A

ANATOMY AND SYSTEMATICS AND OF XYRIDACEAE, WITH SPECIAL REFERENCE TO *ARATITIYOPEA* STEYERM. & P.E. BERRY

by

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A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

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ABSTRACT

ANATOMY AND SYSTEMATICS AND OF XYRIDACEAE, WITH SPECIAL REFERENCE TO *ARATITIYOPEA* STEYERM. & P.E. BERRY

by

Lisa M. Campbell

Adviser: Dr. Dennis Wm. Stevenson

The monocot family Xyridaceae comprises about 385 species in five genera: *Abolboda*, *Achlyphila*, *Aratitiyopea*, *Orectanthe*, and *Xyris*. Xyridaceae are a morphologically diverse assemblage that occur in seasonally wet, usually exposed habitats, such as savannas and boggy meadows. Ninety-five percent of the species comprise the widespread genus *Xyris*; the smaller genera are known only from northern South America, particularly in the Guayana Highlands.

The family is considered related to Eriocaulaceae, and is presently included in the broadly defined order Poales. While systematists generally agree about these relationships, hypotheses that Xyridaceae are not monophyletic have not been critically evaluated. Assessments of relationship have thus far been hindered by the fact that many Xyridaceae are morphologically poorly characterized, particularly the rare, monospecific genera *Achlyphila* and *Aratitiyopea*. Presented here are structural descriptions of *Aratitiyopea lopezii*, a morphological survey of Xyridaceae and related taxa, analyzed using parsimony, and summarized in a generic monograph.

Although the gëstalt of *Aratitiyopea* is aberrant in Xyridaceae, it is structurally consistent with the family, and unusual features are interpreted as adaptations to its relatively mesophytic habitat, shared by few Xyridaceae. The vegetative anatomy exhibits a combination of mesomorphic features and adaptations to seasonal drying. The family is characterized by plants with a basal rosette of leaves and a scapose spike. Plants of *Aratitiyopea* have relatively long, decumbent stems, with broad, cauline leaves, and a congested, showy, compound raceme. The large, tubular flowers have a uniseriate androecium of epipetalous stamens, and fleshy appendages on top of the ovary. These features, along with highly ornamented, inaperturate pollen are most similar to those exhibited by *Orectanthe* and *Abolboda*.

Parsimony analysis resolved Xyridaceae as monophyletic with two main lineages: one consisting of *Xyris*, and the other of *Achlyphila* sister to *Aratitiyopea-Orectanthe* and *Abolboda*. This represents a novel hypothesis of relationship in Xyridaceae, because *Achlyphila* is generally considered to be sister to *Xyris*, and highlights the need for a critical evaluation of the structure of *Achlyphila*. Synapomorphies of *Aratitiyopea* and *Orectanthe* are the presence of large flowers, a protruding anther connective, and the gynoecium appendages located on the ovary (vs. on the style).

RESUMEN

ANATOMY AND SYSTEMATICS AND OF XYRIDACEAE, WITH SPECIAL REFERENCE TO *ARATITIYOPEA* STEYERM. & P.E. BERRY

by

Lisa M. Campbell

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La familia Xyridaceae de las monocotiledóneas incluye cerca de 385 especies en cinco géneros: *Abolboda*, *Achlyphila*, *Aratitiyopea*, *Orectanthe* y *Xyris*. Xyridaceae son un ensamblaje morfologicamente diverso que se encuentra en ambientes estacionalmente húmedos, usualmente al descubierto, tales como sabanas y campos inundados. Un 95% de las especies pertenecen al género *Xyris*, de amplia distribución; los géneros más pequeños se conocen sólo del norte de Sudamérica, particularmente del Macizo de Guayana.

La familia se considera relacionada a Eriocaulaceae, y en estos momentos se incluye en un orden Poales ampliamente definido. Aunque la sistemática moderna generalmente esta de acuerdo con estas relaciones, las hipótesis que tratan la monofilia de Xyridaceae no han sido críticamente evaluadas. El estudio de estas relaciones ha estado hasta ahora retrasado porque algunos géneros de Xyridaceae están morfológicamente poco caracterizados, particularmente los géneros monoespecíficos *Achlyphila* and *Aratitiyopea* que son poco comunes tanto en el campo como en los herbarios. Aquí se presentan la descripción estructural de *Aratitiyopea lopezii*, un reconocimiento morfológico de Xyridaceae y taxones relacionados, utilizando análisis de parsimonia y resumidos en una monografía genérica.

Aunque el aspecto de *Aratitiyopea* es aberrante en Xyridaceae, a su vez es estructuralmente consistente con la familia, y sus rasgos no usuales dentro de Xyridaceae se interpretan como adaptaciones a su ambiente mesolítico típico, que comparte con muy pocos otros miembros de la familia. La anatomía vegetativa muestra una combinación de rasgos mesomórficos y adaptaciones a sequías estacionales. Plantas en la familia presentan característicamente una roseta basal y una espiga escapiforme. Las plantas de *Aratitiyopea* tienen tallos decumbentes, relativamente largos, with hojas anchas caulinares, y un racimo compuesto relativamente grande y vistoso. Las flores grandes, tubulares, tienen un androceo uniseriado de estambres epipétalos, y apéndices carnosas sobre el ovario. Estos rasgos, junto con el polen altamente ornamentado e inaperturado, son más similares a los que muestran *Orectanthe* and *Abolboda*.

Análisis de parsimonia resuelven Xyridaceae como un grupo monofilético con dos linajes principales: uno que contiene a *Xyris*, y el otro a *Achlyphila* como grupo hermano de *Aratitiyopea-Orectanthe* y *Abolboda*. Estos resultados representan una hipótesis novel de relaciones filogenéticas en Xyridaceae, porque *Achlyphila* generalmente se consideraba un grupo hermano a *Xyris*, y a su vez demuestra la necesidad de tener una evaluación más crítica de la estructura de *Achlyphila*. Entre las sinapomorfias de *Aratitiyopea* y *Orectanthe* se encuentran las flores relativamente grandes, el conectivo de la antera protuberante, y las apéndices sobre el ovario (*versus* sobre el estilo en otras Xyridales).

To my mother, Carol, and in loving
memory of my father, Richard.

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1. AN INTRODUCTION TO XYRIDACEAE

Xyridaceae are a morphologically diverse assemblage of monocots included in the broadly defined Poales, part of the large commelinid clade (Chase et al. 2000, Soltis et al. 2000, APG 2003). The family is usually considered closely related to Eriocaulaceae (Cronquist 1981, Dahlgren et al. 1985, Thorne 2000) and was included in Dahlgren et al.'s (1985) petaloid Commelinales. As presently understood, Xyridaceae includes the wide spread genus *Xyris* (ca. 360 spp.), and four genera endemic to northern South America: *Abolboda* (21 spp.), *Achlyphila* (1 sp.), *Aratitiyopea* (1 sp.), and *Orectanthe* (2 spp.). Species of the latter four are mostly endemic to the Guiana Shield, especially the isolated table-top mountains (tepuis) of the Roraima formation. The monotypic genera, *Achlyphila* and *Aratitiyopea*, are known from only a few localities. The greatest species diversity of *Xyris* is in the neotropics, but species are found throughout tropical to subtropical regions (from Australia, through Indonesia to southern Asia, Africa, and the Americas), and a minor number of species occur in adjacent temperate Australia and North America.

As the number of taxa ascribed to Xyridaceae accelerated in the mid 1900's, it was noted that the family is morphologically heterogeneous, but without concordant discrepancies (Maguire and Wurdack 1960, Dahlgren et al. 1985, Rudall and Sajo 1999). Phylogenetic studies have shown conflict with respect to the monophylesis of the family (e.g. Bremer 2002, Michelangeli et al. 2003, Davis et al. 2004) and its placement within monocots(e.g. Chase et al. 1995, APG 1998, APG 2003). Some of these discrepancies rest in the understandable lack of samples and basic data about the two rare and difficult to collect genera, *Aratitiyopea* and *Achlyphila*.

Aratitiyopea lopezii (L. B. Sm.) Steyerm. & P. E. Berry is an herbaceous perennial with long, decumbent stems that terminate in a congested inflorescence. Isolated populations occur in semideciduous forests in areas of high annual precipitation (2800–4000 mm) that are located on ancient sandstone and granite in the Guayana region of northern South America, and on the geologically similar, although younger (Foster and Beltran 1997), Cordillera del Cóndor in northern Peru. The habit and escapose inflorescence, with large flowers and colorful bracts, is strikingly different from species in the more familiar genera *Xyris* and *Abolboda*. Indeed, *Aratitiyopea lopezii* (L. B. Sm.) Steyerm. & P. E. Berry was originally ascribed to *Navia*, a moderate-sized genus in the Bromeliaceae, also endemic to the Guayana region (Holst and Luther 2004). Interestingly, the features of this species that were unique within *Navia*, the flower size and magenta corolla (Smith 1951), are also unusual for Xyridaceae. The morphology and possible systematic affinities of the species remained obscure until additional material from an expedition to Cerro Aratitiyope (Amazonas state, Venezuela) was examined. The authors realized that the species doesn't exhibit the combination of features found in Bromeliaceae, and concluded that the uniseriate androecium, and appendages on the ovary were consistent with Xyridaceae (in Steyermark 1984). They remarked on its similarity to *Orectanthe ptaritepuiana* (Steyerm.) Maguire, a little-known species with stems that trail over high elevation scrub vegetation.

The purpose of this contribution is to further describe structural aspects of *Aratitiyopea* based on field studies and collections, to incorporate the data in assessment of the monophylesis of the family, and to summarize these results in a systematic treatment.

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2. VEGETATIVE ANATOMY AND MORPHOLOGY

Introduction

Xyridaceae are delicate to relatively robust herbs, the majority of which are sympodially branched and perennial. Most species are characterized by a basal rosette of leaves that are either ranked or spiraled and a long naked scape that bears the inflorescence. Xyridaceae occur in oligotrophic habitats that are seasonally or permanently wet or moist, such as grasslands and savannas, or on rock faces, particularly sandstone and granitic outcrops, and other exposed habitats.

Modern contributions on the anatomy of Xyridaceae were prepared for the New York Botanical Garden's series *The Botany of the Guayana Highlands* (Carlquist 1960) and Metcalfe's *Anatomy of the Monocotyledons* (Tomlinson 1969). Both summarized the anatomical literature for Xyridaceae. These treatments were prepared prior to the description of *Aratitiyopea*, and included *Abolboda*, *Achlyphila*, *Orectanthe* and *Xyris*.

The habit of *Aratitiyopea* and the habitats that it occupies are different from most other Xyridaceae and similarities are known only in *Orectanthe ptaritepuiana* (Steyerm.) Maguire (Fig. 2.1) and, more remotely, in a few species of *Xyris*. As with many species in the family, *Aratitiyopea* is endemic to granite and sandstone mountains in northern South America; however, while most species occur in open-canopied sites, *Aratitiyopea* occurs under dense to

Figure 2.1. A herbarium specimen of *Orectanthe ptaritepuiana* (*Steyermark and Wurdack 523* [NY]).

moderate canopy, often in very shallow debris, or scrambling over understory scrub vegetation. The distribution of *Aratitiyopea* appears to be confined to areas of high annual precipitation for the region (3,000–4,000 mm). Plants have relatively flexible, thin, broad leaves that occur along a decumbent rhizome, becoming very congested just below the inflorescence.

Materials and Methods

Observations are based on specimens that were fixed in formalin-propionic acid-alcohol (1:1:18 v/v, 50% ethanol), and later transferred to 70% ethanol (*L. M. Campbell et al. 734, 766, 813* [NY, TFAV, VEN]). Additionally, specimens of *Aratitiyopea* from the following herbaria have been studied: COL, F, GH, K, MO, NY, SEL, US, and VEN. Some stem was sectioned using a sliding microtome, and the presence of lignin detected with saturated phloroglucinol acidified with HCL (Jensen 1962). Other sectioned material (including stem) was embedded in Paraplast+® using standard procedures, sectioned with a rotary microtome, and stained with safranin and astra blue. Figure 2.2 was drawn using camera lucida, and edited in Adobe Illustrator® (ver. 8.0) and PhotoShop® (ver. 7.0).

For scanning electron microscopy, specimens were dissected in 70% ethanol, dehydrated in a series to 100% acetone and critical point dried. Samples were coated with gold palladium in a Hummer 6.2 sputtering system and viewed with a JEOL JSM-5410LV scanning electron microscope.

The following abbreviation is used: T.S., for transverse section.

Observations and Discussion

Root

Aratitiyopea.—Fleshy, densely covered by uniseriate, multicellular hairs (Fig. 2.2). Hairs from one end of cell, epidermal cells of the same length. Exodermis many cell layers thick, cells thick-walled and heavily lignified, staining red with safranin (Fig. 2.3A). Middle cortical cells of a similar size, usually with a ring of very large cells near the endodermis (Fig. 2.3B), some areas of cell death (Fig. 2.3A). Aerenchyma present in some roots (Fig. 2.3C). Endodermis very conspicuous of thick-walled cells, with the small lumen near the exterior, staining bright orange with safranin (Figs. 2.3A,B). Central cylinder containing a continuous pericycle, polyarch, with the vessels forming a single ring, and little or no phloem. Toward the endodermis vessels invested in fibers, the cells grading to sclerenchyma, and parenchyma of the wide pith that appear to be somewhat lignified. (Fig. 2.3B).

Relative to other Xyridaceae (Carlquist 1960, Tomlinson 1969), the roots of *Aratitiyopea* present a relatively wide cortex and pith. The thickened endodermal cell walls are characteristic of the family, and Carlquist (1960) found the pattern to be taxonomically diagnostic in *Abolboda*. Carlquist (1960) observed in *Achlyphila* that the endodermis stained orange, whereas other lignified cells stained red, as found here for *Aratitiyopea*. In *Abolboda* vessels are uniformly distributed throughout the stele (Carlquist 1960), otherwise, in the taxa studied, vessels are distributed near the periphery of the central cylinder in Xyridaceae (Tomlinson 1969). The roots of *Aratitiyopea* that include aerenchyma are

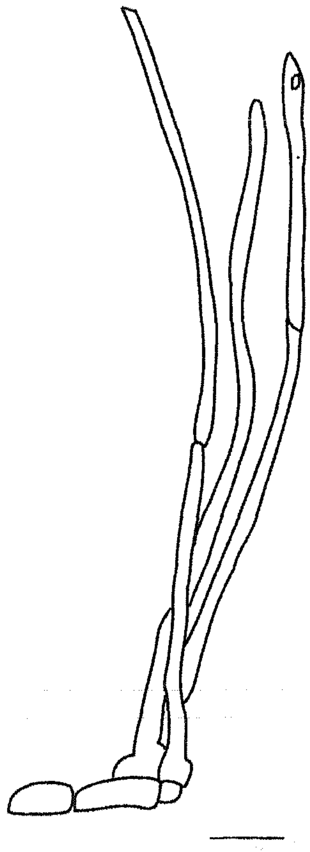

Figure 2.2. Root hairs of *Aratitiyopea lopezii*. (Scale bar = 0.25 mm).

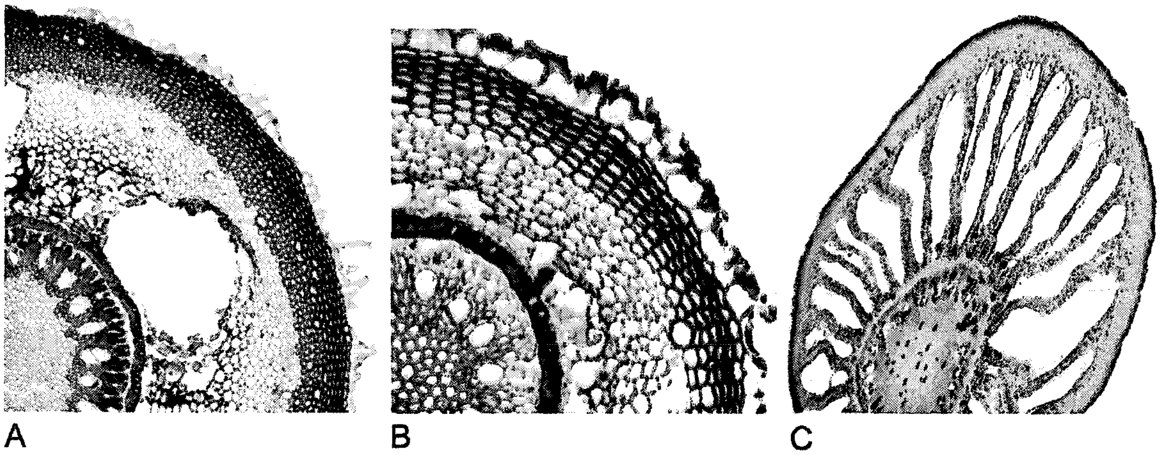

Figure 2.3. Transverse sections of roots of *Aratitiyopea lopezii*. A. A mature root. B. A young root. C. An aerenchymatous root.

probably formed during periods of inundation. The patches of cell death between the exo- and endodermis appear to be the result of seasonal drought (see Dickison 2000). Roots observed here exhibit variation in the development of sclerification. Nilsson (1892) considered highly sclerotic roots as mechanical, and distinguished them from typically functioning roots. As Carlquist (1960) pointed out, the differences are probably not clear cut, and they are more a matter of degree.

Stem

Aratitiyopea.—Epidermal cells without suberin. A narrow cortex is composed of dense, starchless, isodiametric parenchyma cells, and is delimited by a multi-layered sheath of small, thick walled sclereids (Fig. 2.4). Internal to this sheath, the majority of the vascular bundles are embedded in lignified ground tissue, the cells of which become progressively larger and more parenchymatous centripetally. Vascular bundles amphivasal and surrounded by lignified cells. Central pith of dense, unlignified parenchyma.

Most Xyridaceae have a short vertical stem, with short internodes, and the leaves usually form a congested rosette. A few species, including *Aratitiyopea*, have longer stems and internodes, that become distally congested in *Aratitiyopea*.

Anatomically, stems of most Xyridaceae are characterized by a sclerotic sheath demarcating the central cylinder (Carlquist 1960, Tomlinson 1969). In *Achlyphila*, the sclerotic sheath has been interpreted as an endodermis (Carlquist

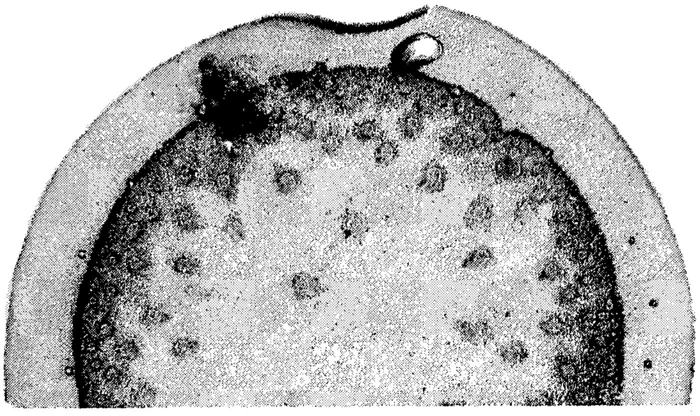

Figure 2.4. Transverse section of a stem of *Aratitiyopea lopezii.*

1960, Tomlinson 1969) because the staining properties and pattern of the cell wall thickenings resemble those of the root endodermis (Carlquist 1960). The twenty-one species of *Abolboda* can be roughly divided into two groups based on overall robustness of the plants. This distinction correlates with anatomical features and is how data has been presented (Carlquist 1960, Tomlinson 1969). A sclerotic sheath was not found in larger species of *Abolboda* or *Orectanthe sceptrum* (Oliv. ex Thurn) Maguire, although it was present in *O. ptaritepuiana* (Carlquist 1960). In stems of the former, the cortical cells contain abundant starch.

Within the family, variation occurs in the relative width of cortex, the presence of spongy ground tissue in some *Xyris* and the small species of *Abolboda*, and presence of a sclerotic central pith in *Orectanthe sceptrum*. Leaf traces are surrounded by a sclerotic sheath, except in *Achlyphila*, where sclerenchyma occurs only near the protoxylem pole.

