CALYDOREA HERBERT (IRIDACEAE–TIGRIDIEAE): NOTES ON THIS NEW WORLD GENUS AND REDUCTION TO SYNONYMY OF *SALPINGOSTYLIS*, *CARDIOSTIGMA*, *ITYSA*, AND *CATILA*[1]

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ABSTRACT

Subequal tepals spreading from the base, free stamens, and short slender style branches with simple, obtuse to emarginate apices, the defining generic criteria for the southern South American *Calydorea* (Iridaceae–Tigridieae) (Herbert, 1843a) also characterize the Florida (U.S.A.) monotypic *Salpingostylis* (Small, 1931), the Mexican *Cardiostigma* (Baker, 1876), and the Venezuelan *Itysa* Ravenna (1986). *Salpingostylis* and *Cardiostigma* hardly differ from one another and are congeneric; they can be distinguished from *Calydorea* only by their secund flower, weakly eccentric style that divides near the apex of the anthers, and short style branches. *Itysa* also has secund flowers with spreading subequal tepals, free stamens and slender, simple style branches. It is unusual only in having the anthers coherent at their bases and a style that divides above the level of the anthers. Typical *Calydorea* has upright flowers and a central style that divides near the bases of the anthers into relatively longer style branches that twist weakly so that they come to lie between, rather than opposite, the style branches. We consider the differences between *Calydorea*, *Cardiostigma*, *Salpingostylis*, and *Itysa* too insignificant to merit generic segregation and unite them all under *Calydorea*. An unusual species of *Calydorea*, *C. pallens*, which has unequal inner and outer tepals and style branches that lie opposite the anthers, is strikingly similar to *Catila amabilis* (Ravenna, 1983), the latter having somewhat larger and more intensely colored flowers, the anthers of which clasp the style branches after anthesis. These two species belong in the same genus, and we recommend treating both as *Calydorea* in which we consider them to be relatively unspecialized. Other members of Tigridieae, notably *Onira*, *Eleutherine*, and *Gelasine*, that have free stamens and simple style branches are considered in relation to *Calydorea*. The phylogenetic position of the species or species clusters of *Calydorea* are analyzed cladistically and are discussed in relation to other taxa of Tigridieae and the basic character states of the tribe and its sister taxon Mariceae.

Described in 1843 by the British botanist William Herbert, *Calydorea* was erected to include a species of bulbous and plicate-leafed Iridaceae from Chile, *Sisyrinchium speciosum*, which was misplaced in *Sisyrinchium*. Two features distinguished *Calydorea* from other genera of Iridaceae then known that also had a bulbous rootstock and plicate leaves, and the same basic vegetative morphology: free stamens; and a style with long, slender, undivided branches loosely alternating with the stamens.

By 1843, 11 genera with similar vegetative morphology had already been described, and more than 15 additional ones have since been added. Except for some obvious synonyms, each differed largely in its floral morphology and was characterized by unusual stamen and/or stylar specializations, and sometimes by differences in the relative size and shape of the inner and outer tepal whorls. The bulbous and plicate-leafed genera of Iridaceae are now treated as members of Tigridieae, one of four tribes (Goldblatt, 1990) of Iridoideae, the others being Sisyrinchieae, Irideae, and Mariceae. Iridoideae is the only one of the

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four subfamilies of Iridaceae that occurs in the New World (Goldblatt, 1982, 1990). A notable feature of Tigridieae (Figs. 1, 2) is the unusual degree of variability in the style branches, which frequently form a highly specialized and complex structure, intimately associated with the stamens, which are also sometimes specialized. This contrasts markedly with the vegetative uniformity in the tribe.

