual cues to pollinators and thus enforce some degree of short-term floral constancy. For example, a drepanid that recently learned to associate a unilabiate corolla with an abundant supply of nectar may temporarily defend a territory containing several such individuals, and ignore sympatric species with bilabiate, rotate, or tubular flowers (Carothers 1982, Pimm & Pimm 1982, Rathke 1983, van Riper 1984). Typically, each series of Clermontia (and thus
each major structural type) is represented in a given region by just one species. Thus, most sympatric congeners will differ significantly in their floral structure. These differences in floral morphology possibly could serve to effectively partition pollinators among sympatric species of Clermontia.

Occasionally, two members of a series are sympatric. Although these closely-related pairs of species are not separated by major structural differences, they do exhibit differences in coloration, size, and/or mode of presentation (Table 8). These differences might also be visual cues that would serve to partition pollinators. For example, a drepanid that has learned through association that large purple bilabiate flowers are a rich source of nectar might ignore small white bilabiate flowers while foraging. Differences in habitats and presentation of the flowers (i.e., pendent, deflexed, or spreading) might also enforce short-term floral constancy due to differences in foraging behavior.

A single pollinator might be partitioned between two or more species, through differential placement of pollen loads (Stebbins 1977, Brantjes 1982). This phenomenon is known to occur in plants pollinated by hummingbirds (Apodiformes: Trochilidae) in Central America (Stiles 1975, Brown & Kodric-Brown 1979, Feinsinger 1983). On any given bird, the placement of pollen will be determined by the length of the staminal column. If two sympatric species of Clermontia differ in the lengths of their staminal columns (Table 8), a single bird theoretically could pollinate both with only minimal improper
Table 8. Floral features distinguishing closely-related sympatric species of *Clermontia*. Islands: EM = East Maui; Ko = Kohala Mts., Hawai'i; MN = Maui Nui; Mo = Moloka‘i; O = O‘ahu. Species acronyms derived from first three letters of specific epithet. Characters: cor = corolla, tub = corolla tube, stam = staminal column, infl = inflorescence

<table>
<thead>
<tr>
<th>Series</th>
<th>Island</th>
<th>Species</th>
<th>Distinguishing characters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sarcanthae</td>
<td>EM</td>
<td>ARB</td>
<td>cor green, tub 2.2-3.4 cm long; ventral lobes 0.5-1.5 cm long.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>TUB</td>
<td>cor rose, tub 1-2 cm long; ventral lobes 2-3 cm long.</td>
</tr>
<tr>
<td>Dupliciflorae</td>
<td>O</td>
<td>KAK</td>
<td>cor green; stam magenta, 3.8-5.2 cm long; sheltered sites.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PER</td>
<td>cor white; stam white, 4.8-6.6 cm long; windswept sites.</td>
</tr>
<tr>
<td></td>
<td>Mo</td>
<td>KAK</td>
<td>cor green; stam magenta, 3.8-5.2 cm long; sheltered sites.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PAL</td>
<td>cor purple; stam purple, 5-6.6 cm long; windswept sites.</td>
</tr>
<tr>
<td></td>
<td>Ko</td>
<td>DRE</td>
<td>cor 4-5.6 cm long, tub 1-1.6 cm long; infl deflexed; bogs.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>KOH</td>
<td>cor 5-6.5 cm long, tub 2-3.2 cm long; infl spreading; forest.</td>
</tr>
<tr>
<td>Parviflorae</td>
<td>Ko</td>
<td>CAL</td>
<td>cor dark purple, 3.5-4.5 cm long, tub 1-1.8 cm long; stam 3.5-4.6 cm long.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>PAR</td>
<td>cor white or purple, 1.5-2.8 cm long, tub 0.5-1.1 cm long; stam 2.6-3.3 cm long.</td>
</tr>
<tr>
<td>Clermontia</td>
<td>MN</td>
<td>GRA</td>
<td>Infl pendent; sheltered sites.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>OBL</td>
<td>Infl spreading; windswept sites.</td>
</tr>
<tr>
<td></td>
<td>EM</td>
<td>GRA</td>
<td>Infl pendent; cor 5.1-8.5 cm long.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SAM</td>
<td>Infl spreading; cor 3.6-5.5 cm long.</td>
</tr>
</tbody>
</table>
Although interaction with pollinators ordinarily would result in divergence, it might also lead to convergence of floral traits (Brown & Kodric-Brown 1979, Rathke 1983, Feinsinger 1983). In Clermontia very dark purple ("black") floral pigments have arisen independently in four series: Clermontioideae (Clermontia waimeae); Dupliciflorae (C. drepanomorpha, C. kohala, C. montis-loa); Parviflorae (C. calophylla); and Unilabiateae (C. peleana subsp. peleana). All are endemic to the youngest island, Hawai'i, and are clearly derived from taxa with white, green, or light purple flowers. The co-occurrence of this unique trait in four disparate lineages on one island suggests that some nectarivorous bird endemic to Hawai'i has exerted strong selective pressure for the development of dark floral pigments. Drepanis pacifica and Moho nobilis were both endemic to Hawai'i, are known to have fed preferentially on lobelioid nectar, and had black plumage (Perkins 1903, Munro 1944, Pratt et al. 1987). The unique coloration of these flowers may mimic that of the birds. Due to the strong territoriality of the drepanids, dark floral pigments may have elicited an instinctive response to investigate "intruders". The use of captive individuals as lures or decoys by native bird-catchers (Perkins 1903) lends some credence to this idea. "Black" flowers thus would represent the best possible signal for attracting these pollinators. Further, the dark flowers may have provided camouflage for the birds. Buteo solitarius Peale (Falconiformes: Accipitridae) is a hawk endemic to Hawai'i that preys upon passerines (Shallenberger 1977). Perhaps a
hawk would have difficulty discerning a black bird feeding among "black" flowers. Unfortunately, this intriguing speculation can never be tested experimentally, as both passerines became extinct early in this century (Greenway 1967, Pratt et al. 1987).

*Clermontia drepanomorpha* (ser. *Dupliciflorae*) and *C. pyrularia* (ser. *Clermontioideae*), both endemic to Hawai'i, share a type of inflorescence that is unique in the genus. The peduncle is long and deflexed with two very short abruptly ascending pedicels. However, in all other aspects, these two species are literally as different as night and day: the former has "black" flowers, the latter has white. The parallel development of this unique inflorescence type may find an explanation in the foraging and/or perching behavior of some nectarivorous bird endemic to Hawai'i.

The available data support the hypothesis that interactions with drepanid and meliphagid pollinators have played an important role in the evolution of the diverse floral morphology that characterizes the species of *Clermontia*. Selection pressures generated by these birds have resulted in a general pattern of divergence and speciation, but also in some apparent instances of convergence. The ornithophilous flora has generated reciprocal pressures on the drepanids and meliphagids, leading to the evolution of nectarivory from insectivory. Consequently, it is appropriate to conclude that *Clermontia* and the endemic nectarivorous passerines are involved in a diffuse mixed-process coevolutionary relationship.
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