Leaf

Aratitiyopea.—Leaves are bifacial, lingulate in outline, and spirally arranged. Epidermis with a thin cuticle, without epicuticular wax, glabrous. Stomata abaxial (hypostomatic), paracytic (Fig. 2.5A), the outer periclinal walls of the guard cells thickened, and with cuticular extensions (Fig. 2.5B). Epidermal cell, in surface view rectangular, the end walls mostly truncate, sometimes oblique, the lateral walls becoming sinuous near the leaf apex. In T.S., the walls evenly thickened, cells of the adaxial epidermis elongate (Fig. 2.6). Along the leaf margins a narrow band of cells sclerotic. Mesophyll not differentiated into adaxial palisade

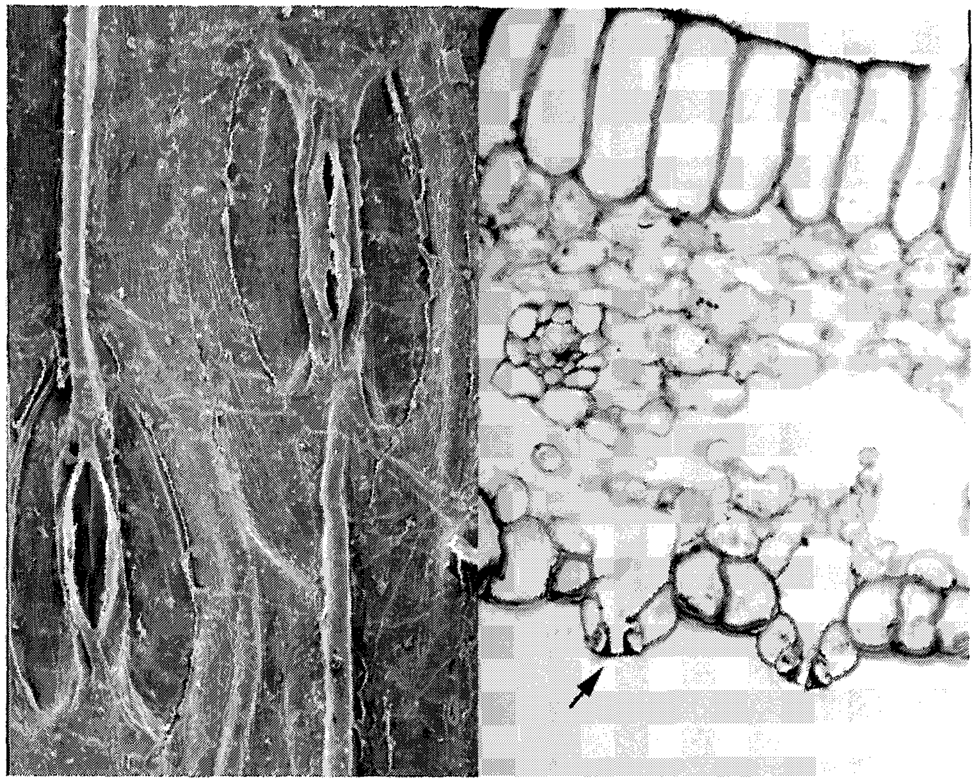

Figure 2.5. Leaf anatomy of *Aratitiyopea lopezii*. A. Scanning electron micrograph of leaf surface showing paracytic stomata (x 500). B. Transverse section of a leaf (arrow: guard cell with cuticular extension covering the stoma).

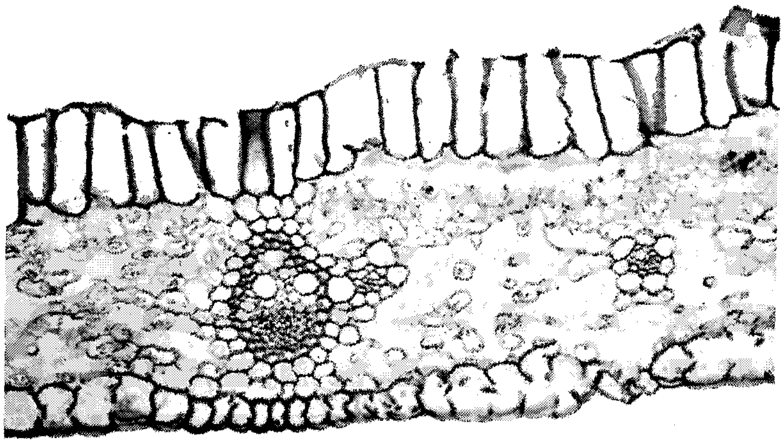

Figure 2.6. Transverse section of a leaf of *Aratitiyopea lopezii*.

parenchyma, with numerous intercellular spaces, including substomatal chambers (Fig. 2.6). Parenchyma adjacent to the dermal layers more or less isodiametric, those of the spongy central tissue irregular in shape and elongate. Vascular bundles equidistant from each surface, surrounded by a sclerotic sheath of 1- or 2-cell layers, which is surrounded by a single layer of large, colorless parenchyma. Together with mesophyll cells, the sheath forms a girder between the ad- and abaxial surfaces. Smaller vascular bundles alternate with larger ones. A few compound vascular bundles, surrounded by a common sclerotic sheath occur. In the terete tip, three large vascular bundles consisting mostly of xylem, are invested in dense chlorenchyma.

The leaf sheath is broad and without a distinct articulation from the lamina. In T.S. it differs from the lamina in that the cells of both dermal layers are similar in length, and the mesophyll is uniform with tightly arranged parenchyma that includes regularly spaced intercostal lacunae.

The genera of Xyridaceae are often considered in two groups, which correspond to leaf type and phyllotaxy (Nakai 1943, Takhtajan 1997, Sajo & Rudall 1999). *Xyris* and *Achlyphila* have unifacial leaves that are ranked, and *Abolboda*, *Aratitiyopea*, and *Orectanthe* have bifacial leaves that are spirally inserted. Most Xyridaceae have xeromorphic adaptations, such as sclerophylly, to the intense exposure and seasonal dryness they endure. Sclerophylly is also associated with deficiency in some minerals (Dickison 2000) and Xyridaceae habitats are typically nutrient poor (e.g. acidic peat soils and sand savannas). In the Guayana Highlands, where Xyridaceae are most diverse, sclerophylly is paralleled in other unrelated groups (e.g., Mutisieae [Carlquist 1958] and Bonnetiaceae [Dickison and Weitzman 1996]). When turgor pressure is low, thickened cell walls and fibrous bundle sheath extensions provide mechanical support. Epidermal cells of many Xyridaceae have either uniformly thickened walls, or thickened periclinal walls, which are rugose or papillate in *Achlyphila* and some *Xyris* species (Carlquist 1960, Tomlinson 1969). *Xyris* has leaf axil hairs that are associated with mucilage (Tomlinson 1969, pers. obs.); mucilage is otherwise unknown in the family.

Leaves of *Orectanthe* and *Abolboda* have a multi-layered, colorless, adaxial hypodermis. Additionally, an abaxial hypodermis is present in *Orectanthe sceptrum* (Carlquist 1960). The hypodermis may be confined to only the distal portion of leaves in some *Abolboda* species. Carlquist (1960) related a continuous hypodermis to the large-stemmed *Abolboda* species sampled in his study. However, additional sampling and a re-identification of one specimen sampled by Carlquist (*Maguire et al. 41439*, *A. ebracteata* Maguire & Wurdack var. *brevifolia* Maguire) reveals an ecological correlation of a reduced hypodermis formed by species that inhabit relatively moister sites, such as high elevation bogs.

Aratitiyopea occurs in a moister, shadier habitat, and has a relatively thin lamina that contains less sclerotic tissue. Despite this, there is no distinct palisade parenchyma typical of mesophytes (Esau 1965). The internally elongate adaxial epidermal cells in *Aratitiyopea* comprise a substantial portion of the leaf and may function in water storage (cf. Eriocaulaceae, Tomlinson 1969). Other internal features of the leaf, such as the mesophyll, which is spongy in the lamina and dense and lacunate in the sheath, are similar to that found in *Abolboda* and *Orectanthe*. Irregularly shaped chlorenchyma is also found in the mesophyll of representatives of all the genera except *Achlyphila* (Carlquist 1960, Tomlinson 1969).

Conclusions

Carlquist (1960) concluded, based on gross morphology and anatomy, that *Abolboda* and *Orectanthe* are closely related, and that both *Xyris* and *Achlyphila* are quite different from them, and from each other. In gross vegetative morphology, plants of *Aratitiyopea* are most similar to those of the more robust genus *Orectanthe*, particularly the longer-stemmed *O. ptaritepuiana*. Considering vegetative features, the simplest distinction of two groups of genera in Xyridaceae based on leaf type (e.g. Takhtajan 1997) is not well substantiated by other characters. For example, *Xyris* and some *Abolboda* species have uniformly thickened cell walls in the endodermis, while the remaining taxa have thin peripheral walls. Naturally, all of the bifacially-leaved genera have some leaf anatomical features common to leaves with this type of development. *Aratitiyopea* does not have a hypodermis, which is also not found in *Xyris* and *Achlyphila*, and presents an epidermis type unique in the family. The vegetative morphology and anatomy of *Aratitiyopea* reflect adaptations to periodic inundation (aerenchymatous roots), and seasonal water depletion (sclerification of the endodermis) typical of the habitat it occupies. Other vegetative features of

Xyridaceae not expressed by *Aratitiyopea*, such as reduced leaf size and a hypodermis, are considered specializations for xeromorphic conditions.

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3. INFLORESCENCE ARCHITECTURE AND FLORAL MORPHOLOGY

Introduction

Aratitiyopea is a monospecific genus of herbaceous perennial plants with long, decumbent stems that terminate in a congested inflorescence (Figs. 5.4, 5.5). The habit and escapose inflorescence, with large flowers and colorful bracts is strikingly different from species in the more familiar genera *Xyris* and *Abolboda*. Indeed, *Aratitiyopea lopezii* (L. B. Sm.) Steyerm. & P. E. Berry was originally ascribed to *Navia*, a moderate-sized genus of Bromeliaceae endemic to the Guayana region (Holst and Luther 2004). Interestingly, the features of this species that were unique within *Navia*, the flower size and magenta corolla (Smith 1951), are also unusual for Xyridaceae. The morphology and possible systematic affinities of the species remained obscure until additional material from an expedition to Cerro Aratitiyope (Amazonas state, Venezuela) was examined; the authors concluded that the uniseriate androecium, and appendages on the ovary were consistent with Xyridaceae (in Steyermark 1984). They remarked on its similarity to *Orectanthe ptaritepuiana* (Steyerm.) Maguire (Figs. 2.1, 5.7), a little-known species with stems that trail over high elevation scrub vegetation.

Xyridaceae are characterized by a scapose spike inflorescence, and the few exceptions to this growth form (i.e. some *Abolboda* species and *Aratitiyopea*) have not been critically evaluated. In the taxonomic literature, the inflorescence of *Aratitiyopea* is described as a bracteate hemispheric capitulum (Steyermark

1984; Kral 1992, 1998) of fascicles '*...in foliorum centro nidulans...*' (Smith 1951). While the inflorescence structure is largely uniform in Xyridaceae, it has long been noted that floral morphology is heterogeneous (Maguire and Wurdack 1960, Dahlgren et al. 1985, Rudall and Sajo 1999) but without concordant discrepancies (Table 5.1). The purpose of this contribution is to further describe the floral morphology and clarify the inflorescence architecture of *Aratitiyopea lopezii*.

Materials and Methods

Specimens of *Aratitiyopea* from the following herbaria have been studied: COL, F, GH, K, MO, NY, SEL, US, and VEN. Henk van der Werff (MO) kindly provided a pickled flower from a population in Peru (*van der Werff 16131*; *MO, SEL*). Living samples were fixed in formalin-propionic acid-alcohol (1:1:18 v/v, FPA), and transferred to 70% ethanol (*L. M. Campbell et al. 734, 766, 813* [NY, TFAV, VEN]). Sectioned material was embedded in Paraplast+® using standard procedures, sectioned with a rotary microtome, and stained with safranin and astra blue. Figure 3.1B was drawn using camera lucida, and edited in Adobe Illustrator® (ver. 8.0) and PhotoShop® (ver. 7.0).

For scanning electron microscopy, flower buds were dissected in 70% ethanol, dehydrated in a series to 100% acetone and critical point dried; pollen grains were dissected from ethanol preserved flowers, and air dried on stubs. All samples were coated with gold palladium in a Hummer 6.2 sputtering system and viewed with a JEOL JSM-5410LV scanning electron microscope.

Observations and Discussion

Inflorescence Architecture

As mentioned above, the inflorescence of most Xyridaceae (98%) is a globose to turbinate or capitulate spike, borne on a scape. One or more pairs of subopposite bracts occur along the scape of many *Abolboda* species. The reproductive system of *Aratitiyopea* terminates the vegetative axis as a double raceme of six to 16 racemes (Fig. 3.1). Occasionally the main axis bears a fully developed green leaf. The individual racemes are short-pedunculate, subtended by a foliose bract, and bear a bicarinate addorsed prophyll (Fig. 3.1). These secondary racemes are formed by several to many flowers in a 3/8 tactic spiral, meaning that three parastiches intersect with five parastiches spiraled in the opposite direction, with a divergence angle of 135°. The integers comprising the fraction are part of the Fibonacci series (i.e. 1, 1, 2, 3, 5, 8…; see Leppik 1961, Esau 1965, Jean 1994). The Fibonacci summation series for tactic patterns (i.e. 1/2, 1/3, 2/5, 3/8, 5/13…) is widespread in plants with spiraled organs, particularly in the arrangement of leaves (Leppik 1961, Esau 1965, Jean 1994).

The suite of inflorescence features presented by *Aratitiyopea* (a compound inflorescence, with many-flowered branches, not borne on a scape) is not known in other Xyridaceae. Escapose inflorescences are encountered in two diminutive *Abolboda* species that have reduced inflorescences. Compound, scapose inflorescences occur in *Achlyphila disticha* Maguire & Wurdack and a few *Abolboda* species, all with a reduced number of flowers per branch.

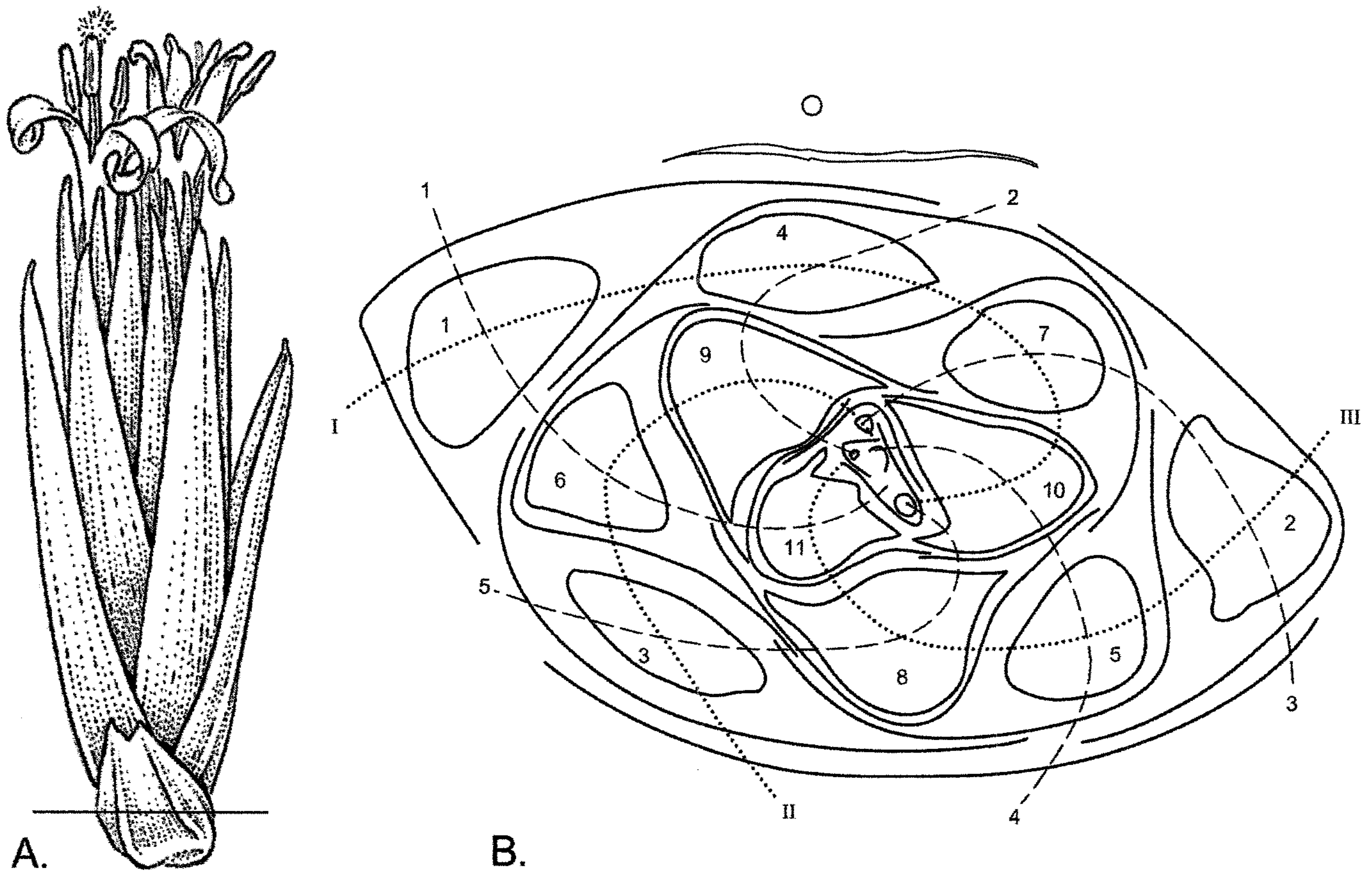


Figure 3.1. An inflorescence branch of *Araitityopea lopezii*. An indivdual raceme, with an adaxial prophyll. A1-A2 indicates the transection in B. B. Cross section through the base of the raceme, and parastiches of the tactic spiral (not the abaxial view is reversed from A). (A drawn by Bobbi Angell.)

Flower Structure

Typical of Xyridaceae, the flowers of *Aratitiyopea* open in the early morning and the corolla withers after several hours. A striking feature of *Aratitiyopea lopezii* is the robustness of the plants, and the concomitant large flowers (ca. 6.5 cm) relative to most Xyridaceae. Flowers are composed of four whorls (Fig. 3.2) and subtended by a foliose, persistent magenta bract. Two color morphs have been collected thus far, and, in at least the one population studied, they are sympatric, and flower simultaneously. Plants bear flowers with either a white corolla and stigma, or a magenta corolla and stigma (but a white style and filaments).

Perianth.— The Xyridaceae perianth is trimerous and bicyclic, with a distinct calyx and corolla. Variation occurs in the form and persistence of the median (abaxial) sepal and in the fusion of the corolla (Table 5.1). In *Aratitiyopea*, the median sepal is subequal to the lateral sepals (Figs. 3.2, 3.3C) and all are persistent in fruit. The sepals contain numerous vascular bundles. The corolla is fused into a long (5.5 cm) tube and, unique to Xyridaceae, the free petal limbs are contorted (Figs. 3.2, 5.4). Within the parenchymatous ground tissue of each petal there are numerous more-or-less equal vascular bundles and a central larger bundle from which the epipetalous stamen trace diverges. The petals are delicate, but lack the fimbriate apex typical in the family (e.g. Fig. 5.4C). A calyx of subequal, persistent sepals is also found in the genus *Achlyphila disticha* Maguire & Wurdack, which occurs at high elevations, whereas in the other genera the sepals are strongly dimorphic and fugacious (*Abolboda* and *Xyris*) or