More than 25 genera of plicate-leafed Iridaceae with bulbs have been described, and all but a few of these appear to be very weakly founded. They are largely based on trivial differences in style or stamen structure. Compared with Iridaceae–Iridoideae in Africa and Eurasia, the generic limits of the Tigridieae seem too finely drawn, and it seems timely to attempt to reduce some of the genera that differ so little from each other. Not only is some degree of consistency in the criteria for recognition of genera desirable at least within the family, but there is a need to define the New World genera of Iridaceae so that usable keys and descriptions can be written. *Cardiostigma* Baker (1876), *Salpingostylis* Small (1931), *Catila* Ravenna (1983), and *Itysa* Ravenna (1986) are four such examples of weakly defined genera, and they are reduced to synonymy in *Calydorea* here. Also critically considered in relation to *Calydorea* are *Gelasine*, *Onira*, and *Eleutherine*, which are at least partly defined by, or contain species with, slender, undivided style branches.

Cardiostigma

Based on the southern Mexican *C. longispathum* (Klatt) Baker, *Cardiostigma* (Baker, 1876: 102) was reduced to synonymy in *Sphenostigma* Baker (1876: 124) by Bentham & Hooker (1883) soon after it was described. The latter is founded on the Brazilian *S. sellowianum* (Klatt) Baker. Baker (1892) expanded *Sphenostigma* to include 11 species, and Foster (1945) added three more. Ravenna (1977) has, however, made a convincing argument for transferring the type of *Sphenostigma*, but not other members of the genus, to *Gelasine*, in which it is now known by an earlier synonym, *G. coerulea* (Vellozo) Ravenna. With *Sphenostigma* thus included in *Gelasine*, Ravenna (1977, 1979, 1986) transferred most of the erstwhile species of that genus to *Ennealophus* N.E. Br., *Phalocallis*, *Cardiostigma*, and the new genera *Ainea* and *Lethia*. One species that Ravenna has not dealt with to date is *Sphenostigma coelestinum* (= *Salpingostylis coelestinum*), and this is discussed in detail below.

Cardiostigma sensu Ravenna comprises three species, *C. longispathum* (the type), *C. mexicanum* (R. Foster) Ravenna, and *C. hintonii* (R. Foster) Ravenna. Ravenna never explained his concept of *Cardiostigma*, but its only notable feature seems to be its flower. This is secund and consists of a blue perianth of subequal spreading tepals, not clearly divided into a limb and claw and without perigonal nectaries; free stamens; and a slender, eccentric style with three short, simple branches. This at least applies to *C. longispathum* and *C. mexicanum*. In *C. hintonii* the three well-defined style branches are each deeply forked for about two-thirds of their length. This style corresponds exactly to that of *Ainea* (Ravenna, 1979) and *Alophia* (Herbert, 1840), and we assume that it is related to these genera rather than to the other species of *Cardiostigma*. We will not deal further with *C. hintonii* here.

Salpingostylis

This genus is monotypic, containing only the Florida species *Salpingostylis coelestinum* (basionym *Ixia coelestina* Bart.), which was, as recently as 1974, regarded as a not particularly unusual member of *Sphenostigma* (Goldblatt, 1974). Small (1931) described *Salpingostylis* and regarded it as monotypic, but his opinion was largely ignored (Foster, 1945; Goldblatt, 1974). Only after 1977, when Ravenna reduced *Sphenostigma* to synonymy in *Gelasine*, has *Salpingostylis*, more or less by default, been recognized.

A careful comparison of the available collections of *Salpingostylis* and *Cardiostigma* sensu Ravenna leaves us in no doubt that, with the exception of *C. hintonii* (mentioned above), these are congeneric. *Salpingostylis coelestinum* has the identical flower described above for *C. longispathum* and *C. mexicanum*, secund in orientation with subequal tepals, free stamens, and a long style. Examination of ample herbarium material and some accompanying illustrations made from live plants also makes it clear that the style is divided into distinct branches, not obscurely lobed as is sometimes thought (Fig. 1A). A reading of the literature and examination of living and preserved specimens have not indicated any reason to separate *Salpingostylis* and *Cardiostigma* from one another, and little to distinguish them from *Calydorea* (Fig. 1B).

Itysa

Described by Ravenna in 1986, *Itysa* comprises two species of northern South America. Both are broadly similar to *Calydorea* and *Cardiostigma* in

FIGURE 1. Flowers, style, and stamen detail and enlargement of style apex in species of *Calydorea*.—A. *C. coelestina* (*Salpingostylis*) (with habit).—B. *Calydorea* sp.—C. *C. gardneri* (*Itysa*).—D. *C. pallens*.—E. *C. amabilis* (*Catila*). Habit and flowers full size; stamens and style × 3; style branch apices much enlarged.

vegetative morphology, and they have secund flowers with subequal inner and outer tepals lacking differentiation into a limb and claw. The filaments are free, and the long style divides above the level of the anthers into three short, slender branches (Fig. 1C), the structure of which closely resembles that in *Calydorea*. One peculiarity of the genus is that the bases of the anthers are coherent around the style. Except for this unusual feature, both species of *Itysa* seem to correspond to the species of *Cardiostigma* in particular.

CALYDOREA

Flowers of *Cardiostigma*, *Salpingostylis*, and *Itysa* correspond closely to the type and most other

species of *Calydorea* (Fig. 1B) with the following differences. The flower is upright not secund, and the style is shorter, dividing opposite the base of the anthers. The style branches are thus comparatively longer and more slender, and by a weak twisting lie loosely between the anthers. (This is not a fundamental difference in the position of the ovary or style branches in relation to the stamens.) In *Salpingostylis* and *Cardiostigma*, the style divides just above the apex of the anthers and the exact position of the style branches relative to the anthers is obscured because the style is weakly eccentric (whether by design or the effect of gravity in the secund flower is not known) (Fig. 1A). However, the structure of the style and style branches of *Salpingostylis*, *Cardiostigma* sensu Ravenna, *Itysa*, and *Calydorea* is very similar (compare details of style arms in Fig. 1A–D).

As far as we can tell from live specimens of a *Calydorea* sp. from Argentina, and an illustration of the closely related *C. xiphioides* (Poeppig) Espin. (synonym *C. speciosa*), there are no other taxonomically significant differences between *Calydorea*, *Cardiostigma*, *Salpingostylis*, and *Itysa*. The secund flower, longer style, short style branches, and basally connate anthers are inadequate criteria on which to base genera in Iridoideae. Thus, as presently understood, *Cardiostigma*, *Salpingostylis*, and *Itysa* cannot be upheld and are here reduced to synonymy. The minor differences that we have outlined, in conjunction with the correlated geographic disjunction, appear to merit sectional separation within one genus at best. The necessary nomenclatural changes are presented below, together with short notes about each species.

Calydorea pallens and *Catila* Ravenna

When other species currently assigned to *Calydorea* are taken into account, the circumscription of the genus is somewhat expanded. In *C. pallens* Griseb., the style is shorter than in *C. xiphioides* and *Calydorea* sp., and the branches lie opposite the anthers, though not appressed to them (Fig. 1D); the tepals are weakly unguiculate; and the inner tepals are smaller than the outer. *Calydorea pallens* bears a remarkable resemblance to *Catila amabilis* Ravenna (Fig. 1E), the type and only species of *Catila* (Ravenna, 1983), which differs significantly from it only in having a larger flower with more strongly unguiculate tepals of a darker purple color and in the anthers being closely applied to the style branches. The inner tepals of *Catila* resemble many other *Tigridieae* in having the base of the limb folded back on itself and bearing a median zone of nectariferous tissue. There is no basis for the generic separation of *Calydorea pallens* and *Catila*.

Phylogenetic Considerations

The basic floral morphology in Tigridieae appears to be similar to the complex structure encountered in *Cypella* (e.g., Ravenna, 1981a, b), which is very similar to the basic flower of Mariceae (Fig. 2A), sister taxon of Tigridieae (Goldblatt, 1990). Here the tepals are clawed with the claws forming an open cup, and the inner tepals are smaller than the outer, each folded back on itself at the base of the limb, in which area there is a zone of nectaries surrounded by an area of contrasting coloration. The style branches are thickened and compressed, and terminate in a pair of flat appendages, called crests because of their resemblance to similar structures in *Iris*. The filaments are free, usually threadlike, and too weak to support the anthers, which are closely applied (not united) to the abaxial side of the style branch. The anthers usually reach to just below the stigma, a transverse band of tissue (Fig. 2A) at the base of the crests on the abaxial surface of the style branch. (The stigma may bear a pair of small appendages similar to the crests.)