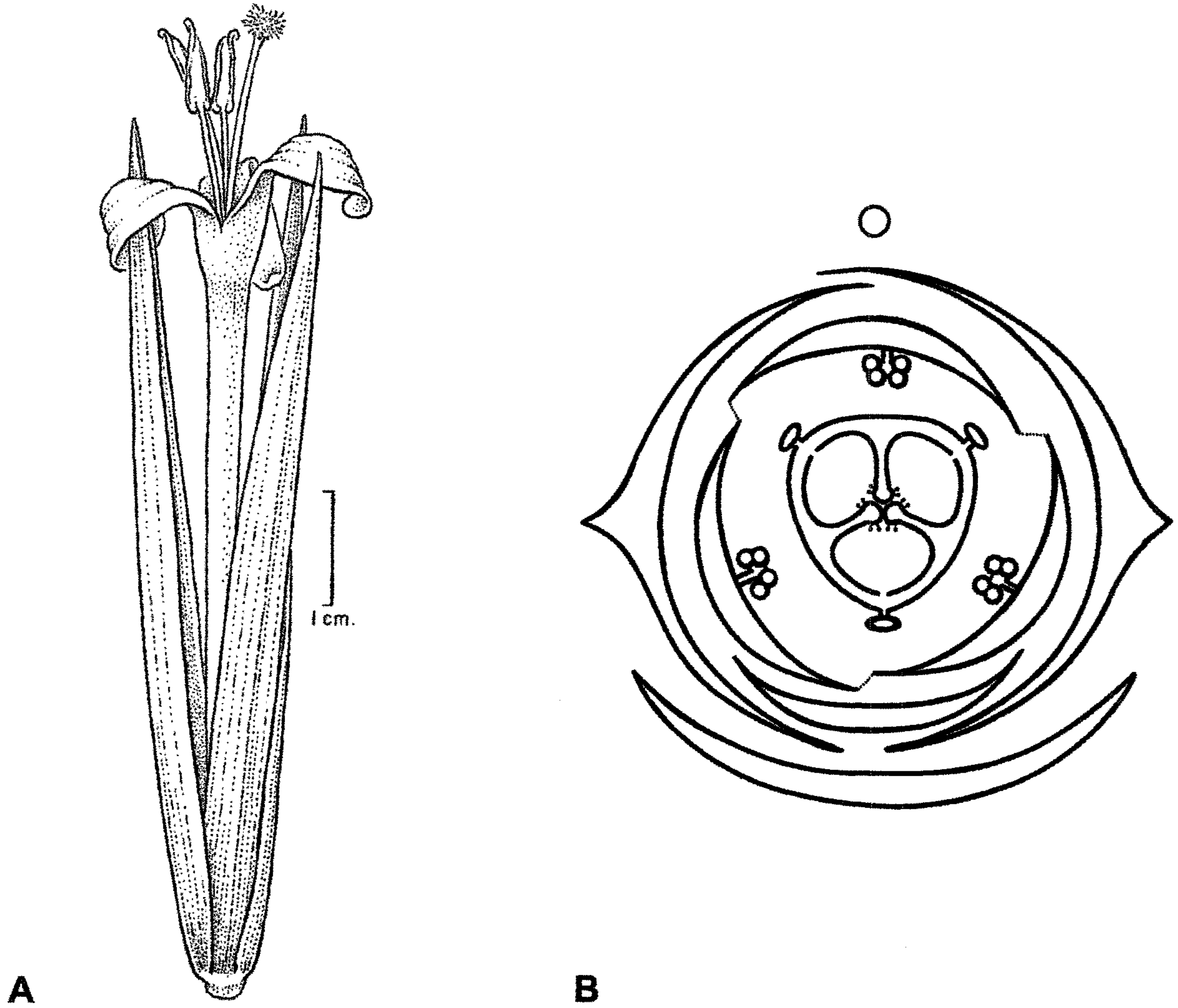
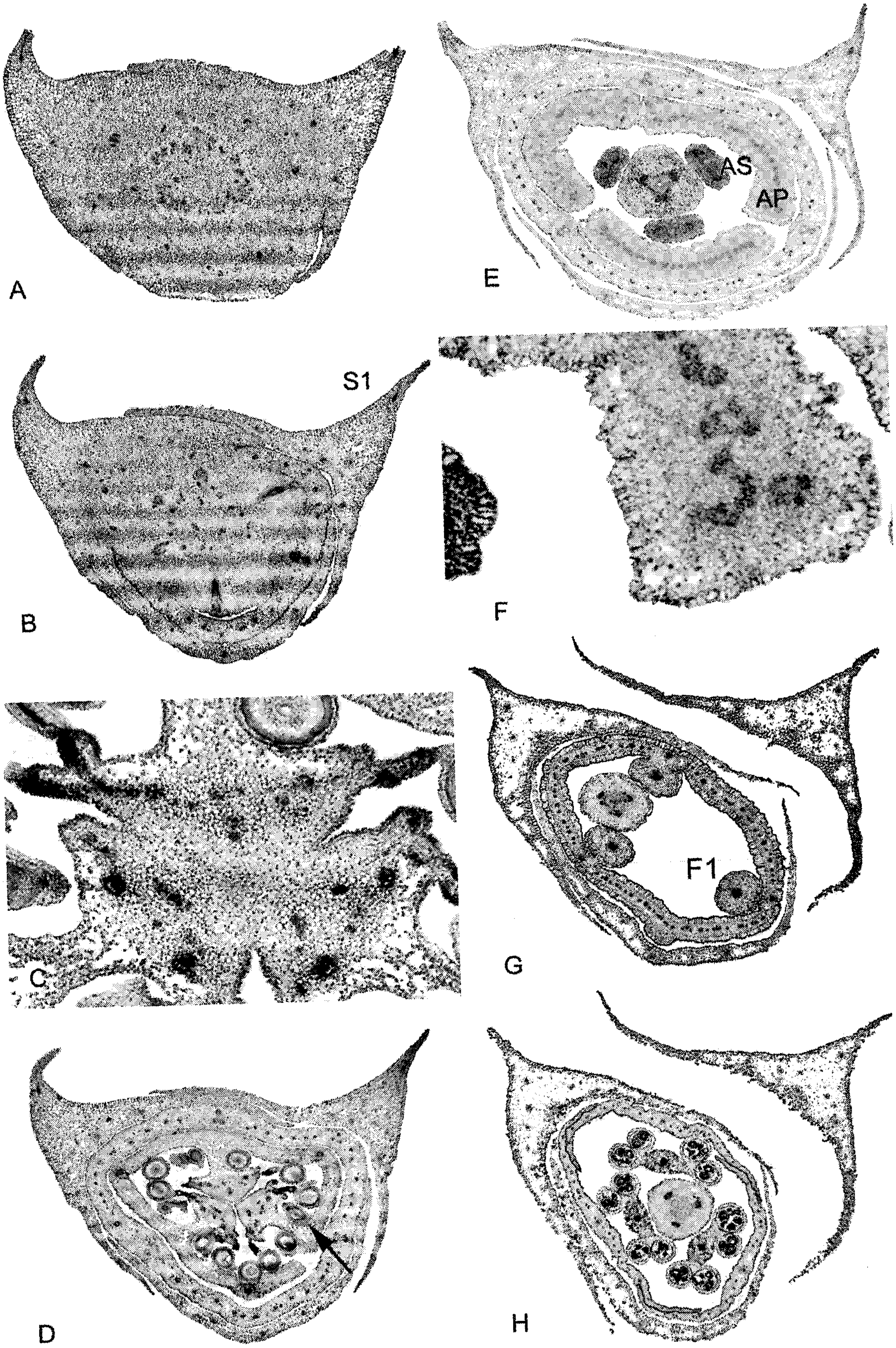


Figure 3.2. Floral morphology of *Aratitiyopea*. A. Abaxial view of a flower. B. Floral diagram of *Aratitiyopea*. The large dorsal gynoecial appendages are depicted; dorsal stigma lobes not shown. (A drawn by Bobbi Angell.)

Figure 3.3. Acropetal sections through a flower of *Aratitiyopea lopezii*.. A. Peduncle. B. Calyx initiated (s1 first sepal). C. Septa fused in the base of the ovary. D. Mid-ovary, showing intruded placentae and anatropous ovule (arrow). E. Near the ovary apex, showing the appendages (ap distal portion of an appendage, as an appendage stalk). F. Detail of the distal portion of an appendage. G. Divergence of the staminal filaments (f1 filament 1). D. At the level of the anthers. Note the solid style.


A
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caducous (*Orectanthe*). Sympetalous corollas are found in *Abolboda* and *Orectanthe*.

Androecium.—The form of the stamens and presence of an outer androecium whorl, if present expressed solely as staminodia, varies in the family. The anthers are hypogenous or epipetalous, basifixed or dorsifixed and tetrasporangiate with longitudinal dehiscence of varying orientation. In *Aratitiyopea*, the androecium is uniseriate with three antepetalous fertile stamens. The filaments are epipetalous, and supplied by a single vascular trace from the petal midvein (Figs. 3.3G, H). The anthers are basifixed, dehisce latrorsely, and the connective projects slightly beyond the thecae (Fig. 5.5F). The yellow pollen grains are large (to 180 µm), inaperturate, with a dense surface ornamentation of very large bacula interspersed among smaller ones (Fig. 5.12A).

Anthers of *Orectanthe* are also basifixed, and have a slight connective protrusion (Fig. 5.7F), whereas in other Xyridaceae the connective is sunken. Inaperturate pollen occurs in *Achlyphila*, *Abolboda* and *Orectanthe*; pollen of the latter two have surface ornamentation similar to *Aratitiyopea* (Carlquist 1960, Nilsson & Praglowski1992; see Chapter 5). Antesepalous staminodia occur in some *Abolboda*, and are well-developed structures in *Xyris*, forming a conspicuous part of the floral display.

Gynoecium.—In all Xyridaceae, the gynoecium is tricarpellate and the ovary superior. In *Aratitiyopea*, the ovary is trilocular with the septa basally fused (Fig. 3.3C), but unfused throughout the most of the ovary (Fig.3.3D). Each carpel has a dorsal vascular bundle that continues up and bifurcates with one branch entering an appendage and the other entering the style. Numerous biseriate, anatropous ovules are borne on intruded placentae (Fig. 3.3D). The style contains a solid column of transmitting tissue (compitum; Figs. 3.3E, G, H) and branches distally into three stigmatic lobes that are further ramified into a plumose stigma (Fig.3.4). A large, fleshy gland, or appendage, develops on the dorsal flank of each carpel (Fig. 3.5A). At anthesis, the stalked appendage is atop the ovary and the distal, reflexed massive portion occupies most of the diameter of the floral tube (Fig. 3.3E). In this region, the numerous vascular bundles are mostly composed of phloem, and cells of the ground tissue are densely cytoplasmic with large nuclei. Near the periphery, the tissue becomes aerenchymatous (Fig. 3.3F). In contrast to the regularly-shaped cells of the epidermis along the appendage stalk, the cells in the distal portion form a glandular, papillate epithelium that lacks stomata (Figs. 3.3F, 3.6) .

A trilocular ovary with intruded placentae, usually described as axile placentation in taxonomic descriptions (e.g. Kral 1998) is common, but not uniform, within the family. A reexamination of *Xyris* sect. *Pomatoxyris* and *Achlyphila* is needed in light of this new interpretation. *Orectanthe* and *Abolboda* have solid styles, an uncommon condition in monocotyledons (Rudall et al. 2002), whereas the style is hollow in *Xyris* (but unknown in *Xyris* sect. *Pomatoxyris* and in *Achlyphila*). The gynoecium of *Achlyphila* is incompletely known with respect to the surface of the stigma, the degree of fusion of the

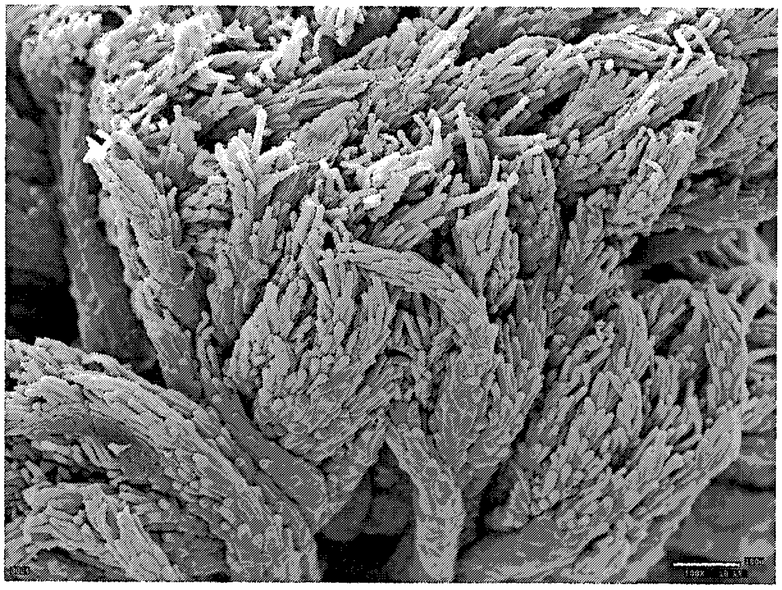

Figure 3.4. Plumose stigma of *Aratitiyopea lopezii* (scale bar = 100 µm).

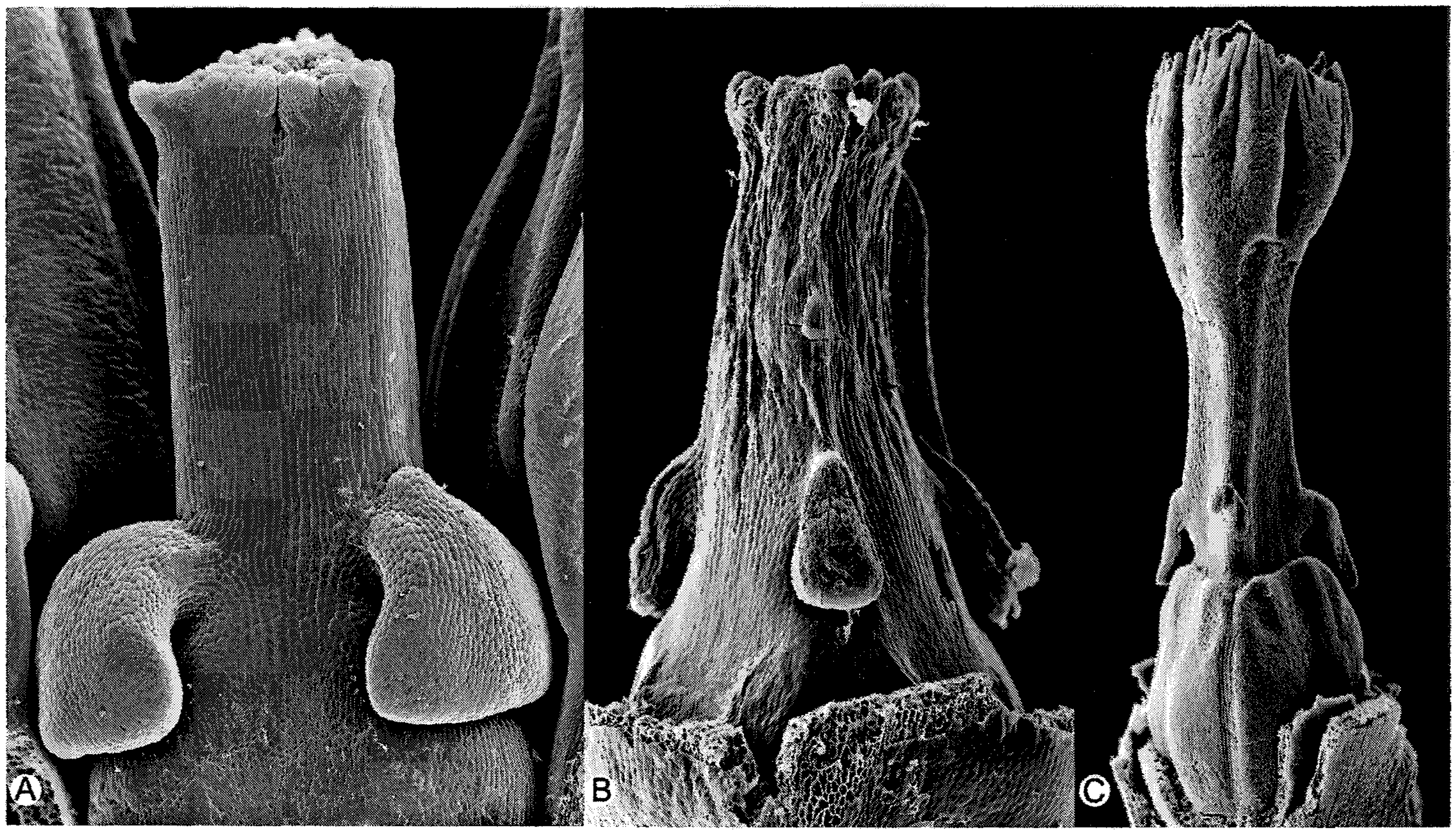

Figure 3.5. Immature appendaged gynoecia of Xyridaceae. A. *Aratitiyopea lopezii*, adaxial view. B. *Orectanthe sceptrum*, abaxial view. C. *Abolboda grandis*, abaxial view. Note the reducded abaxial appendage above the dorsal bundle groove.

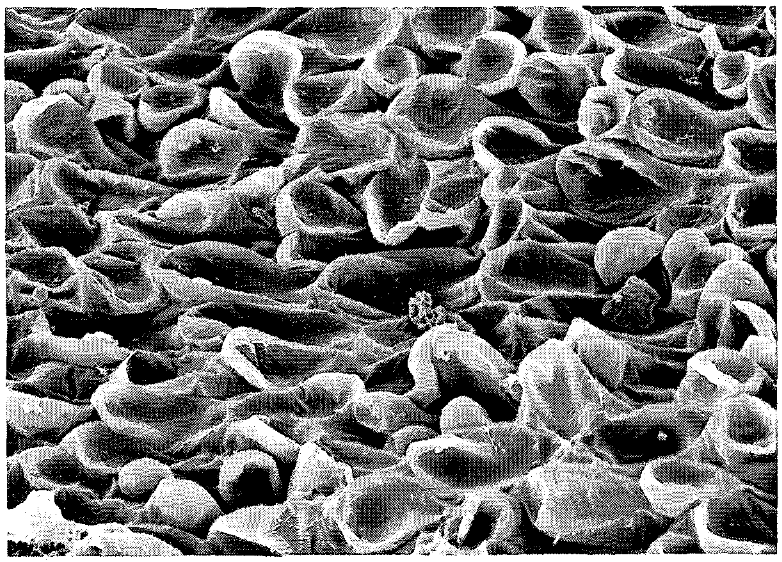

Figure 3.6. Scanning electron micrograph of the epithelium from the distal region of a gynoecium appendage

carpels within the ovary, and the anatomy of the style. While it appears to lack appendages (Maguire and Wurdack 1960, Kral 1998), it should be noted that the delicate appendages in *Abolboda* are sometimes impossible to detect, especially in rehydrated flowers (Kral 1992, pers. obs.).

Gynoecium appendages are large and similarly positioned in *Orectanthe*, and are reduced, unequal, and occur along the style in *Abolboda*. While the tissue of appendages in *Aratitiyopea* is clearly of a secretory type, their physiological function has yet to be determined. A close relationship to Eriocaulaceae, which posses nectar-secreting gynoecial appendages (Stützel 1984, Rosa and Scatena 2003), would lead one to predict that the glands in Xyridaceae have the same function. However, no nectar has been detected in the floral tubes of *Aratitiyopea*, and while glands with a large phloem content is associated with secretion of dilute nectar (Esau 1965), is also found in osmophores (Vogel 1990).

CONCLUSIONS

Aratitiyopea is an unusual Xyridaceae with features such as a trailing habit, long, broad leaves, and a prolific compound inflorescences of large flowers, that are probably adaptations to the habitat it occupies. While the majority of Xyridaceae occur in open-canopied habitats including savannas, rocky out-crops, and bogs, *Aratitiyopea* is found under dense-canopied forest in scrub vegetation and on sheer rock faces, habitats shared with many Bromeliaceae.

Structurally, *Aratitiyopea* is most similar to *Orectanthe*, and the two share with *Abolboda* a fused corolla, an appendaged gynoecium with intruded placentae and a solid style, and inaperturate pollen with conspicuous ornamentation (Table 5.1). The monophylesis of Xyridaceae is still in debate (see APG 2003, Michelangeli et al. 2003, Davis et al. in press), with *Abolboda*, *Aratitiyopea*, and *Orectanthe* often forming a clade independent of *Xyris*. A satisfying resolution of relationship based on morphological synapomorphies awaits pending studies of *Achlyphila*, which presents an interesting combination of features shared by *Abolboda*, *Aratitiyopea*, and *Orectanthe* on the one hand (e.g. a uniseriate androecium, and inaperturate pollen) and *Xyris* on the other (e.g. unifacial leaves, and free, yellow petals; Table 5.1).

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4. PHYLOGENY OF XYRIDACEAE

Introduction

Xyridaceae comprise about 385 species in five genera of petaloid monocots with a mostly tropical to subtropical distribution, and populations occurring in areas that are at least seasonally wet. Over 90% of the species are in the genus *Xyris* Gronov. ex L., and three of the genera consist of only one or two species each. The greatest diversity is found in northern South America where four genera are endemic. Because they occur in areas that are difficult to access, coupled with a usually very brief flowering period, many species have remained poorly characterized, and character state distributions in the family have been unclear (e.g., see Table 1 in Rudall and Sajo 1999). It has long been recognized that the family is morphologically diverse (Maguire and Wurdack 1960, Dahlgren et al. 1985); two subfamilies were described based on the striking differences in pollen, corolla, and staminodia morphologies (Suessenguth and Beyerle 1935) of *Abolboda* Humb. & Bonpl. and *Orectanthe* Maguire (Abolbodoideae) as compared to *Xyris* (Xyridoideae). The more recently described genus, *Aratitiyopea* Steyerm. & P. E. Berry (described in 1984), exhibits features consistent with Abolbodoideae. On the other hand, *Achlyphila* Maguire & Wurdack (described in 1960), with unifacial leaves and a yellow corolla is included in Xyridoideae, but presents an interesting combination of characteristics from both subfamilies, as well as some unique features. These two lineages have been recognized as separate families, with perhaps independent origins (APG 1998, but see APG 2003). The present familial circumscription has been considered paraphyletic with respect to the enigmatic monogeneric family Mayacaceae (Stevenson and Loconte 1995, see below). However, lacking congruent character discontinuities, taxonomists have taken a conservative approach and retained the family (Cronquist 1981, Takhtajan 1997, Kubitzki 1998).

Most systematists currently consider Xyridaceae part of a broadly defined order Poales (Table 4.1) that includes seventeen families (Chase et al. 2000, APG 2003), and is part of a large Commelinid clade. With some realignments, the Commelinids correspond to Dahlgren et al.'s (1985) complex of the superorders Bromeliflorae, Zingiberiflorae, and Commeliniflorae, plus the Areciflorae and Dasypogonaceae. Within this grouping Xyridaceae has been associated either with families Dahlgren et al. (1985) assigned to Poales (e.g., Engler and Prantl 1930) or Commelinales (e.g., Hamann 1961). These classifications relate Xyridaceae to Mayacaceae and Eriocaulaceae (Malme 1930), just Eriocaulaceae (Dahlgren et al. 1985), or Rapateaceae (Hamann 1961).

Studies of monocotyledon biology and systematics, and work toward a systemization for all angiosperms based on sequence data (APG 1998, 2003), have led to several hypotheses about the monophyly and relationships of the Xyridaceae. Many of the early studies were based on limited sampling (e.g., Linder and Kellogg 1995), or were missing data sets for taxa critical to the placement of Xyridaceae (e.g., Chase et al. 1995). As data sets are becoming

Table 4.1. Classification systems for commelinid monocots.

Engler & Prantl (1930)	Hutchinson (1959)	Hamann (1961)
Faninosae	Calyciferae	Commelinales
Flagellariineae	Commelinales	Commelinieae
Flagellariaceae	Commelinaceae	Commelinaceae
	Cartonemataceae	Mayacaceae
Enantioblastae	Flagellariaceae	Rapateaceae
Restionaceae	Mayacaceae	Xyridaceae
Centrolepidaceae		
Mayacaceae	Xyridales	Eriocaulineae
Xyridaceae	Xyridaceae	Eriocaulaceae
Eriocaulaceae	Rapateaceae	
		Restionieae
Bromeliineae	Eriocaulales	Restionaceae
Thurniaceae	Eriocaulaceae	Centrolepidaceae
Rapateaceae		
Bromeliaceae	Bromeliales	Flagellariineae
	Bromeliaceae	Flagellariaceae
Commelinieae		
Commelinaceae s.l.	Corolliferae	Bromeliales
	Liliales	Bromeliaceae
Pontederiineae	Pontederiaceae	
Pontederiaceae		Liliales
Cyanastraceae	Glumiflorae	Pontederiaceae
	Juncaceae	Philydraceae
Philydrineae	Thurniaceae	:
Philydraceae	Centrolepidaceae	etc.
	Restionaceae	
Liliiflorae		Juncales
Juncineae		Juncaceae
Juncaceae		Thurniaceae
Liliineae		
Haemodoraceae		
:		
etc.		