This complex structure is thought to be basal (plesiomorphic) for a tribe in which much simpler stylar structures also occur (as in *Calydorea*) because the flowers of the central genera of Mariceae, *Neomarica* and *Trimezia*, have exactly the same structure. The genera of Mariceae, however, have a rhizomatous rootstock and plane leaves, and these features are less specialized than the bulb and plicate leaves of Tigridieae. In the other New World tribe of Iridoideae, Sisyrinchieae, which also has a rhizomatous rootstock and plane leaves, the inner and outer tepals are similar, not normally unguiculate, lack a zone of nectaries, and have style branches that are always simple, filiform structures sometimes reduced to short lobes.

Thus, the pattern of floral evolution in Tigridieae, as presented in the cladogram (Fig. 3), is best seen as a progressive reduction from the complex to the simple (Figs. 1, 2). Goldblatt (1990) presented this argument in detail. To consider the phylogenetic relationships as having a different pattern, from the simple to the complex, is tempting. It is, however, less parsimonious as this means that either the exact type of flower structure evolved independently in Mariceae and Tigridieae, or that Mariceae are derived from supposedly specialized

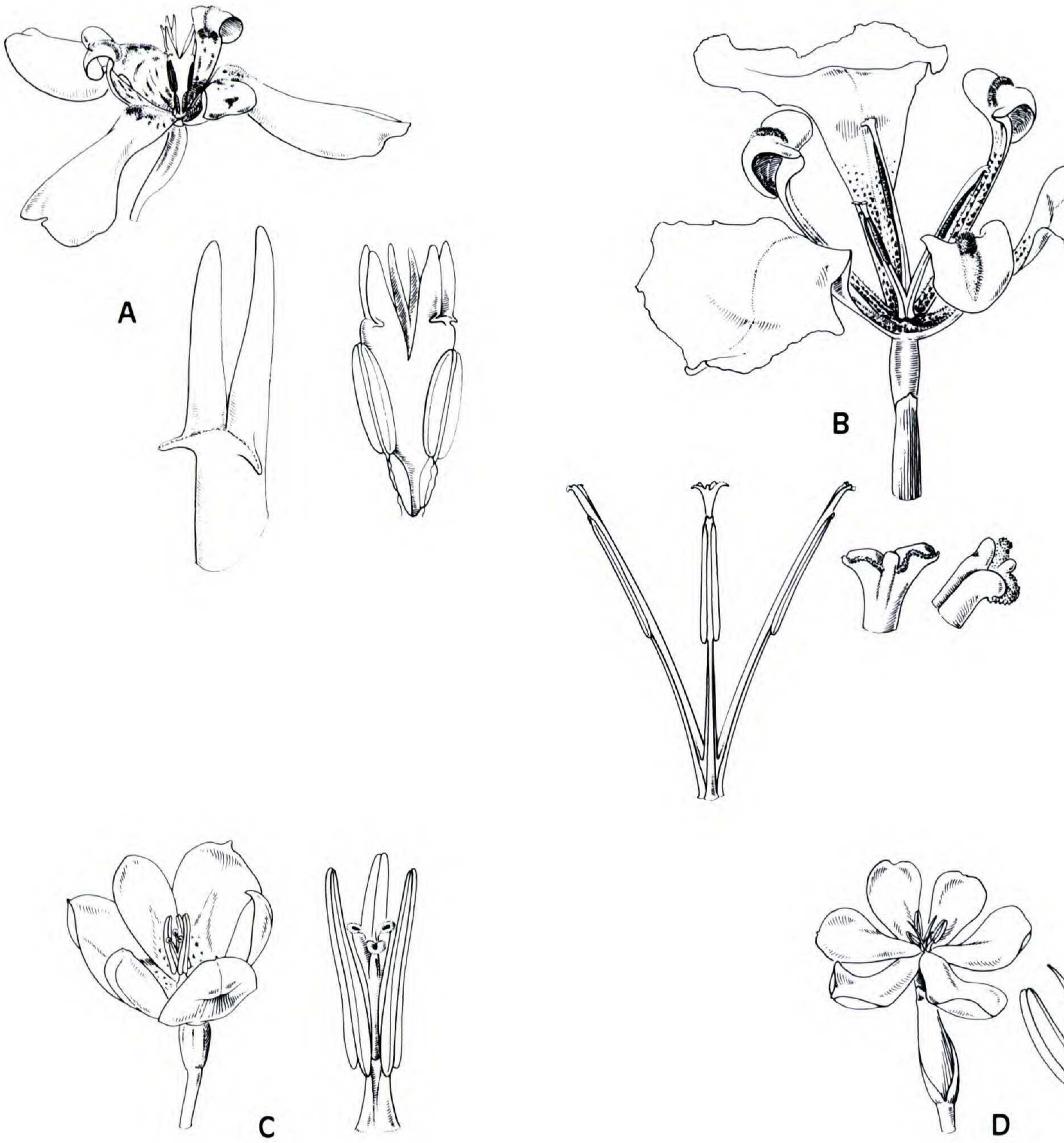

FIGURE 2. Flowers, style, and stamen detail and enlargement of style branch apex in selected Iridaceae.—A. *Trimezia steyermarkii*.—B. *Onira unguiculata*.—C. *Gelasine elongata* (= *G. azurea*).—D. *Eleutherine bulbosa*. Habit and flowers full size; stamens and style × 3; style branch apices much enlarged.

Tigridieae and acquired a rhizome and plane leaves secondarily. Both scenarios seem unlikely. In Irideae, a similar progression from the complex type of flower to the simple seems likely (Goldblatt, 1981, 1986, 1990) and the same pattern seems to have occurred in *Cipura*, a small genus of Tigridieae (Goldblatt & Henrich, 1987).

In the scenario outlined above, *Calydorea* appears to be a moderately specialized member of Tigridieae. It most likely evolved from a *Cypella*-like ancestor in which the style branches lost their thickening and apical appendages, and differences between the inner and outer tepals were reduced (Fig. 3). The flower of *Catila amabilis* is interpreted here as being close to this ancestral type, and *Calydorea pallens* represents another step in this process, leading to species with flowers like *C. speciosa*, and ultimately to such Northern Hemisphere species as *C. coelestina* and *C. longispatha*, with their secund flowers and elongate, eccentric style (Fig. 3).

Other genera of Tigridieae with simple style branches resembling those of *Calydorea* are *Eleutherine* Herbert (1843b), which comprises two species; one species of *Gelasine* Herbert (1840), *G. elongata* (= *G. azurea*); and *Onira* Ravenna (1983). Regarding *Eleutherine* (Fig. 2D), we feel that it is unrelated to *Calydorea*. Its unusual reddish bulb, large subterminal cauline leaf, and short inflorescence spathes seem to isolate it from possible relatives. The reduction of this genus should be considered when its immediate ancestry can be