Table 4.1. (con't.) Classification systems for commelinid monocots.

Dahlgren, et al. (1985)	APG (2003)
Commeliniflorae	Commelinids
Commelinales	Dasypogonaceae
Commelinaceae s.l.	
Mayacaceae	Arecales
Xyridaceae	
Rapateaceae	Commelinales
Eriocaulaceae	Commelinaceae
	Haemodoraceae
Hydatellales	Hanguanaceae
Hydatellaceae	Philydraceae
	Pontederiaceae
Cyperales	
Juncaceae	Poales
Thurniaceae	Anarthriaceae
Cyperales	Bromeliaceae
Cyperaceae	
	Centrolepidaceae
	Cyperaceae
Poales	
	Ecdeiocoleaceae
Flagellariaceae	Eriocaulaceae
Joinvilleaceae	Flagellariaceae
Poaceae	Hydatellaceae
Ecdeiocoleaceae	Joinvilleaceae
Anarthriaceae	Juncaceae
Restionaceae	Mayacaceae
Centrolepidaceae	Poaceae
	Rapateaceae
Bromeliiflorae	Restionaceae
Velloziales	Sparganiaceae
Bromeliales	Thurniaceae
Haemodorales	Typhaceae
Pontederiales	Xyridaceae
Typhales	
Sparganiaceae	Zingiberales
Typhaceae	
Areciflorae	
Arecales	

more robust, Xyridaceae was resolved as monophyletic (APG 2003) and sister to Eriocaulaceae (Givnish et al. 1999, Bremer 2002) based on nucleotide sequence data (but see also Chase et al. 2000, Michelangeli et al. 2003). The monogeneric Mayacaceae has been related to Xyridaceae based on parietal placentation, an embryostega formed from the inner integument, and the location of anther dermal cell wall thickenings (Stevenson and Loconte 1995, Stevenson). A relationship of *Mayaca* to Xyridaceae (Cronquist 1981, Stevenson and Loconte 1995, Michelangeli et al. 2003) or, more recently proposed, to *Trithuria* (Hydatellaceae; Stevenson et al. 2000, Davis et al. 2004) has not been critically evaluated. Like *Mayaca*, *Trithuria* is a reduced plant with specializations to an aquatic habit, and homology assessment is difficult for some characters. The placement of these two genera in phylogenetic analyses varies depends on the taxa included (Stevenson et al. 2000, Bremer 2002, Davis et al. 2004).

The aim of this study is to test the monophyly of Xyridaceae, to identify potential synapomorphies for the family, and to generate hypotheses of relationship within and among the genera.

Materials and Methods

Taxon sampling.— The ingroup taxa include *Aratitiyopea*, *Orectanthe*, *Achlyphila*, all 21 species of *Abolboda* except for the hybrid *A.* ×*glomerata* (see Appendix 3), and twenty-five species of *Xyris*. Analysis of relationships within *Xyris* is necessarily preliminary due to the large number of species and limited material available for study. Exemplar species were selected to sample the morphological variation and geographic distribution of *Xyris* (Table 4.2). The sample includes ten species of section *Xyris*, eight species of sect. *Pomatoxyris*, and seven from sect. *Nematopus*. Widespread species and those with narrow distribution ranges are represented in both the eastern and western hemisphere. Due to a lack of variability between species for the characters scored and subsequent lack of resolution in the analysis, ten species of *Xyris* were eliminated from the analysis to remove redundancy.

Trithuria submersa Hook. f. (representing 9 species, Hydatellaceae) and *Mayaca fluviatilis* Aubl. (representing four species) were included to explore hypotheses of relationship to Xyridaceae and Eriocaulaceae. The outgroup consisted of one species each from three Eriocaulaceae genera and the resulting trees were rooted in a species of *Paepalanthus* subgen. *Platycaulon* (*P. melaleucus* Kunth), based on the results of Giulietti et al. (2000).

Data matrix.— The characters used in the analyses are presented in Appendix 1. Character states were coded as unordered, and are based on original observation and published accounts. Matrix statistics obtained from WinClada (ver. 1.00.24, Nixon 1999–2002) are presented in Table 4.3.

Data analysis.— Parsimony analysis of the equally weighted data were performed in NONA (ver. 1.6, Goloboff 1993) saving up to 10,000 most parsimonious trees (MPTs) created by 1,000 random add sequences on 10 minimum length trees, using the multiple tree bisection-reconnection algorithm (hold 10000; hold/10; multi*1000), followed by swapping to completion. Jackknife support values (Farris et al. 1996) for nodes were calculated from 2,000

Table 4.2. Species of *Xyris* included in the data matrix and their geographic distribution.

Species	Section	Geographic distribution[1]
**X. atrovirida* A. N. Doust & B. J. Conn	*Pomatoxyris*	Au
**X. exilis* A. N. Doust & B. J. Conn	*Pomatoxyris*	Au
**X. inaequalis* N. A. Wakef.	*Pomatoxyris*	Au
**X. lacera* R. Br.	*Pomatoxyris*	Au
**X. lantana* R. Br.	*Pomatoxyris*	Au
**X. laxiflora* F. Muell.	*Pomatoxyris*	Au
**X. operculata* Labill.	*Pomatoxyris*	Au
**X. ustulata* F. Muell.	*Pomatoxyris*	Au
X. capensis Thunb.	*Xyris*	SA, Af
X. cheumatophila A. N. Doust & B. J. Conn	*Xyris*	Au
**X. complanata* R. Br.	*Xyris*	As, In, Pa, Au
X. indica L.	*Xyris*	As, In, Ma, Au
X. iridifolia Chap.	*Xyris*	NA
X. juncea R. Br.	*Xyris*	Au
X. jupicia Rich.	*Xyris*	NA, CA, WI, SA
X. navicularis Griseb.	*Xyris*	CA, SA
X. platylepis Chap.	*Xyris*	NA
**X. pusilla* Sol. ex R. Br.	*Xyris*	Au
X. bicephala Gleason	*Nematopus*	SA
**X. involucrata* Nees	*Nematopus*	SA
X. lomatophylla Mart.	*Nematopus*	SA
**X. spruceana* Malme	*Nematopus*	SA
**X. stenostachya* Steyerm.	*Nematopus*	SA
**X. teniosperma* Idrobo & L. B. Sm.	*Nematopus*	SA
**X. ptariana* Steyerm.	*Nematopus*	SA

[1] Geographic abbreviations in parentheses: Africa (Af), Asia (As), Australia (Au), CA (Central America), India (In) Malaysia (Ma), NA (North America),Pacific (Pa), SA (South America), WI (West Indies)

* Species included in final analyses.

Table 4.3. Matrix statistics for the cladistic analysis.

Total: 3124 cells
Missing values: 2%
Polymorphisms: 0.5%
Subset polymorphisms: 0.48%
No comparison: 10%

replicates of 100 random taxon additions and 3 trees held to a maximum of 10,000. The consistency index (C.I., Kluge and Farris 1969) and retention index (R.I., Farris 1989) were calculated with WinClada. Tree manipulations and character optimizations using *slow optimization* (= DELTRAN of PAUP*, Swofford 1998) were performed with WinClada.

Results

The analysis resulted in three MPTs with 186 steps (C.I. = 0.46, R.I. = 0.82) and is summarized as a consensus tree in Figure 4.1. The basal lineages form a grade with *Trithuria* sister to *Mayaca* plus Xyridaceae. Xyridaceae form a monophylum, supported by four character state changes (3 unambiguous; Table 4.4). Synapomorphies of Xyridaceae include the possession of noninvolucral inflorescence bracts, imbricate sepals, the outer androecial whorl represented by staminodia, and a sunken connective. Of these, only imbricate sepals are universal in Xyridaceae. Involucral bracts are independently derived in one sister pair of *Xyris*, and the other characters are lost in several lineages.

The genera are resolved into two main clades with *Xyris* sister to the remainder of the family (Fig. 4.1). In that major clade *Achlyphila* is sister to the traditional circumscription of subfamily Abolbodoideae (Fig. 4.1). Characters that define this clade are the inflorescence not subtended by bracts, verrucate pollen ornamentation and inaperturate pollen, although the former two characters undergo transformations in the *Aratitiyopea-Orectanthe* clade. Ten character state changes occur on the *Achlyphila* lineage, of these, unifacial leaves, ranked

Figure 4.1A. Strict consensus of the three most parsimonious trees obtained from parsimony analysis, with Abolbodoideae collapsed (see Fig 4.1B). Unambiguous character state changes are represented by circles with the character number (Appendix 1) listed above the symbol and the state change listed below. Black circles indicate unique origins of character states; character states that are not uniquely derived are indicated by white circles. Large numbers below the branches are jackknife support values for clades with support of 50 or greater.

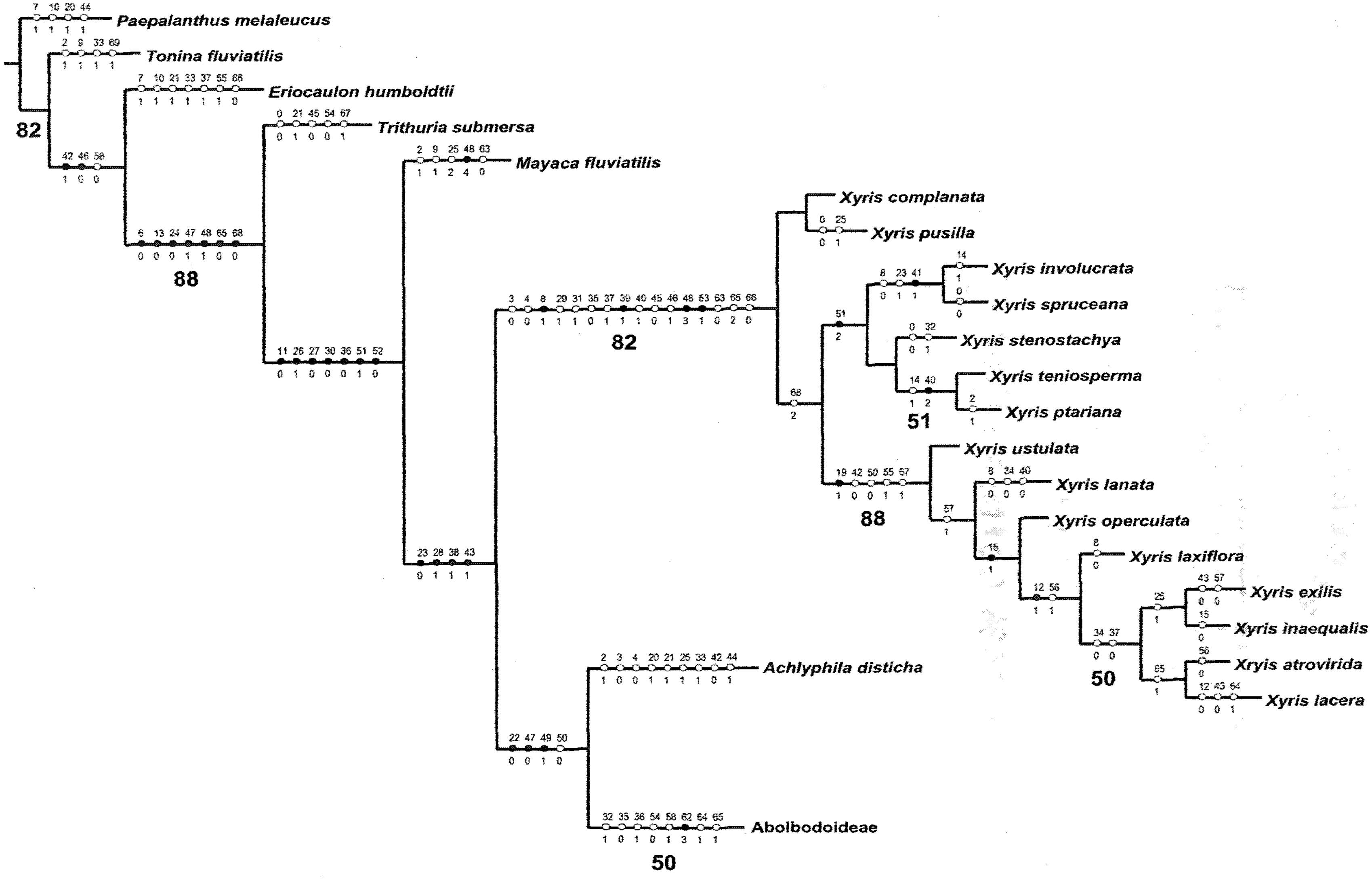

7 10 20 44
1 1 1 1
Paepalanthus melaleucus
2 9 33 69
1 1 1 1
Tonina fluviatilis
7 10 21 33 37 55 68
1 1 1 1 1 1 0
Eriocaulon humboldtii
0 21 45 54 67
0 1 0 0 1
Trithuria submersa
2 9 25 48 63
1 1 2 4 0
Mayaca fluviatilis
82
42 46 58
1 0 0
6 13 24 47 48 65 68
0 0 0 1 1 0 0
88
11 26 27 30 36 51 52
0 1 0 0 0 1 0
23 28 38 43
0 1 1 1
3 4 8 29 31 35 37 39 40 45 46 48 53 63 65 66
0 0 1 1 1 0 1 1 1 0 1 3 1 0 2 0
82
Xyris complanata
0 25
0 1
Xyris pusilla
14
1
Xyris involucrata
8 23 41
0 1 1
0
0
Xyris spruceana
51
2
0 32
0 1
Xyris stenostachya
Xyris teniosperma
14 40
1 2
2
1
Xyris ptariana
51
68
2
Xyris ustulata
19 42 50 55 57
1 0 0 1 1
88
8 34 40
0 0 0
Xyris lanata
57
1
Xyris operculata
15
1
8
0
Xyris laxiflora
12 56
1 1
43 57
0 0
Xyris exilis
25
1
15
0
Xyris inaequalis
34 37
0 0
50
56
0
Xryis atrovirida
65
1
12 43 64
0 0 1
Xyris lacera
2 3 4 20 21 25 33 42 44
1 0 0 1 1 1 1 0 1
Achlyphila disticha
22 47 49 50
0 0 1 0
32 35 36 54 58 62 64 65
1 0 1 0 1 3 1 1
Abolbodoideae
50

Figure 4.1B. Continuation of strict consensus of the three most parsimonious trees obtained from parsimony analysis, with Abolbodoideae detailed (see Fig 4.1A).

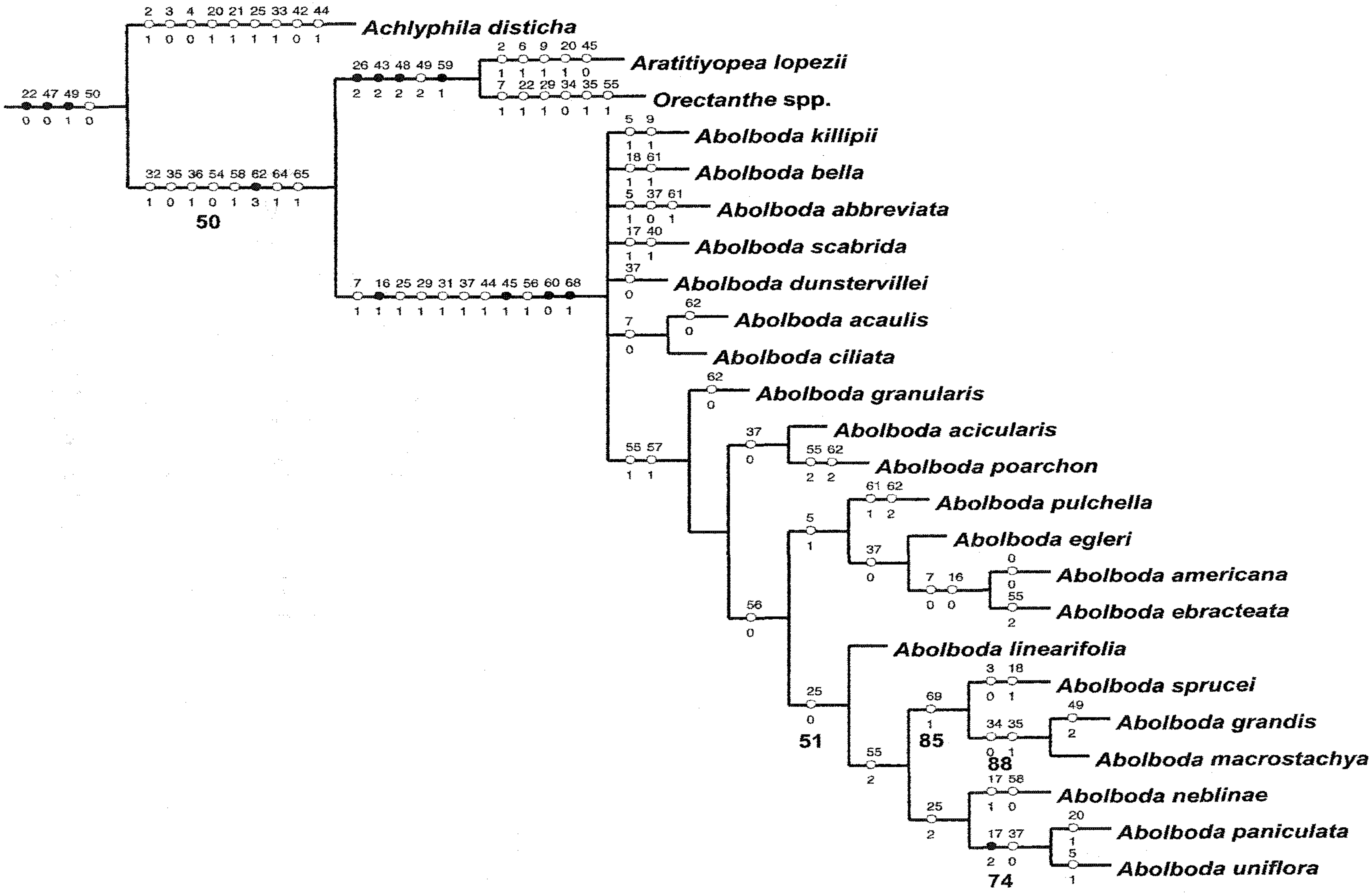

22 47 49 50
0 0 1 0
2 3 4 20 21 25 33 42 44
1 0 0 1 1 1 1 0 1
Achlyphila disticha
32 35 36 54 58 62 64 65
1 0 1 0 1 3 1 1
50
26 43 48 49 59
2 2 2 2 1
2 6 9 20 45
1 1 1 1 0
Aratitiyopea lopezii
7 22 29 34 35 55
1 1 1 0 1 1
Orectanthe spp.
7 16 25 29 31 37 44 45 56 60 68
1 1 1 1 1 1 1 1 1 0 1
5 9
1 1
Abolboda killipii
18 61
1 1
Abolboda bella
5 37 61
1 0 1
Abolboda abbreviata
17 40
1 1
Abolboda scabrida
37
0
Abolboda dunstervillei
7
0
62
0
Abolboda acaulis
Abolboda ciliata
55 57
1 1
62
0
Abolboda granularis
37
0
Abolboda acicularis
55 62
2 2
Abolboda poarchon
56
0
5
1
61 62
1 2
Abolboda pulchella
37
0
Abolboda egleri
7 16
0 0
0
0
Abolboda americana
55
2
Abolboda ebracteata
25
0
51
Abolboda linearifolia
55
2
69
1
85
3 18
0 1
Abolboda sprucei
34 35
0 1
88
49
2
Abolboda grandis
Abolboda macrostachya
25
2
17 58
1 0
Abolboda neblinae
17 37
2 0
74
20
1
Abolboda paniculata
5
1
Abolboda uniflora

Table 4.4. Character state changes in the main lineages of Xyridaceae resolved from parsimony analysis (non-homoplasious character state change*).

Xyridaceae

Inflorescence bracts not forming an involucrum
Sepals imbricate*
Outer androecium whorl staminodia*
Connective apex sunken

Xyridoideae (s. str.)

Leaves ranked
Leaves unifacial
Leaves with a ligule
Sepals dimorphic
Median sepal caducous
Corolla salverform
Staminodia distally enlarged*
Staminodia once-branched
Anther dehiscence latrorse
Pollen oblong
Pollen foveolate*
Ovules multiseriate*
Styles hollow
Stylodia
Styles branching simple

Abolbodoideae (including *Achlyphila*)

Inflorescence not subtended by bracts
Pollen inaperturate*
Exine verrucate
Placentae intruded into the locule

Achlyphila

Internodes elongate
Leaves unifacial
Leaves ranked
Inflorescence compound
Flowers pedicellate
Inflorescence units few-flowered
Petals clawed
Androecium uniseriate
Stamens hypogenous

Anthers dorsifixed

Abolbodoideae s. str.

Corolla sympetalous
Corolla salverform
Petals with a midvein
Ovules anatropous
Gynoecium appendaged
All three appendages pendulous
Style arcuate
Styles short-branched into stigmatic lobes

Aratitiyopea-Orectanthe

Flowers large*
Androecium uniseriate
Connective protruding*
Exine clavate/baculate*
Secondary exine sculpturing pila
Gynoecium appendages atop the ovary*

Abolboda

Scapes bracteate
Flowers few per inflorescence unit
Sepals dimorphic
Median sepal caducous
Anthers dorsifixed
Dehiscence extrorse*
Ovary apex tuberculate
Gynoecium appendages not uniform*
Seeds prismatic*

phyllotaxis, and hypogenous stamens are paralleled in *Xyris*, and dorsifixed anthers are paralleled in *Abolboda*.