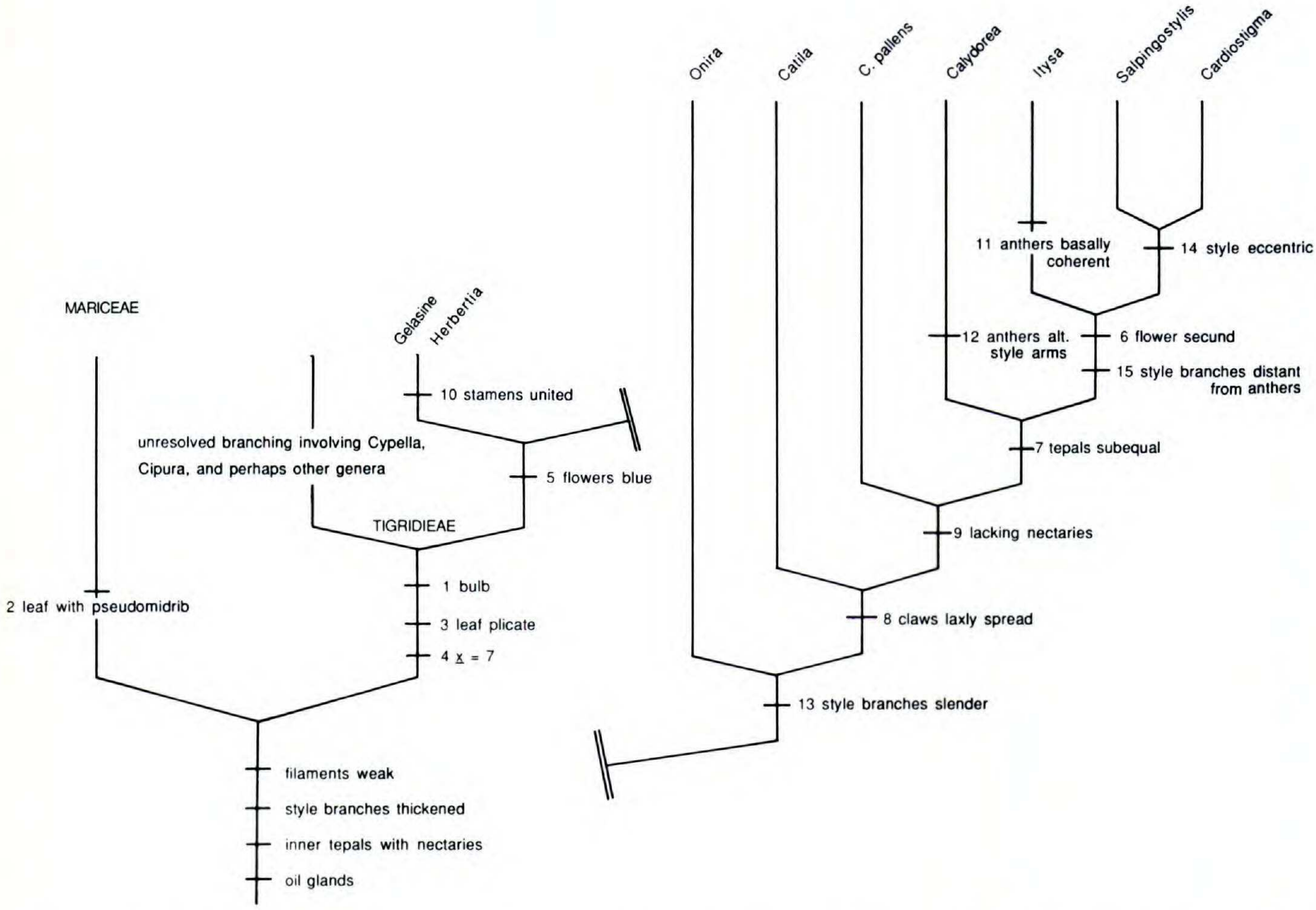

FIGURE 3. Phylogeny of the genera and species closely allied to *Calydorea* suggested by the cladogram based on the character list and data matrix presented in Table 1. The major branching patterns in Tigridieae and sister tribe Mariceae (from Goldblatt, 1990) are indicated to give some perspective to the *Onira–Calydorea* clade. Polarity of unnumbered characters from Goldblatt (1990).

TABLE 1. Data matrix and character list for the cladogram (Fig. 3). Presence of the specialized condition is denoted by 1; absence by 0; state inapplicable by ?