Eight character state transformations define the Abolbodoideae s. str. A synapomorphy for the subfamily is all three gynoecium appendages pendulous, with transformations within *Abolboda*. A salverform corolla is paralleled in *Xyris*, and styles shortly-branched into stigmatic lobes (vs. stylodia) is found in one clade of *Xyris*.

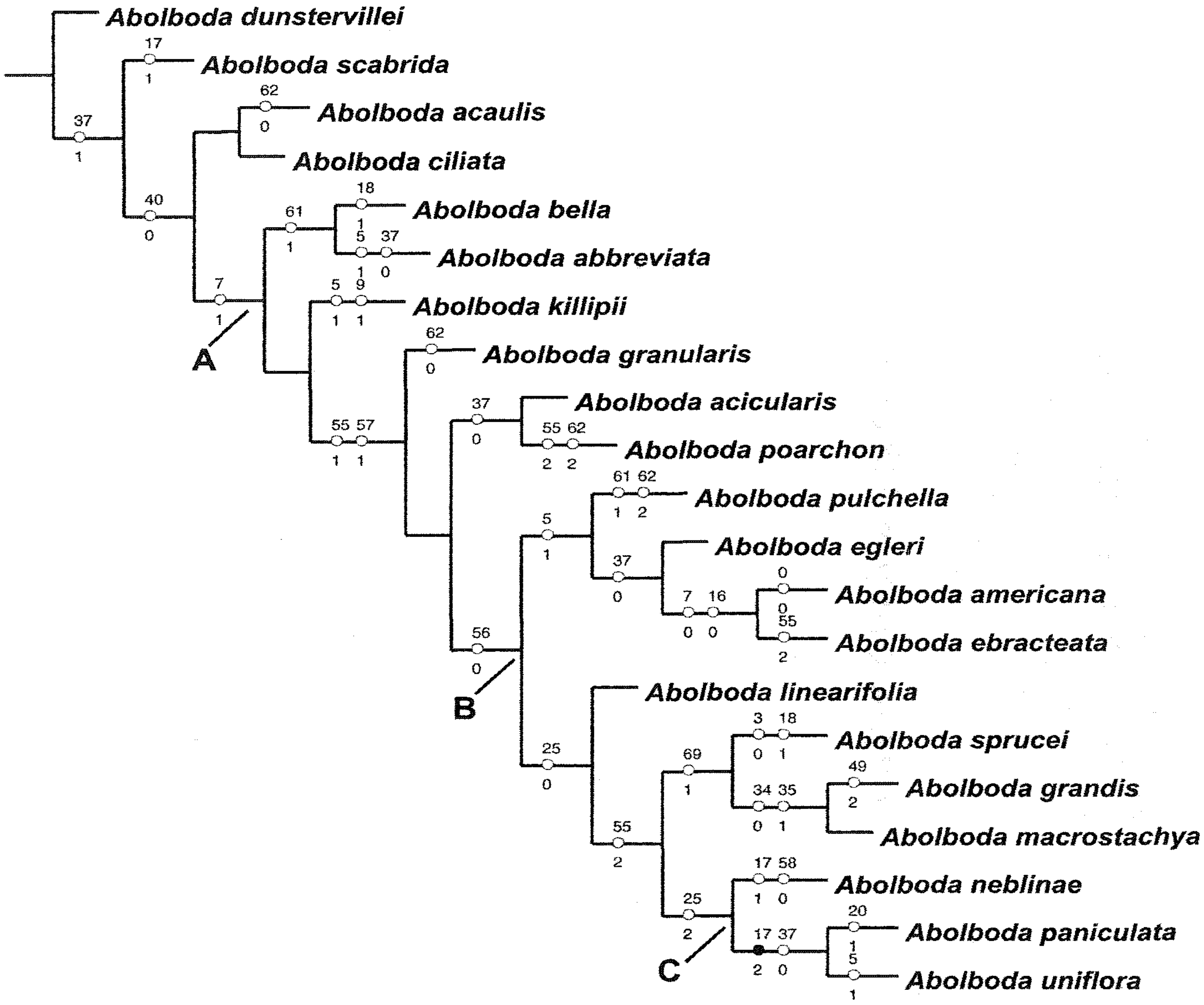
Three of the synapomorphies that describe the sister group *Aratitiyopea-Orectanthe* are large flowers, a protruding connective, and the location of gynoecium appendages on top of the ovary. The data also support clavate/baculate pollen as a nonhomoplasious transformation; however this condition is also found in one of the two varieties of *Abolboda grandis* (thus the taxon is resolved as ambiguous for this character). This lineage is also supported by a reversal to the plesiomorphic condition of a uniseriate androecium.

Nine character transformations, three of which are nonhomoplasious, define the genus *Abolboda*. Of these, bracts on the scape, extrorse anther dehiscence, gynoecium appendages of unequal size, and prismatic seeds are synapomorphic for the genus. The loss of scape bracts occurs in one sister pair of *Abolboda*. Dimorphic sepals and the median sepal caducous are two character states found universally in *Abolboda* and *Xyris*, and a tuberculate ovary apex is paralleled in one clade *Xyris*.

In the consensus tree, *Abolboda* is resolved with a basal polytomy of seven species that includes a single sister pair (Figure 4.1). *Abolboda dunstervillei* is resolved in the phylogenetically basal position in two of the three MPTs. In the preferred hypothesis of relationship for *Abolboda* (Fig. 4.2), the basal lineages represent species that occur at high elevation. The character state uniting *A. bella* and *A. abbreviata* is the presence of horned gynoecial appendages, which is paralleled in *A. pulchella*. Within *Abolboda* there are four reversals to a uniseriate androecium, and this character state supports the sister relationship of *A. poarchon* and *A. acicularis*. Loss of a tuberculate ovary apex occurs in the lineage marked B in Fig. 4.2. Within this lineage, the *A. pulchella* clade is supported by dimorphic leaves, which is independently derived four times in *Abolboda*. The *A. sprucei* lineage is defined by white pollen, unique within Xyridaceae. A porrect corolla is independently derived in *Orectanthe* and *A. grandis*-*A. macrostachya*. The high elevation *A. neblinae* clade has single-flowered spikelets, and a single synapomorphy (many scape nodes) defines the sister relationship of *A. paniculata* and *A. uniflora*.

The genus *Xyris* is supported by more character transformations than any other lineage in the analysis (Fig. 4.1, Table 4.3). Synapomorphies for genus are leaves with a ligule, distally enlarged staminodia, foveolate pollen, and multiseriate ovules. The leaf ligule is lost three times. Some characters that define the genus, such as ovule arrangement (seriation) and exine, are unknown in sect. *Pomatoxyris*. The character state staminodia bifurcate undergoes further independent transformations in two lineages. Dimorphic sepals, a caducous sepal and salverform corollas are variously paralleled in the Abolbodoideae s. str.

Figure 4.2. The preferred hypothesis of phylogeny (one of three) for *Abolboda*. Unambiguous character state changes are represented by circles with the character number (Appendix 1) listed above the symbol and the state change listed below. Black circles indicate unique origins of character states; character states that are not uniquely derived are indicated by white circles.


Abolboda dunstervillei
Abolboda scabrida
Abolboda acaulis
Abolboda ciliata
Abolboda bella
Abolboda abbreviata
Abolboda killipii
Abolboda granularis
Abolboda acicularis
Abolboda poarchon
Abolboda pulchella
Abolboda egleri
Abolboda americana
Abolboda ebracteata
Abolboda linearifolia
Abolboda sprucei
Abolboda grandis
Abolboda macrostachya
Abolboda neblinae
Abolboda paniculata
Abolboda uniflora
A
B
C

Within *Xyris* the three taxonomic sections are resolved as monophyletic with the two species of sect. *Xyris* forming a sister pair based on symplesiomorphies, which is in turn sister to the remainder of the species. Sections *Nematopus* and *Pomatoxyris* are united by the condition of oblong seeds, also found in the outgroup. The species of sect. *Nematopus* form a clade with the synapomorphy of ovules attached proximally in the ovary. Two species pairs are resolved in the section each with a synapomorphy concerning features of the staminodia. In clade with *X. involucrata*, the staminodia are adnate to adjacent corolla limbs; and in *X. teniosperma-X. ptariana*, they are distally multifurcate. Within *Xyris*, the clade representing sect. *Pomatoxyris* is the most robust hypothesis in the analysis. Some of the characters defining the sections are flowers that last at least a full day, hypogenous stamens, and an apically indehiscent capsule. Hypogenous staminodia evolved independently in *Achlyphila*. The deepest branch within sect. *Pomatoxyris* resolves two species pairs, and is supported by a monosymmetric corolla, which evolves independently at least four times in Xyridaceae, and the reversal to a uniseriate androecium. Styles short-branched into stigmatic lobes (vs. stylodia) is paralleled in *Xyris atrovirida-X. lacera* and the Abolbodoideae s. str.

Discussion

Several points should be considered in assessing the robustness of hypotheses drawn from this analysis. First, there is a dearth of hypotheses of relationship in Eriocaulaceae, and only the selection of *Paepalanthus melaleucus*

Kunth. to represent *Paepalanthus* subgen. *Platycaulon* was based on an explicit hypothesis of phylogeny for this large (200–600 spp.), and morphologically diverse genus. As hypotheses about the phylogeny of Eriocaulaceae are developed (see Unwin et al. 2002), outgroup selection for Xyridaceae will be refined.

Another reason for ambiguity in this data set rests in the aforementioned morphological diversity in Xyridaceae, and the distinctiveness of each of the families represented in the analysis. Thus, some characters that are useful in resolving relationships between some of the taxa in the analysis are not present in other taxa in the analysis. For example, a total of five characters were utilized to study gynoecium appendages, but these structures are not present in *Mayaca*, *Trithuria*, *Achlyphila*, or *Xyris*. In this data set *Mayaca* was scored as no comparison for 25% of the characters. Additionally, the genus has several distinctive features not shared by the other taxa studied here, such as poricidal anther dehiscence, and a hollow stigma. Furthermore, *Trithuria* was scored with 42% ambiguous data because structures scored for other taxa are either not present, or reduction (e.g., the androecium a single stamen) makes assessment of homology impossible.

Jackknife support values are low in parts of the topology that address key questions about the phylogeny of Xyridaceae: whether the family is monophyletic, and the placement of *Achlyphila*. Very few relationships within *Abolboda* have strong jackknife support values, and hypotheses of relationship in

Abolboda are considered preliminary, also because of the unresolved basal polytomy.

Relationships in the three topologies obtained for *Abolboda* vary little. The hypothesis of relationship presented was selected based on field-based knowledge of the species, and minimizes shifts between lineages evolving on tepui summits and surrounding low elevation savannas. In the preferred hypothesis of relationship for *Abolboda* (Fig. 4.2), the basal lineages are high elevation species and low elevation taxa appear at the node labeled A Figure 4.2. The other *Abolboda* species that occur exclusively at high elevation are resolved together deeper in the genus (node C, Fig. 4.2). The topology is supported by transformations in characters that the data indicate are very plastic, and may be ecologically induced (e.g., dimorphic leaves arise four times, probably a xeromorphic adaptation to seasonal drought [see Chapter 2; Dickison 2000]).

The resultant hypothesis that *Achlyphila* is more closely related to the Abolbodoideae than to *Xyris* diverges from the traditional subfamilial classification (Suessenguth and Beyerle 1935). Based on character state distributions it is predicted that *Achlyphila disticha* has a solid style (unknown for the species), and highlights the need to reexamine the gynoecium for the presence of appendages. Altering the topology to reflect the traditional subfamilies requires two steps, and changes character optimizations for leaf type, phyllotaxis, and presence of a petal midvein.

Additional exemplars of *Xyris* need to be analyzed in order to make robust hypotheses of species relationship and to assess the infrageneric classification. Notably, the two species of sect. *Xyris* are resolved as sister species based solely on symplesiomorphies. There is more non-homoplasious support for some clades of *Xyris* than was found within *Abolboda*, which may be due to fewer species of the former being analyzed. Despite thorough descriptions in recent revisions (Doust and Conn 1994, Conn and Doust 1997), some features of species of sect. *Pomatoxyris* are unknown, but from this analysis it can be predicted that they have hollow styles, and pollen with foveolate exine.

Several characters are often invoked when discussing phenetic similarities or distinctiveness of Xyridaceae genera. Of these, characters interpreted here to be derived are unifacial and ranked leaves; a fused corolla; staminodia, which evolved as elaborated structures in the *Xyris* lineage, and as delicate filamentous structures in *Abolboda*; sulcate pollen; and anatropous ovules.

Kral (1992) predicted that Xyridaceae evolved in the Guayana region of northern South America, and envisioned two main clades: one comprised of *Achlyphila* and *Xyris* and the other with *Orectanthe* derived. This analysis agrees with his hypothesis that the ancestor to Xyridaceae was a rhizomatous perennial with polystichous leaves, scapose, bracteate racemes, and choripetalous flowers with a superior tricarpellate ovary. However, this study does not concur with his suggestion that six free stamens, and axile placentation are plesiomorphic character states for Xyridaceae lineage.

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5. MONOGRAPH OF THE GENERA OF XYRIDACEAE

Introduction: A Brief Taxonomic History

Xyridaceae are a morphologically diverse assemblage of monocots. As currently understood, the family comprises about 385 species in five genera: *Abolboda*, *Achlyphila*, *Aratitiyopea*, *Orectanthe*, and *Xyris* (Kral 1998). The family is mostly tropical to subtropical in distribution, with some *Xyris* species occurring in temperate America, Asia, and Australia (Fig. 5.1). The greatest diversity in the family is in South America, and only species of *Xyris* occur outside of the region (Fig. 5.2).

The taxonomic history of Xyridaceae began in 1737 with the establishment of *Xyris* Gronov. ex L., and until the mid 1900's included only a second genus, *Abolboda* Humb. & Bonpl. During this time *Abolboda* was sometimes placed in a separate subfamily (Suessenguth and Beyerle 1935) or family (Nakai 1943) based on a suite of vegetative, floral, and pollen (Nilsson and Praglowski 1992: 136) characters that differed from the known morphology of *Xyris* species. The subsequent recognition of a new genus, *Orectanthe* Maguire, for the species *Abolboda sceptrum* Oliv. ex Thurn (Maguire 1958), and the discovery of *Achlyphila disticha* Maguire & Wurdack (1960), which shares characteristics with both *Xyris* and the *Abolboda-Orectanthe* alliance, led most workers to recognize a single, morphologically heterogeneous family (Maguire and Smith 1964, Cronquist 1981, Dahlgren 1985, Thorne 1992, Takhtajan 1997, Kral 1998, Thorne 2000; see Table 5.1). The fifth genus of Xyridaceae, *Aratitiyopea*, was

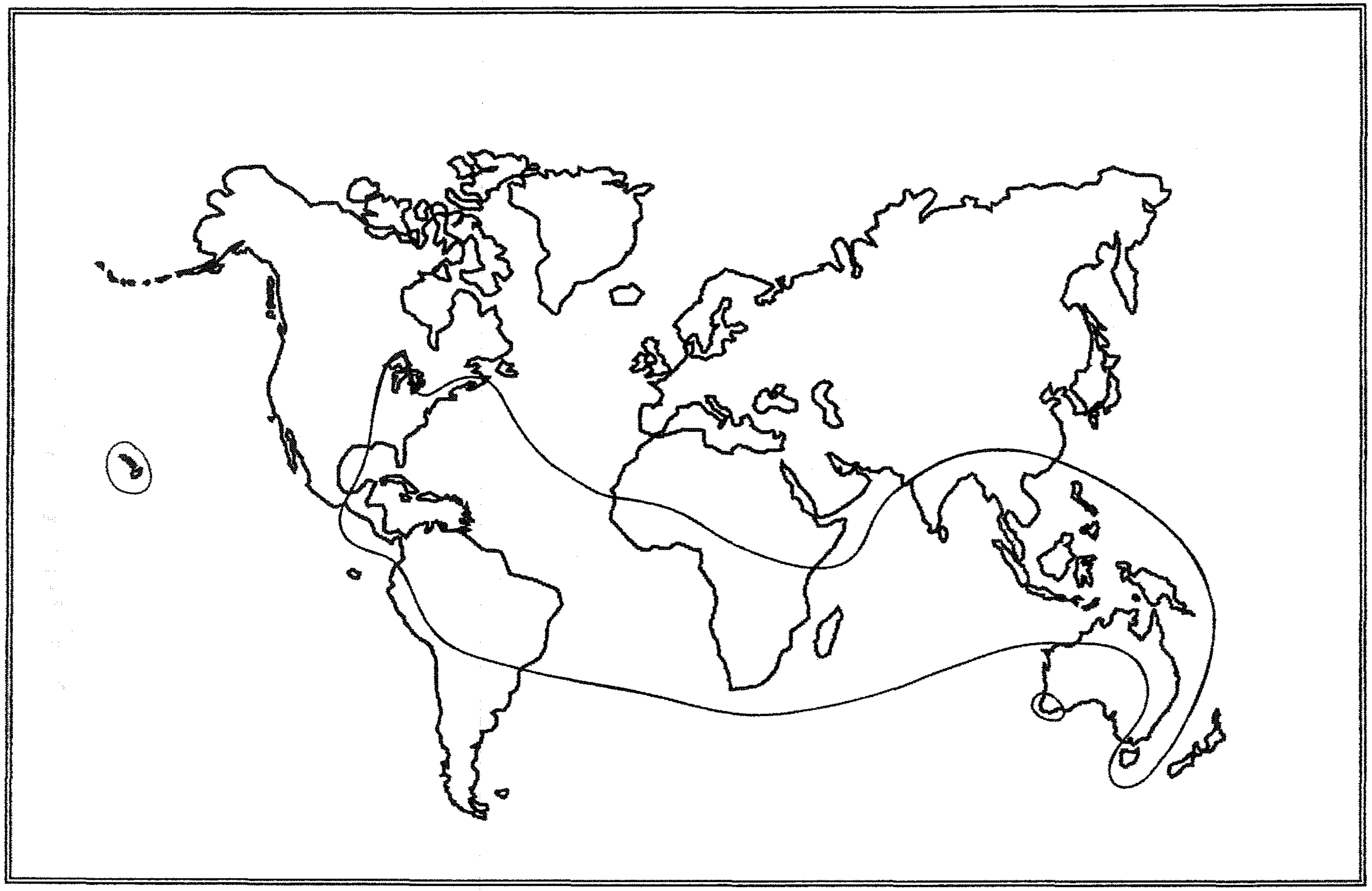

Figure 5.1. Distribution map of Xyridaceae. Two naturalized *Xyris* species occur in the Hawaiian Islands.

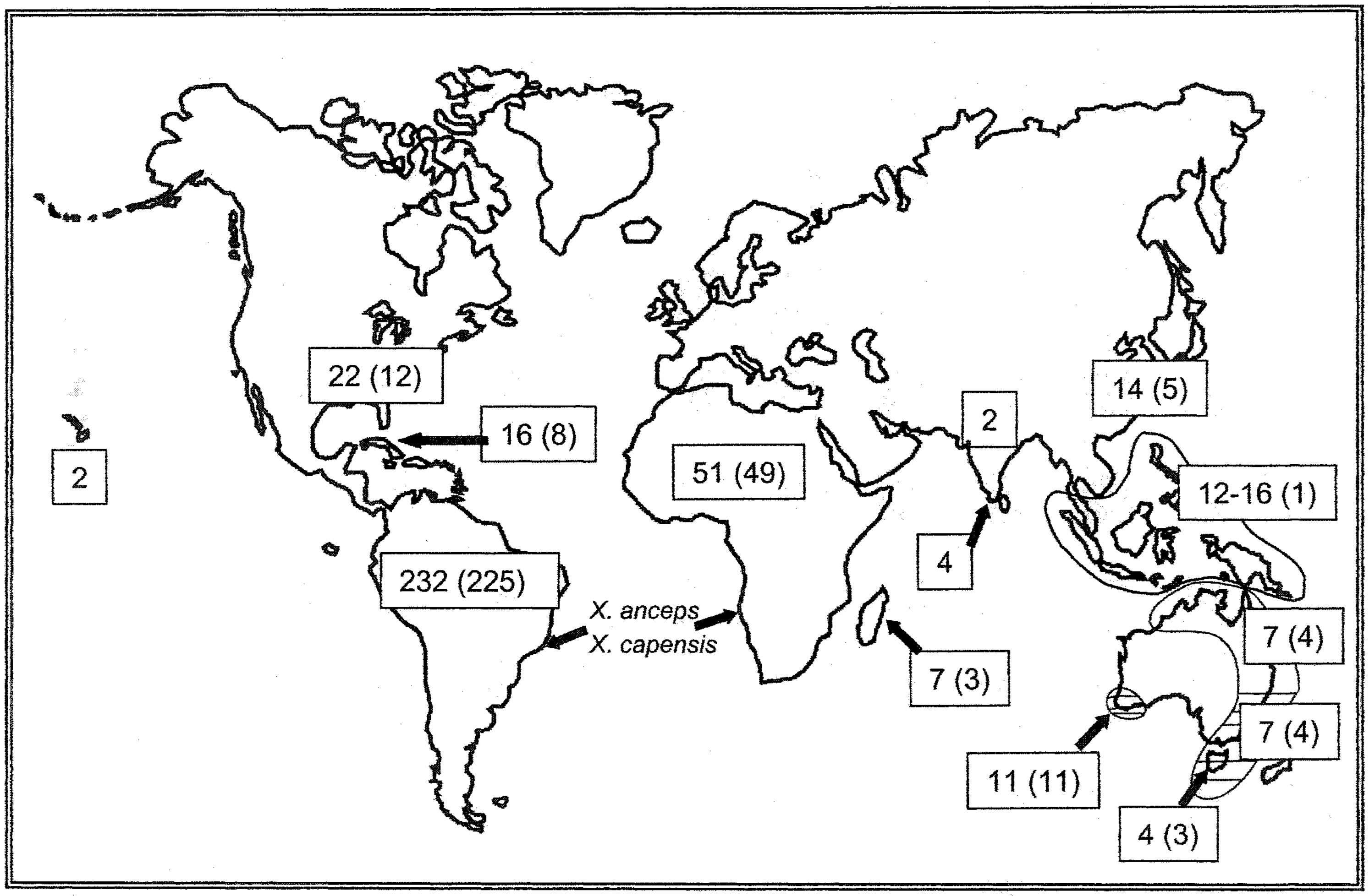

Figure 5.2. Species abundance in *Xyris*. The number of endemic species in parentheses. Section *Pomatoxyris* is indicated by hatching. Only two species occur in both the eastern and western hemispheres. The two species in the Hawaiian islands are naturalized.

Table 5.1. Distinguishing floral characteristics of the genera of Xyridaceae.

Genus	Sepals	Corolla	Staminodia
Aratitiyopea	3, subequal all persistent	sympetalous salverform white or magenta polysymmetric	absent
Orectanthe	3, dimorphic median caducous	sympetalous porrect yellow monosymmetric	absent
Abolboda	2 or 3, then dimorphic if 3, median fugacious	sympetalous salverform or porrect blue, purple, white poly-, sometimes monosymmetric	present or absent filamentous
Achlyphila	3, subequal all persistent	choripetalous dish yellow polysymmetric	absent
Xyris	3, dimorphic median fugacious	chori- or sympetalous tubular yellow poly-, occasionally monosymmetric	rarely absent usually elaborate usually distally adnate to the corolla

Table 5.1 (con't.). Distinguishing floral characteristics of the genera of Xyridaceae.

Genus	Stamens	Pollen	Gynoecium	Ovules
Aratitiyopea	basifixed dehiscence latrorse	spherical inaperturate	trilocular ovary 3-appendaged style solid stigma branched	anatropous
Orectanthe	basifixed dehiscence introrse	spherical inaperturate	trilocular ovary 3-appendaged style solid stigma branched	anatropous
Abolboda	dorsifixed dehiscence extrorse	spherical inaperturate	trilocular style solid, usually 3-appendaged stigma branched	anatropous
Achlyphila	dorsifixed dehiscence latrorse	spherical inaperturate	trilocular style? stigma capitate	anatropous
Xyris	basifixed dehiscence latrorse, extrorse	elongate sulcate	uni- or trilocular style hollow stylodia or stigma branched	orthotropous

described in 1984 for the transference of a single enigmatic species of Bromeliaceae, *Navia lopezii* L. B. Sm. (Steyermark 1984).

The majority of Xyridaceae species are in the wide-spread genus *Xyris*, which presently includes about 360 species (Campbell, in prep.). Early workers recognized three sections of *Xyris* based mainly on placentation type and geographic distribution. As traditionally circumscribed, section *Xyris* have parietal placentation and occur pantropically to temperate North America; sect. *Nematopus* Seub. have basal or free central placentation and occur in the neotropics; and sect. *Pomatoxyris* Endl. have axile placentation and species distributed in either southeastern or southwestern Australia. Section *Pomatoxyris*, the smallest section, was recently further characterized by a hardened, sometimes apically indehiscent capsule, and flowers that are not ephemeral, lasting a full day or longer (Conn and Doust 1997). A fourth section of species, endemic to the Espinhaço range in Brazil, has been suggested but not formally proposed (Wanderley et al. 1993; pers. comm.). Kral (1988) reported axile placentation in some species of sect. *Nematopus*, and varying degrees of septa development throughout some ovaries, as also occurs in some species of sect. *Xyris* (Tukshetty et al. 1968), a condition well documented in other families (Puri 1952). Although Kral (1988) questioned using placentation as a basis for a classification, the sections are still referred to in taxonomic treatments (e.g. Doust and Conn 1994) and new species descriptions (e.g. Kral and Duivenvoorden 1993, Kral and Jansen-Jacobs 1998). Primary observations and a literature review has failed to identify any *Xyris* species with free central placentation with a fully developed central column of tissue; at most ovules are borne on a short stalk, often accompanied by rudiments of septa. Because other Xyridaceae genera described as having axile placentation are here interpreted as having intruded placentae, considered to be parietal by Puri (1952), sect. *Pomatoxyris* are also characterized as having a multilocular ovary with parietal placentation. Additional characters, such as connation of the corolla, adnation or mere adherence of the filaments to the corolla, fusion of the staminodia branches to adjacent corolla limbs, and anther dehiscence orientation need to be investigated and assessed in the context of developing a classification of the genus.

In the early part of the last century Malme presented revisionary studies (1913, 1924, 1930) and regional treatments (1896, 1898, 1901, 1914, 1925, 1927, 1929a, 1929b, 1929c, 1931, 1933), concentrating on the genus *Xyris*. More recently, a regional treatment of *Xyris* is in progress for Minas Gerais state, Brazil (Wanderley, in prep.), that includes a large number of new species and the undescribed section (Wanderley et al. 1993; pers. comm.). Others have been presented for North America (Kral 2000), northern South America (Kral 1988, 1992), Australia (Doust and Conn, 1994, Conn and Doust 1997), Cameroon (Lewis 1981), central Africa (Lisowski et al. 2001), tropical east Africa (Lock 1999), southern Africa (Lewis and Obermeyer 1985, Lock 1999), and parts of tropical Asia (Hansen 1983, 1987; Wijesundara 2000). A modern revision considering the entire genus is needed, but is beyond the scope of the present work.

The taxonomic knowledge of Xyridaceae was greatly expanded in the latter half of the last century due to concerted botanical exploration of northern South America (see Huber 1995). Three genera were added to the family, and the number of recognized *Abolboda* taxa increased by over 60%. Smith and Downs (1968) included 115 species of *Xyris* in their treatment for *Flora Brasílica*, and presently about 165 species are recognized for that area. Kral revised the four non-*Xyris* genera in 1992, recognizing twenty-one species of *Abolboda*, two species of *Orectanthe*, and one species each of *Achlyphila* and *Aratitiyopea.*

Materials, Methods, and Presentation

The present study is part of on-going field-oriented research into the biology and systematics of Xyridaceae. Field-based systematic study enables observation and documentation of features that are not well preserved or represented by herbarium specimens (see Hopkins et al. 1998). Moreover, while herbarium specimens maybe be sufficient for recognizing and describing taxa, in most cases they alone are inadequate for understanding the biology of a group (Prance and Mori 1998) and the forces driving character evolution (Prance 1990). The short-lived flowers and persistent hard bracts and sepals that characterize Xyridaceae inflorescences complicate preparation of herbarium specimens and render removal of flowers for dissection very difficult. The present research was greatly enhanced by specimens collected for morphological dissections and anatomical studies, which were killed and fixed in formalin-propionic acid- alcohol (1:1:18, FPA), and transferred to 70% ethanol. For example, the small, delicate gynoecium appendages and staminodia in *Abolboda* are now better characterized from examination of 3-dimensional preparations using high-resolution stereo microscopy (Wild M5 and Nikon SMZ1500 and fiber optic illumination).

The taxonomic treatment, including abbreviation standards, follows the format of *Flora Neotropica Monographs*[1]. The term "ligule" is used for extensions of the leaf sheath in descriptions of *Xyris* (e.g. Kral 1988); its usage is continued here for consistency, and is not meant to infer homology with the lamina-derived ligule of Poaceae. The term "caducous" is used for structures that fall off before other similar structures, that persist longer than ephemeral or fugacious ones. The key to genera was developed using characters generally observable from herbarium specimens without removing flowers, including label data (e.g. flower color). Genera are recognized for monophyletic lineages. By necessity circumscription of species and infraspecific taxa is morphologically based as field studies have not reached an advanced enough state to incorporate ecological information (e.g. breeding system data) for all taxa. Species are recognized based on suites of characters. Infraspecific taxa have morphological distinction; subspecies are recognized for geographically separated variants and the rank of variety is recognized for ecologically separated variants (Grant 1981). Historical precedent was not a criterion for determining rank except for the sections of *Xyris* and *Orectanthe*, in order to maintain nomenclatorial stability as further

[1] (*A Guide for Contributors*: http://www.nybg.org/bsci/ofn/fn-1gnd1.html)

investigation is required to make a taxonomic decision. species of

Specimens from the following herbaria have been studied: B-W, BM, BR, C, COAH, COL, F, FI, G, GH, GOET, HAL, K, L, M, MG, MO, NY, P, PORT, S, SEL, SP, TFAV, U, US, and VEN. No specimens of Xyridaceae were found by staff at KIEL; loans are pending from MYF, R, and RB.

Structures examined with scanning electron microscopy (SEM) were either dehydrated to 100% acetone and critical point dried, or air dried; coated with gold palladium in a Hummer 6.2 sputtering system; and viewed with a JEOL JSM-5410LV SEM. Pollen was examined using light and scanning electron microscopy. Whole mounts were prepared with Calberla's solution (Ogden et al. 1974), and pollen was viewed in sectioned flowers that were embedded in Paraplast+® using standard procedures, sectioned with a rotary microtome, and stained with safranin and astra blue. Measurements were made on SEM images using Carnoy 2.0 software (Schols and Smets 2001). Palynological terminology follows Punt et al. (1994).

Taxonomic Treatment

XYRIDACEAE C. Agardh, Aphor. Bot. 158. 1823, 'Xyrideae', *nom. conserv.* Eichler, *Gen. Pl.* 2: 123–124. 1836. Kunth, *Enum. Pl.* 4: 1–29. 1843. Nilsson, Kongl. Svenska Vetensk. Akad. Handl. 24(14): 1–75. 1892. Baillon, *Hist. Pl.* 13: 224–227. 1895. Seubert in Martius, *Fl. Bras.* 3 (1): 211–224.1855. Malme in Engler & Prantl, *Nat. Pflanzenfam.* 15a. 1930. Malme, Ark. Bot. 25A(12):

1–18. 1933. Maguire, Mem. New York Bot. Gard. 10(1): 1–19. 1958. Type genus: *Xyris* Gronov. ex L. The English name for the family is yellow-eyed grass (Gray 1848). Figs. 5.1, 5.3, 5.4; Appendix 2, 3.

Plants robust or slender to delicate herbs, perennial or annual, often sedge-like, rarely bromeliad-like, rarely aquatic; axes usually stout, seldom rhizomatous, sympodial or monopodial. *Roots* filiform to coarse, firm or spongy, sometimes with a sand-binding sheath of hairs. *Leaves* unifacial or bifacial, alternate, ranked or spiraled, sheath open, forming a ligule or not. *Inflorescence* axillary or terminal, usually scapose, simple or compound, each unit several to many-flowered, bracteate, bracts conspicuous, brown, green, or rarely brightly colored (*Aratitiyopea*), persistent. *Flowers* usually sessile, 3-merous, without scent, rarely malodorous (*Orectanthe*, *S. S. Tillett 45097*); perianth differentiated with a petaloid corolla; sepals unequal, rarely subequal, irregularly imbricate, margins of the median (abaxial) sepal included by the lateral (adaxial) sepals, 3 or 2 (some *Abolboda* spp.), usually dimorphic, the lateral sepals basally connivent or connate, carinate, firm and cartilaginous, the median usually caducous, usually membranous; petals free or basally connate, delicate and ephemeral; rarely not, staminodia when present (*Xyris*, *Abolboda*) antesepalous, branched or simple, elaborate and a conspicuous part of the blossom (*Xyris*) or filiform (*Abolboda*); stamens antepetalous, epipetalous or hypogenous, anthers basifixed or dorsifixed, tetrasporangiate, dehiscence latrorse, extrorse, or rarely introrse, pollen yellow (rarely white); gynoecium tricarpellate, compound, sometimes

Figure 5.3. Floral diagrams of the genera of Xyridaceae. A. *Aratitiyopea* with large dorsal gynoecial appendages depicted; dorsal stigma lobes not shown (*L. M. Campbell 766*). B. *Orectanthe.* without gynoecial appendages depicted (from Maguire 1958). C. *Abolboda poarchon* with only two dorsal gynoecial appendages and a uniseriate androecium depicted (from Suessenguth and Beyerle, 1935). D. *Achlyphila disticha* with all parts free and only the second androecial whorl (from Maguire 1960). E–G. *Xyris* section *Xyris.* E. With a choripetalous corolla, free androecial elements, and three dorsal stigmatic branches depicted (from Eichler 1875). F. The staminodia adnate to adjacent corolla limb and epipetalous stamens (from Melchior and Werdermann 1964). G. With a sympetalous corolla and epipetalous staminodia (from Seubert 1855). H. *Xyris* section *Nematopus*, differing from the previous in having free central placentation (from Seubert 1855).

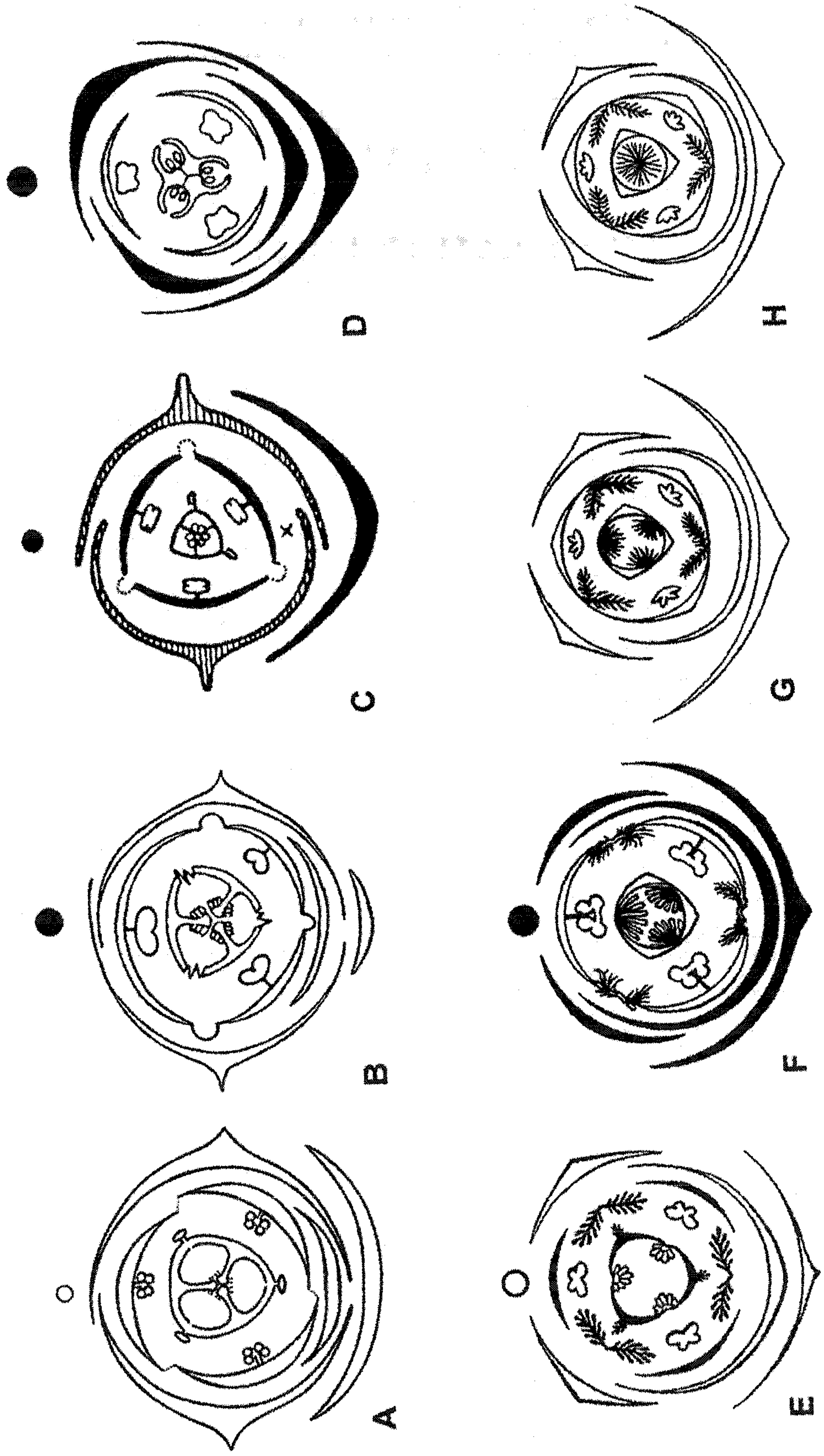
A
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Fig. 5.4. Floral morphologies in Xyridaceae. A. *Abolboda killipii* with solitary flowers. B. *Abolboda pulchella* with a bilaterally symmetrical corolla. C. *Xyris* sp. with staminodia bearing moniliform hairs. D. *Abolboda acicularis* var. *granularis* with a salverform corolla. E. *Orectanthe sceptrum* with monosymmetric flowers. F. *Aratitiyopea lopezii* with reflexed, contorted corolla lobes. G. *Abolboda grandis* with a porrect corolla. H. *Abolboda macrostachya* exhibiting a stigma concolorous with the corolla. (Scale bars = 2.5 cm. Images by: G. A. Romero-González (A, F, G), K. J. Wurdack (C), G. Gerlach (D), F. A. Michelangeli (E).


A
B
C
D
E
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appendaged, ovary unilocular or trilocular, at least basally, placentation basal (some *Xyris*) or parietal, often on intruded placentae; style hollow or solid, flattened, terete, or triquetrous, branched into stylodia or merely stigmatic branches (simple in *Achlyphila*); stigma plumose (*Achlyphila* ?). *Fruit* a loculicidal capsule, usually many-seeded. Seeds minute to small, with prominent longitudinal striations, and usually weaker cross striations, operculate.

Key to the Genera

1a. Leaves unifacial
  2a. Leaves borne along an ascending caudex
    3a. Caudex branching only from a subterranean rhizome, inflorescence single, terminal, branched, flowers pedicellate............ 4*. Achlyphila.*
    3b. Aerial caudices branched, inflorescence solitary to several, a spike borne on an ebracteate scape.. 5. *Xyris.*
  2b. Leaves forming a congested rosette on a stout caudex
      4a. Inflorescence scape with subopposite, chlorophyllous bracts, corolla blue...3. *Abolboda.*
      4b. Inflorescence scape ebracteate, corolla yellow.............. 5. *Xyris.*
1b. Leaves bifacial
  5a. Stem elongate, plants decumbent, internodes not congested, or if congested leaf margins brown

6a. Inflorescence compound, of congested, numerous-flowered branches, bracts foliose, magenta, corolla magenta or white .... 1. *Aratitiyopea.*

6b. Inflorescence a broad, head-like spike, bracts firm, brownish, corolla yellow... 2. *Orectanthe.*

5b. Stem stout, plants erect and usually rosulate, internodes congested

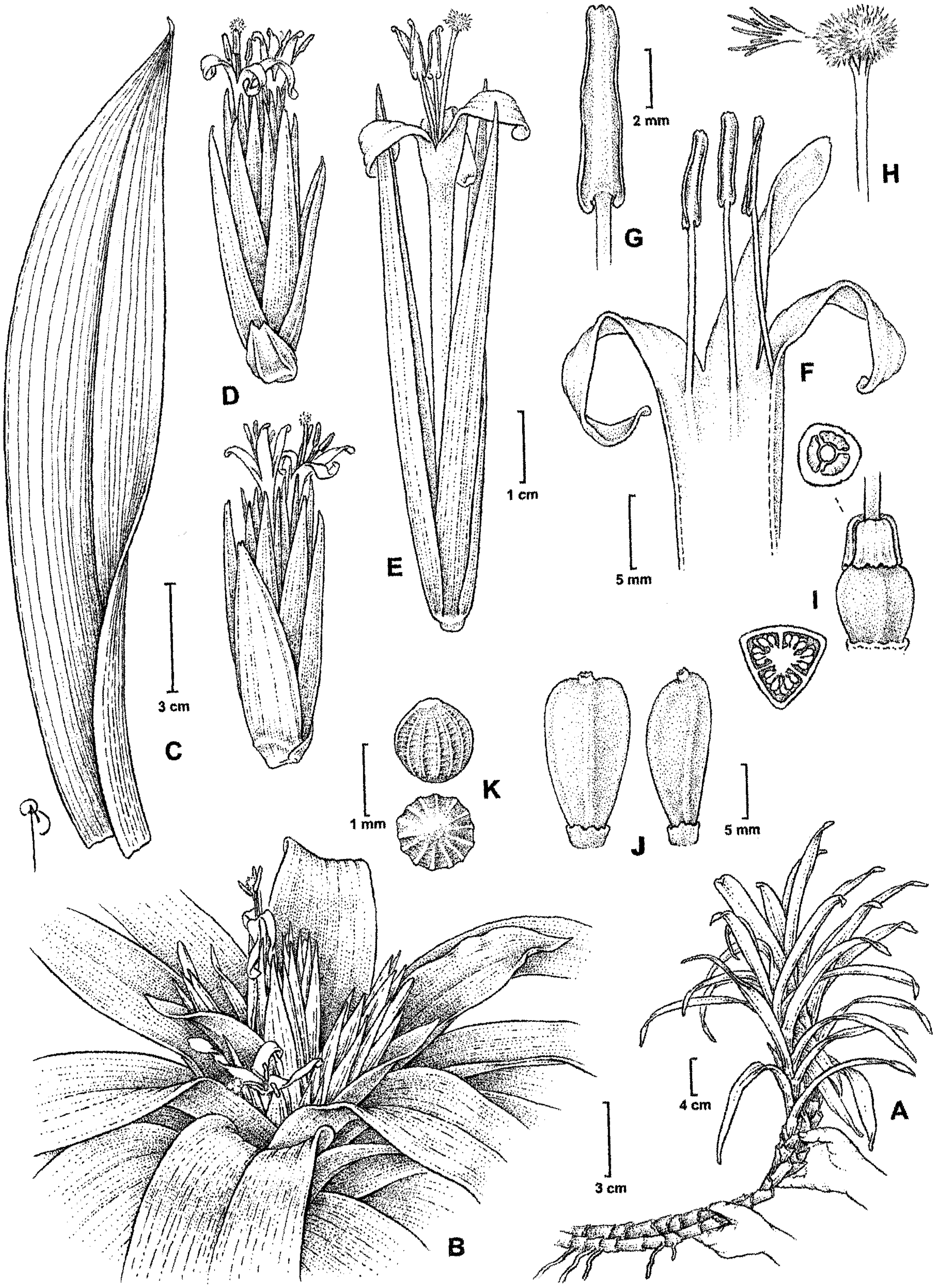
7a. Leaves glaucous and silvery above, margins brown, inflorescence scapose, scape ebracteate, > 4 cm wide, a head-like, many-flowered spike, corolla yellow .... 2. *Orectanthe.*

7b. Leaves not glaucous, green, linear, lanceolate or oblanceolate sometimes forming moss-like rosettes, inflorescence a spike borne on a bracteate or ebracteate scape, < 4 cm. broad, or inflorescences a solitary flower and escapose, corolla blue, purple, or white .... 3. *Abolboda.*

1. *Aratitiyopea* Steyerm. & P. E. Berry , Ann. Missouri Bot. Gard. 71: 297. 1984. Schultes, Bot. Mus. Leafl. 15: 40. 1951. Kral, Ann. Missouri Bot. Gard. 79: 819–885. 1992. Type species: *Aratitiyopea lopezii* (L. B. Sm.) Steyerm. & P. E. Berry. Figs. 5.3A, 5.5, 5.6.