Genus	Character number														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Mariceae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Calydorea	1	0	1	1	1	0	1	?	1	0	0	1	1	0	0
C. pallens	1	0	1	1	1	0	0	1	1	0	0	0	1	0	0
Salpingostylis	1	0	1	1	1	1	1	?	1	0	0	0	1	1	1
Cardiostigma	1	0	1	1	1	1	1	?	1	0	0	0	1	1	1
Itysa	1	0	1	1	1	1	1	?	1	0	1	0	1	0	1
Catila	1	0	1	1	1	0	0	1	0	0	0	0	1	0	0
Onira	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0
Cypella	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
other genera, e.g.,															
Gelasine, Herbertia	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0

Characters: the derived (apomorphic) states listed first followed by the presumed ancestral (plesiomorphic) condition.
1. rootstock a bulb—rootstock a rhizome; 2. leaf with pseudomidrib—leaf without pseudomidrib; 3. leaf plicate—leaf plane; 4. basic chromosome number $x = 7$—base number not $x = 7$ (but unknown); 5. flowers shades of blue—flowers shades of yellow; 6. flower secund—flower upright; 7. tepals subequal and not clawed—tepals unequal and clawed; 8. tepal claws laxly spread—claws forming an open cup; 9. tepals lacking nectaries—zone of nectaries present on inner tepals; 10. stamens united—stamens free; 11. anthers coherent at base—anthers separate from one another; 12. anthers alternating with the style branches—anthers opposite the style arms; 13. style branches slender and not forked—style arms thickened and apically forked; 14. style eccentric—style central; 15. style branches distant from the anthers—style branches at same level as anthers.

identified. The subterminal cauline leaf, rather fleshy bulb scales, and basic chromosome number, $x = 6$, suggest that it is possibly a derivative of *Gelasine*. Base number in Tigridieae is $x = 7$ (Goldblatt, 1982), and apart from *Eleutherine*, $x = 6$ is known in the tribe only in *G. elongata* (reported as *G. azurea*) (Kenton & Rudall, 1987). The similarity in the karyotypes in these two is striking and may indicate a relationship.

Gelasine elongata (Fig. 2C) has united filaments and is a large plant, resembling *G. coerulea* and *G. uruguaiensis* vegetatively. These two species also have united filaments but more elaborate style branches that have paired crests and a broad transverse, abaxial stigma (Ravenna, 1984). *Gelasine elongata* is an autogamous, complex heterozygote (Kenton & Rudall, 1987) with a reduced basic chromosome number, $n = 6$, unlike most Tigridieae, which have $x = 7$. It seems likely that the apparently simple flower and style of *G. elongata* are the result of reduction from the more complex structures present in other species of *Gelasine*. Chromosome number is known in only one other *Gelasine*, *G. uruguaiensis*, $n = 7$ (Ravenna, 1984). Presumably, *Gelasine* evolved from a *Cypella*-like ancestor, and the major distinction between the two genera is in the filaments, free and long in *Cypella*, short and united in *Gelasine*. We assume that similar patterns of floral evolution occurred in *Gelasine* and *Calydorea*. In both genera species have evolved with flowers with subequal unclawed tepals and simple cylindric style branches lacking crests.

Onira

Described in 1983 by Ravenna, *Onira* includes only *O. unguiculata* (Baker) Ravenna, based on *Herbertia unguiculata*. It is a small plant with large, pale blue-green flowers (Fig. 2B). Apart from the color and size of the tepals, and the well-developed tepal claws, the flower is unusual only in the short style, which divides below the middle of the filaments, and the comparatively long, slender style branches (Fig. 2B detail). The filaments are free and the anthers are appressed to the style branches and are closely held to them by the recurving of the anther sacs after anthesis. The style branch apices resemble fairly closely those of *Calydorea pallens* and *Catila* except for the small, irregular outgrowths of nonstigmatic tissue on the stigma lobes (Fig. 2B detail). These may represent the vestigial remains of the style crests that are so prominent in, for example, *Cypella*, and hypothesized as plesiomorphic for the tribe. The tepal whorls are well differentiated, the inner being much smaller than the outer, and strongly folded back at the juncture of the limb and claw. This differentiation is much more pronounced than in *Catila*. We feel that *Onira* and related genera should be studied further before a decision is made regarding their status and disposition.