Plants perennial; rhizome long-trailing, decumbent, distally rosulate and bromeliad-like. *Roots* coarse, firm, densely pubescent. *Leaves* dorsiventral, spiraled, cauline, distal internodes shorter; sheath open, broad; lamina linear-lanceolate and falcate. *Synflorescence* a congested raceme of short-peduncled secondary racemes (paracladia), spikes subtended by a foliose to colored bract

Figure 5.5. *Aratitiyopea lopezii* (*L. M. Campbell 813*). A. Habit. B. Inflorescence. C. Leaf. D. Abaxial view of an inflorescence branch. E. Flower. F. Corolla opened to reveal anther attachment. G. Abaxial view of an anther, note the connective apex. H. Branched and plumose stigma. I. Base of the gynoecium, with dorsal appendages. J. Capsule. K. Seed. (Illustration by Bobbi Angell).



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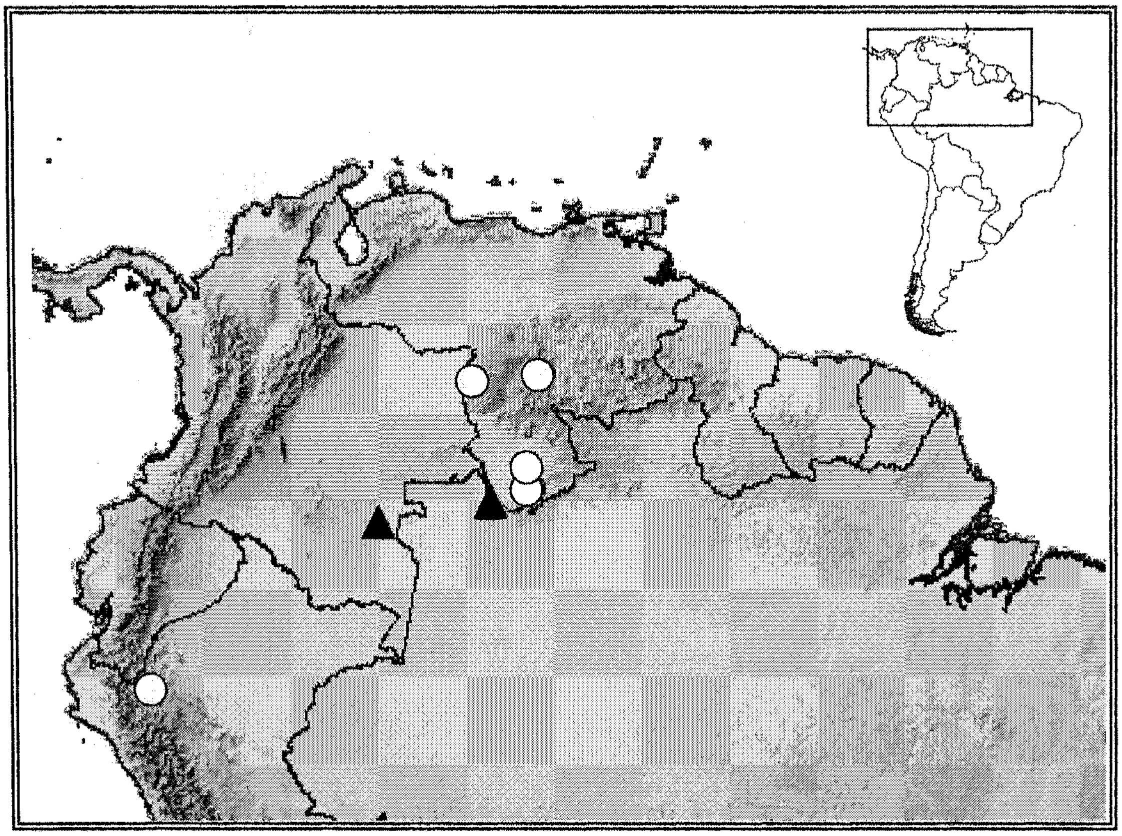


Figure 5.6. Distribution map of *Aratitiyopea lopezii* (○ *A. lopezii var. lopezii,* ▲ *A. lopezii var. columbiana).* Each symbol indicates one or more collections in a degree square. Multiple symbols in a degree square represent collections from individual tepuis.

adaxial prophyll strongly bicarinate, 5–15-flowered. *Flowers* large, sessile, bract magenta, on lower flowers broad, ± flattened, becoming narrow and keeled on upper flowers; sepals magenta, subequal, stiff, median sepal persistent, corolla white or magenta, salverform, monosymmetric, petals delicate, midvein evident, connate, forming a long tube, delicate, the limbs reflexed and contorted, tending toward monosymmetry; androecium uniseriate; stamens epipetalous, filaments white, anthers basifixed, latrorse, connective exceeding the thecae; ovary trilocular, ovules biseriate per placenta, anatropous, ovary apex rounded, each carpel with a large, erect and reflexed, obdeltoid appendage, dorsal near the base of the style, style white, terete, terminally 3-branched, stigmas ramose, colored as the corolla, adaxial surface plumose. *Fruit* ellipsoid, many-seeded. *Seeds* spherical, with pronounced longitudinal striations, and finer cross striations.

Number of species, habitats, and distribution.— *Aratitiyopea* includes one species for which two varieties have been described. It occurs in regions of high annual precipitation on sandstone outcrops and mountains, usually on shallow debris or adjacent high-elevation scrub vegetation. *Aratitiyopea* exhibits a disjunct distribution: the northern populations on the Guiana Shield occur between 250–1200 m; collections from northern Peru are from 400–750 m.

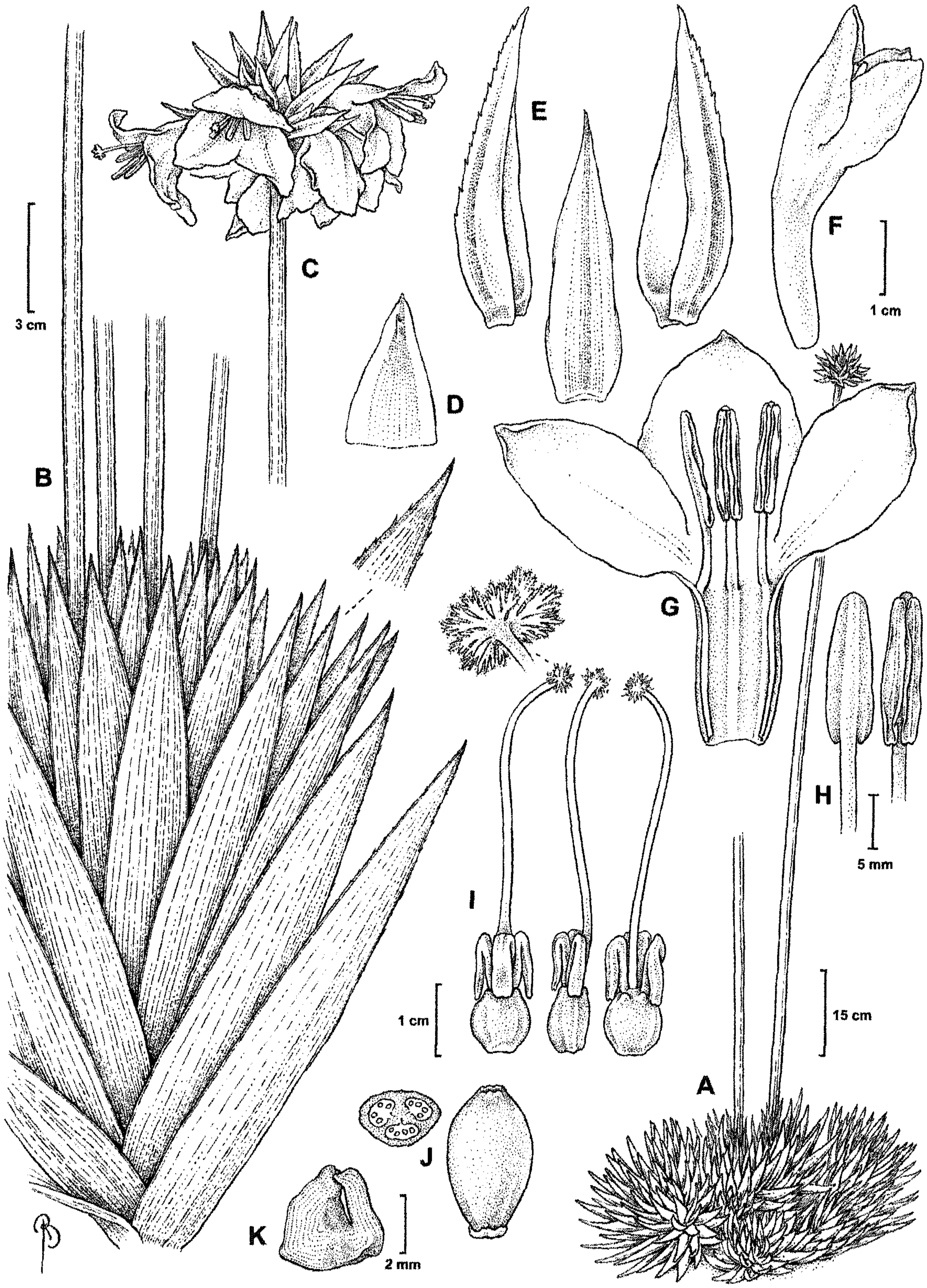
Etymology.— For Cerro Aratitiyope, a sheer granitic inselberg in Amazonas, Venezuela. *Ara* is the genus and local name for Macaws.

2. *Orectanthe* Maguire, Mem. New York Bot. Gard. 10(1): 2. 1958. Suessenguth & Beyerle, Bot. Jahr. 67: 132–142. 1935. Kral, Ann. Missouri Bot. Gard. 79:

819–885. 1992. Type species: *Orectanthe sceptrum* (Oliv. ex Thurn) Maguire. Figs. 5.3B, 5.7, 5.8.

Plants, coarse perennial; rosulate with stout axes, and internodes compressed, or stem decumbent, sympodial branching less evident in decumbent stems. *Roots* coarse, fibrous, firm (seldom spongy). *Leaves* dorsiventral, spiraled, in a dense rosette or cauline; sheath broad; lamina lanceolate to linear-lanceolate, tough and rigid, glaucous or not, base usually white, abscising neatly or the shredded bases persistent (*O. ptaritepuiana*), margins usually sclerified, brown (maroon-brown), apex acuminate, pungent. *Inflorescence* usually terminal, a globose or turbinate cephalium, subtended by 1 or 2 whorls of 3 bracts; cephalium scapose, scapes 1-several, ebracteate. *Flowers* large; lateral sepals persistent, shortly fused at the base, navicular and strongly carinate, strongly thickened towards the keel, firm and sclerotic, median sepal lanceolate-acuminate, unkeeled but midvein obvious, the apex enrolled, pungent, smaller, cartilaginous and thinner than the lateral sepals, caducous; corolla yellow, porrect, monosymmetric, petals connate, the tube fleshy, the limbs delicate, midvein evident; androecium uniseriate; stamens epipetalous, anthers basifixed, introrse, connective exceeding the thecae; ovary trilocular, ovules biseriate per placenta, anatropous, each carpel with a large, erect and recurved, oblong appendage, dorsal, near the base of the style, style triquetrous, terminally 3-branched, stigmas ramose, adaxial surface plumose. Immature *fruit* with 6 crenae above the septa, mature fruit widely elliptic, many-seeded. *Seeds* spherical-ovoid, longitudinally striated, covered by a persistent, triangular, papery

Figure 5.7. *Orectanthe sceptrum* (*L. M. Campbell 789*). A. Habit. B. Base of a plant. C. Inflorescence. D. Persistent floral bract. E. Sepals. F. Corolla. G. Corolla opened to reveal stamen attachment, introrse dehiscence. H. Anthers, note the connective apex. I. Gynoecium. J. Mature capsule, showing intruded placentae with biseriate ovules. K. Seed with obturator. (Illustration by Bobbi Angell).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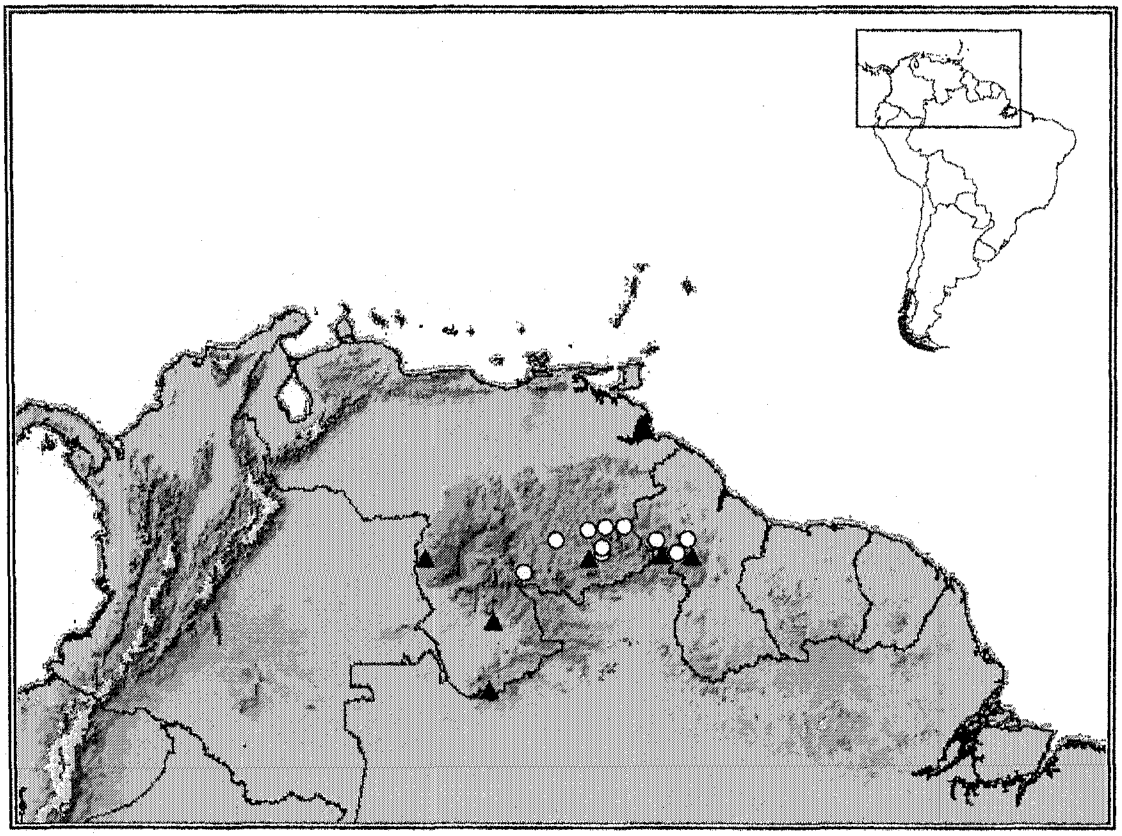

Figure 5.8. Distribution map of *Orectanthe* (▲ *O. sceptrum*, ○ *O. ptaritepuiana*). Each symbol indicates one or more collections in a degree square. Multiple symbols in a degree square represent collections from individual tepuis.

obturator.

Number of species, habitats, and distribution.— *Orectanthe* occurs in savannas and low-canopy scrub vegetation at high elevations (above 1000 m) in the Guayana region of Venezuela and adjacent Brazil and Guyana. Two sympatric species are recognized (Maguire 1958, Kral 1992); however, *Orectanthe ptaritepuiana* (Steyerm.) Maguire is probably better treated as a variety, adapted to high-elevation tepui vegetation (pers. obs., O. Huber, pers. comm.). Herbarium specimens of the two entities exhibit a morphological continuum, even collections from an individual mountain may show morphological intergradation between the two entities. Maguire (1958) formally named or indicated on herbarium specimens additional infraspecific taxa of *Orectanthe sceptrum.* To ascertain the most appropriate taxonomy, field-based studies are needed to assess the variation within *Orectanthe.*

Etymology.— From Greek *orect*, 'stretched', and *anthus*, 'flower', referring to the porrect corolla.

3. *Abolboda* Humb. & Bonpl., *Pl. Aequinoct.* 2: 25, pl. 114. 1813. Suessenguth & Beyerle, Bot. Jahr. 67: 132–142. 1935. Nakai, Ord., fam., trib., ... novis edita. Appendix. 221. 1943. Kral, Ann. Missouri Bot. Gard. 79: 819–885. 1992.
Type species: *Abolboda pulchella* Humb. & Bonpl. Fig. 5.3C, 5.9.

Plants rosulate perennials, rarely annual, sometimes with a high ratio of below ground to above ground biomass, seldom rhizomatous. *Roots* coarse, firm, often with a sand-binding sheath of hairs. *Leaves* dorsiventral, spiraled (except *A. sprucei*), in a dense or loose rosette, sheath short, broad; lamina linear to

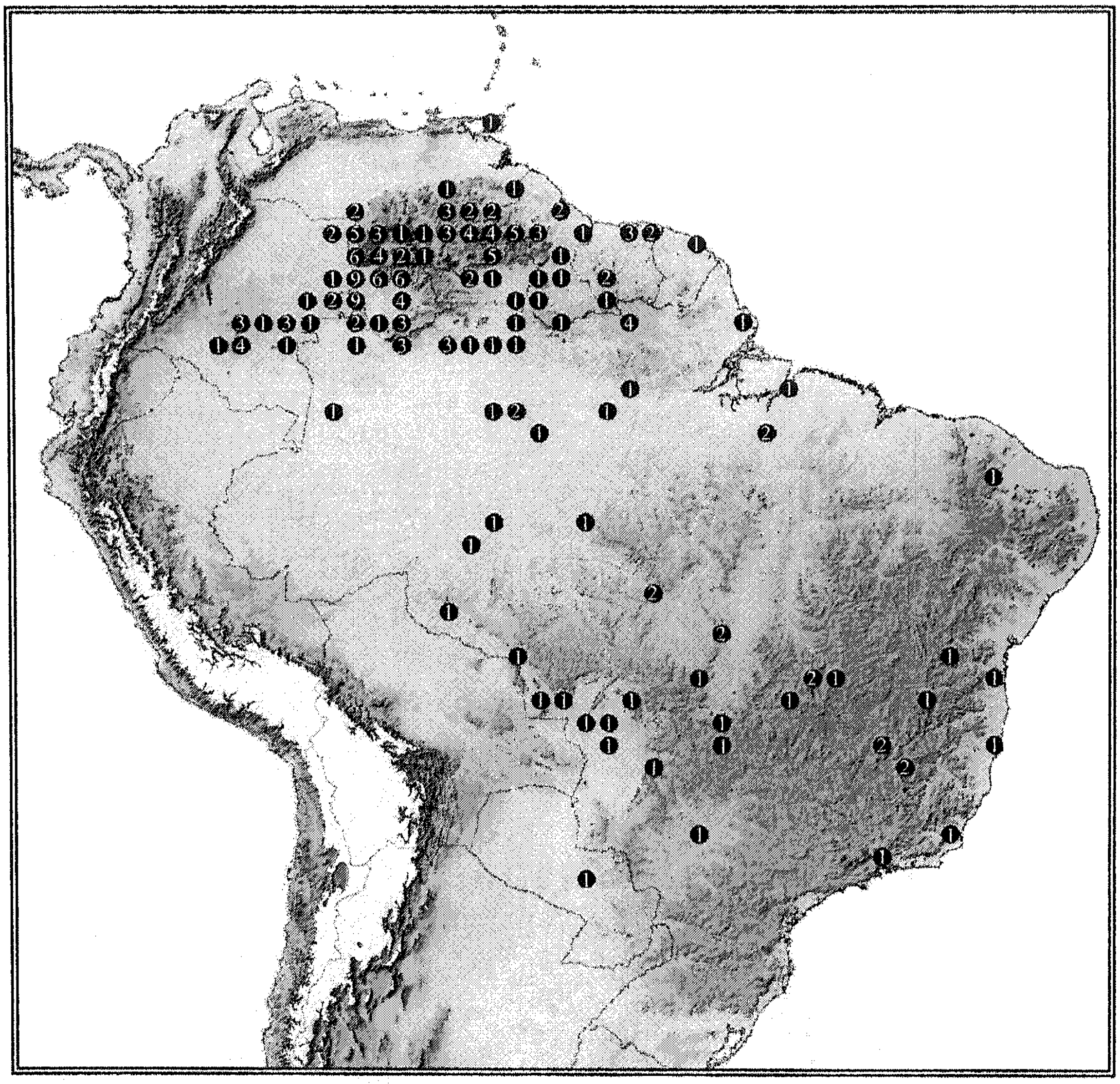

Figure 5.9. Distribution map of *Abolboda.* The numbers indicate the number of *Abolboda* species collected in a degree square.

lanceolate, usually tough and rigid, sometimes dimorphic. *Inflorescence* terminal, usually simple, globose to elongate, or compressed, a raceme of several to many, occasionally a solitary flower, bracts stiff, mostly green, persistent, usually scapose, scapes with 1 to several pairs of subopposite chlorophyllous bracts, occasionally ebracteate. *Flowers* with median sepal translucent, cartilaginous, caducous, sometimes very reduced or failing to develop, lateral sepals often keeled, firm and sclerotic; corolla blue, violet, lavender, or white, salverform or porrect, polysymmetric or monosymmetric, petals connate, delicate, midvein evident; staminodia 3 or reported absent, hypogenous, filamentous, rarely distally branched; stamens epipetalous, filaments white or concolorous with the corolla, anthers dorsifixed, sagittate, extrorse, connective apex sunken; ovary trilocular, ovules biseriate per placenta, anatropous, apex crested or rounded, sometimes tuberculate, style sunken or not, triquetrous, terminally 3-branched, with or without 3 unequal, vascularized, delicate appendages, appendages dorsal, usually midstyle, ± linear, sometimes horned, pendulous, rarely one erect, stigmas ramose, adaxial surface plumose. *Fruit* elliptic, usually many-seeded. *Seeds* prismatic to obovate or oblong, with pronounced longitudinal striations, and finer cross striations.