Systematic Treatment

Calydorea Herbert, Bot. Reg. 29, Misc. Matter.: 85. 1843. TYPE: *C. speciosa* (Hook.) Herbert (= *C. xiphioides* (Poeppig) Espin.).

Cardiostigma Baker, J. Bot. London 14: 188. 1876. TYPE: *C. longispathum* (Herbert) Baker (= *Calydorea longispathum* (Herbert) Baker).

Salpingostylis Small, J. New York Bot. Gard. 32: 161. 1931. TYPE: *S. coelestinum* (Bartr.) Small (= *Calydorea coelestina* (Bartr.) Goldbl.).

Catila Ravenna, Nordic J. Bot. 1983. TYPE: *C. amabilis* Ravenna (= *C. amabilis* Ravenna) Goldbl.

Itysa Ravenna, Nord. J. Bot. 6: 582. 1986. TYPE: *I. gardneri* (Baker) Ravenna (= *Calydorea gardneri* Baker).

Nomenclature of species of *Calydorea* discussed in this paper, including new combinations

1. **Calydorea coelestina** (Bartr.) Goldbl. & Henrich, comb. nov. BASIONYM: *Ixia coelestina* Bartr., Trav. ed. 1, Philadelphia, 155 (1791) [ed. 1, London, 153 & pl. 3 (1792)]; *Salpingostylis coelestina* (Bartr.) Small, J. New York Bot. Gard. 32: 161 (1931). [See Goldblatt (1974) for additional homotypic synonyms.] TYPE: Illustration in Bartram, Travels, pl. 3.
2. **Calydorea longispatha** (Herbert) Baker, J. Bot. London 14: 189 (1876). BASIONYM: *Gelasine longispatha* Herbert in Benth., Pl. Hartweg. 53 (1840). *Cardiostigma longispatha* (Herbert) Baker, J. Linn. Soc. Bot. 16: 102 (1878); *Sphenostigma longispathum* (Herbert) Benth. & Hook., Gen. Pl. 3(2): 695 (1883). TYPE: Mexico. *Hartweg 403* (BM, G) [See Foster (1945: 12) for additional homotypic synonyms.]
3. **Calydorea mexicana** (R. Foster) Goldbl. & Henrich, comb. nov. BASIONYM: *Sphenostigma mexicanum* R. Foster, Contr. Gray Herb. 155: 13 (1945); *Cardiostigma mexicana* (R. Foster) Ravenna, Notic. Mens. etc. (1978). [Additional homotypic synonyms in Foster (1945).] TYPE: Mexico. México: Temascaltepec, Carboneras, *Hinton et al. 8010* (holotype, GH; isotypes, F, MO, NY, US).

4. **Calydorea gardneri** Baker, J. Bot. London 14: 188. 1876. *Itysa gardneri* (Baker) Ravenna, Nord. J. Bot. 6: 582. 1986. TYPE: Brazil. Piauí: Bôa Esperanca, *Gardner 2322* (holotype, BM not seen). [Known to us from illustrations in Ravenna (1986).]
5. **Calydorea venezolensis** (Ravenna) Goldbl. & Henrich, comb. nov. BASIONYM: *Itysa venezolensis* Ravenna, Nord. J. Bot. 6: 584. 1986. TYPE: Venezuela. Guárico: *Ravenna 2178* (holotype, Herb. Ravenna not seen). [Known to us only from the illustrations in the protologue.]
6. **Calydorea amabilis** (Ravenna) Goldbl. & Henrich, comb. nov. BASIONYM: *Catilla amabilis* Ravenna, Nord. J. Bot. 3: 197. 1983. TYPE: Argentina, Entre-Rios, *Ravenna 3* (holotype, Herb. Ravenna not seen). [Known to us from the illustrations in the protologue and from living material.]

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