Number of species, habitats, and distribution.— *Abolboda* comprises twenty-two species, including one putative natural hybrid, with four species having two varieties each. They occur from 100 m to over 2000 m in seasonally wet, oligotrophic habitats, especially white sand savannas drained by black water rivers, and high elevation boggy meadows. *Abolboda* is distributed from Trinidad

(*A. americana* (Aubl.) Malme ex Lanj.), across the Guiana Shield of northern South America, and south on the Brazilian Shield, where three species (two endemic) occur. *Abolboda* species exhibit a high level of endemism (15 spp., 70%). About one-quarter of the species (six species) are high-elevation, narrow endemics, and of these only one species is known from more than one tepui. One-third of the species are low elevation endemics.

Interestingly, over half of the low elevation endemics occur in the vicinity of the town Maroa (Amazonas state, Venezuela) on the Guainía river, a tributary of the Río Negro. High endemicity in a variety of plant families has been attributed to the edaphic conditions of the low forest and interspersed white sand savannas found there (Steyermark 1982), although sampling bias cannot be discounted. The Maroa area has been botanically well-explored because of its location on the isthmus of Pimichín, on the Yavita-Maroa road, which has historically facilitated travel between the Orinoco and Amazon river basins (Wurdack 1960, see Berry and Aymard 1997, Aymard et al. 1998). Despite intensive sampling, a recent collection from the local airstrip (*G. A. Romero-González s.n.*) appears to represent a new escapose species, and, as a result of this study, another low elevation taxon endemic to the Río Negro basin, *Abolboda acicularis* Idrobo & L. B. Sm. var. *granularis* Maguire, is being elevated to species (Appendix 3). New species in other families and interesting records have also been reported from recent botanical surveys of the area (Berry and Aymard 1997).

Another area with similar white sand savannas may also have a high level of local endemism in *Abolboda*. Maguire informally designated on herbarium specimens several new entities from Cerro Yapacana (Amazonas state, Venezuela). The present study calls attention to the fact that the variation in *Abolboda* is probably not adequately reflected in the current classification. The ability to study well-preserved specimens, not afforded previous workers, has revealed fine structures previously described as absent, and highlights the need for collections of additional species.

Etymology.— From Greek *a,* 'without', and *bolbo*, 'bulb', in reference to an early association of the genus to Iridaceae.

4. *Achlyphila* Maguire & Wurdack, Mem. New York Bot. Gard. 10(2): 12. 1960. Kral, Ann. Missouri Bot. Gard. 79: 819–885. 1992. Type species: *Achlyphila disticha* Maguire. Fig. 5.3D, 5.10.

Plants medium-sized, slender, irioid perennials. *Roots* fine, branched. *Rhizome* subterranean, horizontal, branched, slender, aerial stems unbranched, with several cataphylls, nodes not congested, distally compressed and abruptly naked (ca. 1/3 of the stem), tuberculate. *Leaves* cauline, distichous, equitant, steeply ascending, lamina ensiform, tuberculate, long-aciculate, ligule scarious. *Inflorescence* terminal, subtended by an erect foliaceous bract, compound, the main branching a raceme, each branch bearing a cluster of 2 or 3 flowers and bracts, prophyll erect, as long as the inflorescence, tuberculate. *Flowers* long pedicellate, ± polysymmetric; sepals free, lanceolate, distal margins enrolled and erose, acute, subequal, carinate, firm, median sepal deflexed, persistent; petals free, apert, rhomboid-obovate, unclawed, delicate, numerous equal veins evident; androecium uniseriate; stamens free, hypogenous, apex sunken,

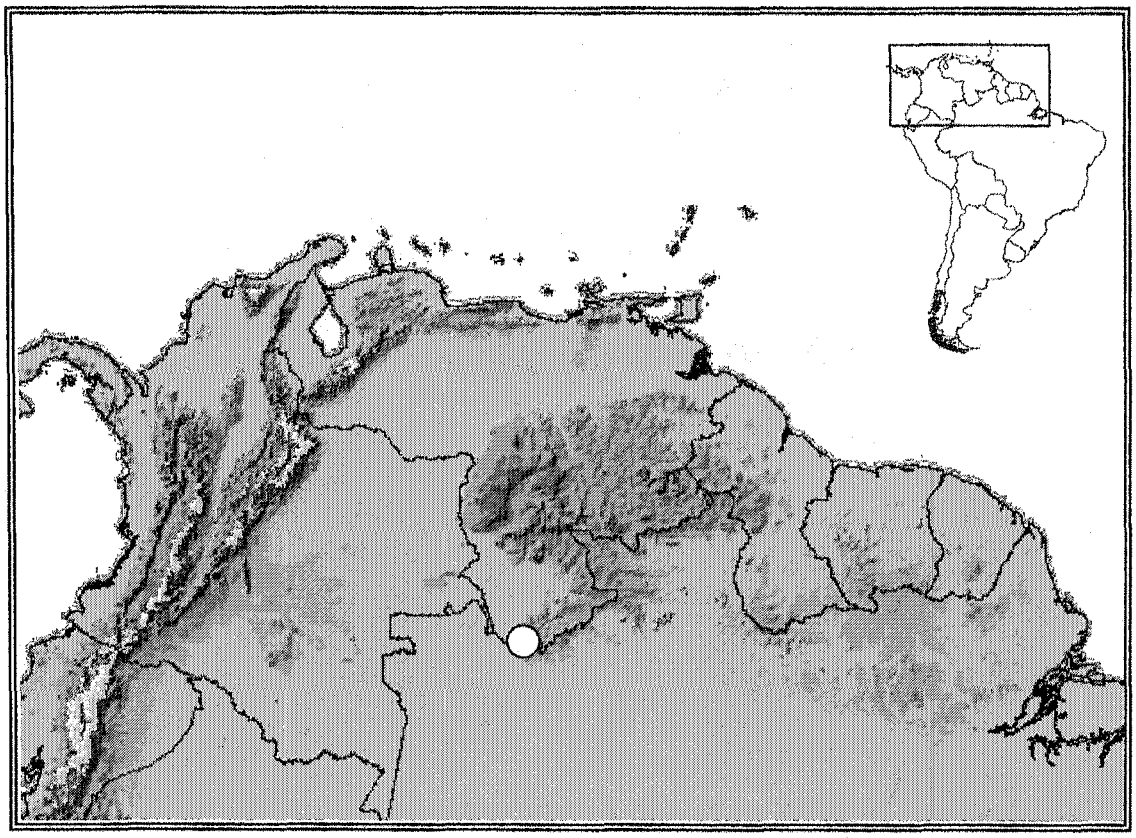

Figure 5.10. Distribution map of *Achlyphila*. The only known locality of *Achlyphila disticha* is Cerro de la Neblina, on the Venezuela/Brazil border. The symbol Indicates more than one collection in a degree square.

anthers dorsifixed, sagittate; ovary with 3 longitudinal shallow grooves, trilocular, ovules biseriate per placenta, anatropous (?), style simple, stigma 3-lobed, lobes small, papillate (?). *Seeds* spherical-ovoid, with minute longitudinal striations.

Number of species, habitats, and distribution.— The single species, *Achlyphila disticha* Maguire & Wurdack, occurs on acidic bogs in the understory of cloud forests. It is known only from Cerro de la Neblina on the Venezuela-Brazil frontier, where it has been collected between 1750 and 2300 m.

Etymology.— From Greek *achly*, 'clouds or mist', and *philo*, 'loving', in reference to the habitat.

5. *Xyris* Gronov. ex L., *Gen. Pl.* 5 ed. 25. 1754. Malme, 1913. Ark. Bot. 13(3): 1–103. 1913. Malme, Ark. Bot. 13(8): 1–32. 1913. Malme, Sven. Bot. Tidskr. 21(4): 381–396. 1927. Idrobo, Caldasia 6: 185–260. 1954. Smith & Downs in Teixeira, *Fl. Brasí.* 9(2). 1968. Wanderley, Ph.D. diss., São Paulo. 1992. Doust & Conn. Aust. Syst. Bot. 7: 455–484. 1994. Conn & Doust, Aust. Syst. Bot. 10: 189–248. 1997. Type species: *Xyris indica* L.

Fig. 5.2, 5.3E-H, 5.11.

Plants slender or robust, perennial or annual, often sedge-like, rarely aquatic; axes usually stout, seldom rhizomatous. *Roots* filiform to coarse, firm or spongy. *Leaves* unifacial, usually ensiform, distichous, equitant, sheath forming a ligule or not. *Inflorescence* terminal or axillary, a (few-) to numerous-flowered globose, turbinate or cylindrical spike, rarely a head, subtended by spiraled bracts, usually initially 1 or 2 pairs, or bracts sometimes large and involucral, spikes scapose, scape ebracteate, terete or compressed, sometimes carinate, sometimes

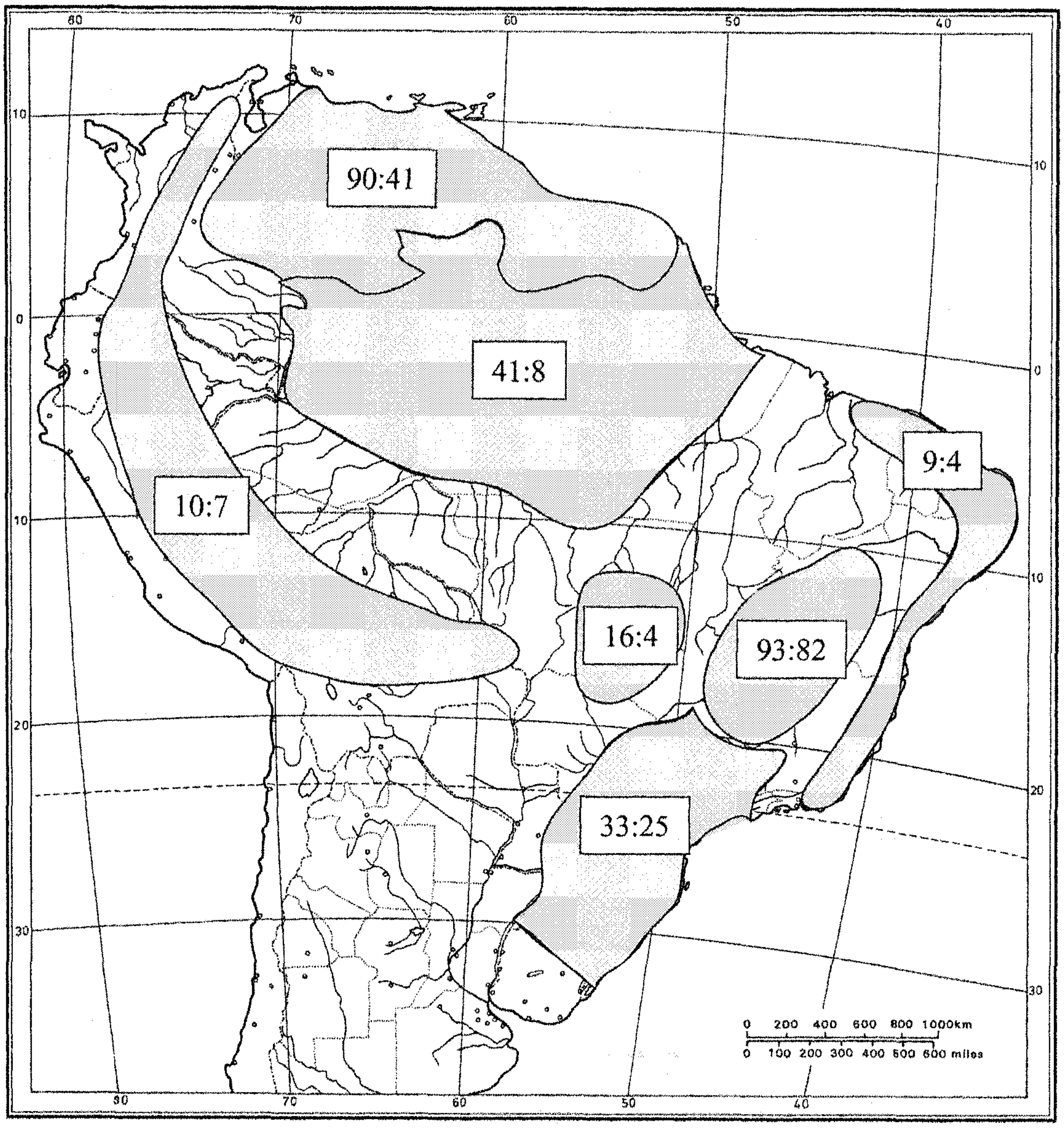

Figure 5.11. Number of *Xyris* species in South America. The first number is the number of species known to occur in a region, followed by the number of species endemic to that region. Redrawn in part from Wanderely (1992).

contorted, occasionally ribbed. *Flowers* subtended by a persistent, firm bract, bract usually with an abaxial, median, colored patch; the median sepal larger, cucullate, translucent, cartilaginous, fugacious, the lateral 2 basally connivent or connate, cymbiform, usually keeled, firm and sclerotic, persistent; corolla yellow, very rarely white or blue (sect. *Xyris*), tubular, usually polysymmetric, rarely not ephemeral (sect. *Pomatoxyris*), petals free or connate basally, clawed, uniform, delicate, numerous equal veins evident; staminodia usually present, hypogenous, antesepalous, distally enlarged, usually distally bifurcated, the branches rarely further branched, often adnate to the adjacent petals, usually with penicillate moniliform hairs; staminal filaments epipetalous or adherent to the petals; anthers basifixed, usually sagittate, latrorse or extrorse, connective broad, apex sunken; gynoecium tricarpellate, ovary unilocular, or trilocular, the septa not always fully formed distally, apex sometimes 3-lobed, rarely tuberculate (Sect. *Pomatoxyris*), placentation basal, shortly free central, parietal, or axile, ovules often long-funiculate, orthotropous, style rarely sunken, flattened or terete, 3-branched distally usually into stylodia, rarely short-branched to unbranched, the branches widely divergent, grooved adaxially, stigma -shaped, plumose. *Fruit* occasionally with an indehiscent apex (sect. *Pomatoxyris*). *Seeds* small to minute, oblong to ovoid, usually longitudinally striated, often with cross ribs.

Number of species, habitats, and distribution.— There are about 360 species of *Xyris* separated into three sections: *Xyris* (ca. 110 spp), *Nematopus* (ca. 230 spp.), and. *Pomatoxyris* (18 spp.). For the number of species, *Xyris* occupies a narrow range of habitats. Many species occur at low elevation in acidic, oligotrophic, wet (at least seasonally) bogs, meadows and savannas. In South America species exhibit greater elevational tolerance and have diversified into a variety of microhabitats. The genus is distributed through out the tropics and subtropics, and occurs in southern North America, the Caribbean Island, South America, Africa, southern Asia, (including Indonesia, Malaysia, and the Philippines), New Caledonia, and Australia. A small portion of species occur in adjacent temperate regions in North America (24 spp.), Asia (1 sp.), and Australia (9 spp.). Species of sect. *Pomatoxyris* are restricted to southwestern and southeastern Australia, and sect. *Nematopus* occur only in South America, where about 65 percent of the species, including many endemics, are found.

Etymology.— Greek for Iris; *xyr-*, 'razor', referring to the ensiform leaves.

Pollen Morphology

Light microscopy studies of pollen morphology, including sectioned material, have been published for species representing all of the genera (Appendix 5). The most important contribution on Xyridaceae pollen is Carlquist's survey using light microscopy (1960). The present study is the first to examine in detail Xyridaceae pollen with scanning electron microscopy (see also Rudall & Sajo 1999; Figs. 5.12, 5.13). Statistically testable quantification of pollen measurements is not yet possible due to limited samples and to different methods of specimen preparation (air dried vs. FPA). The measurements below were made from several uncollapsed grains and a synthesis of published reports (Appendix 5).

Figure 5.12. Xyridaceae Pollen. A, B. *Aratitiyopea lopezii* (*L. M. Campbell 813*, NY). B. Detail of exine sculpturing. C, D. *Orectanthe sceptrum* (*L. M. Campbell 789*, NY). D. Detail of bacula and muri. Scale bars: A, C = 10 µm; B., D = 5 µm.

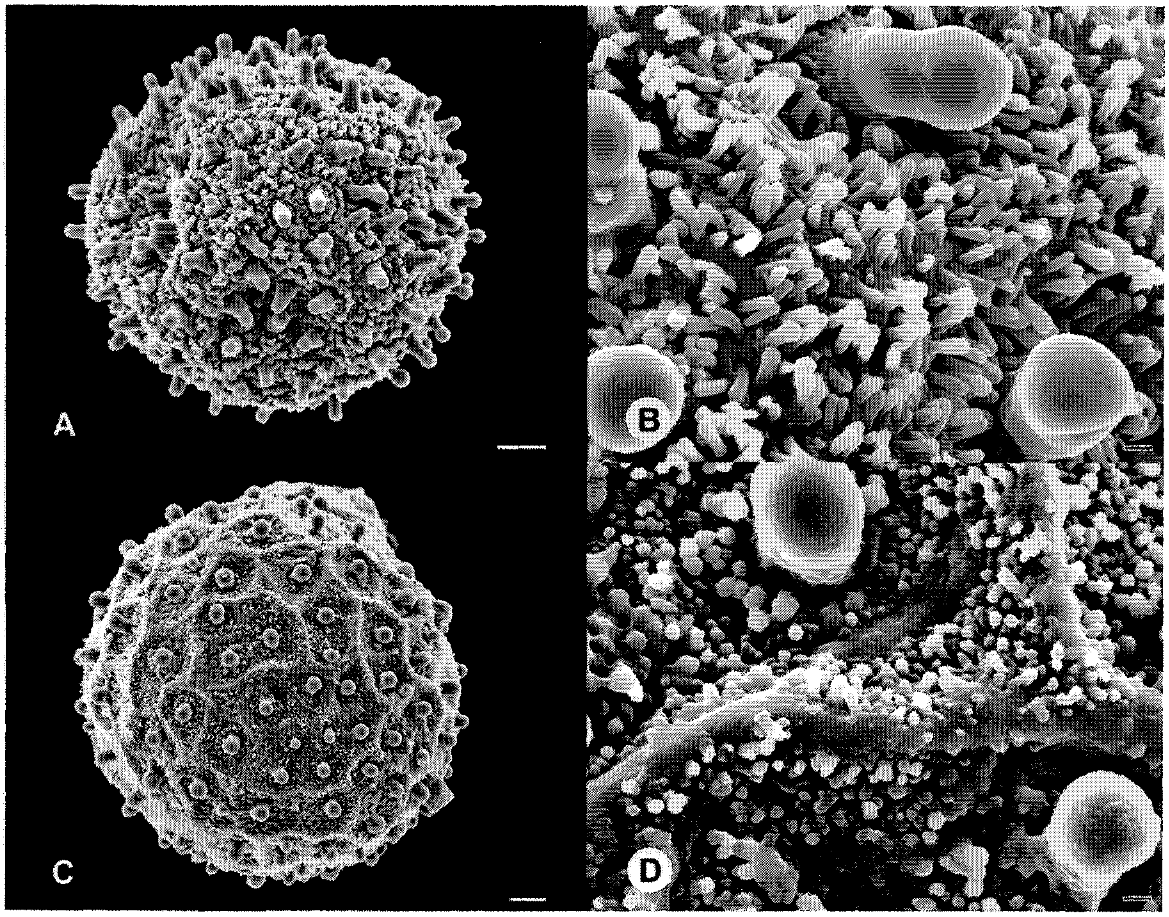
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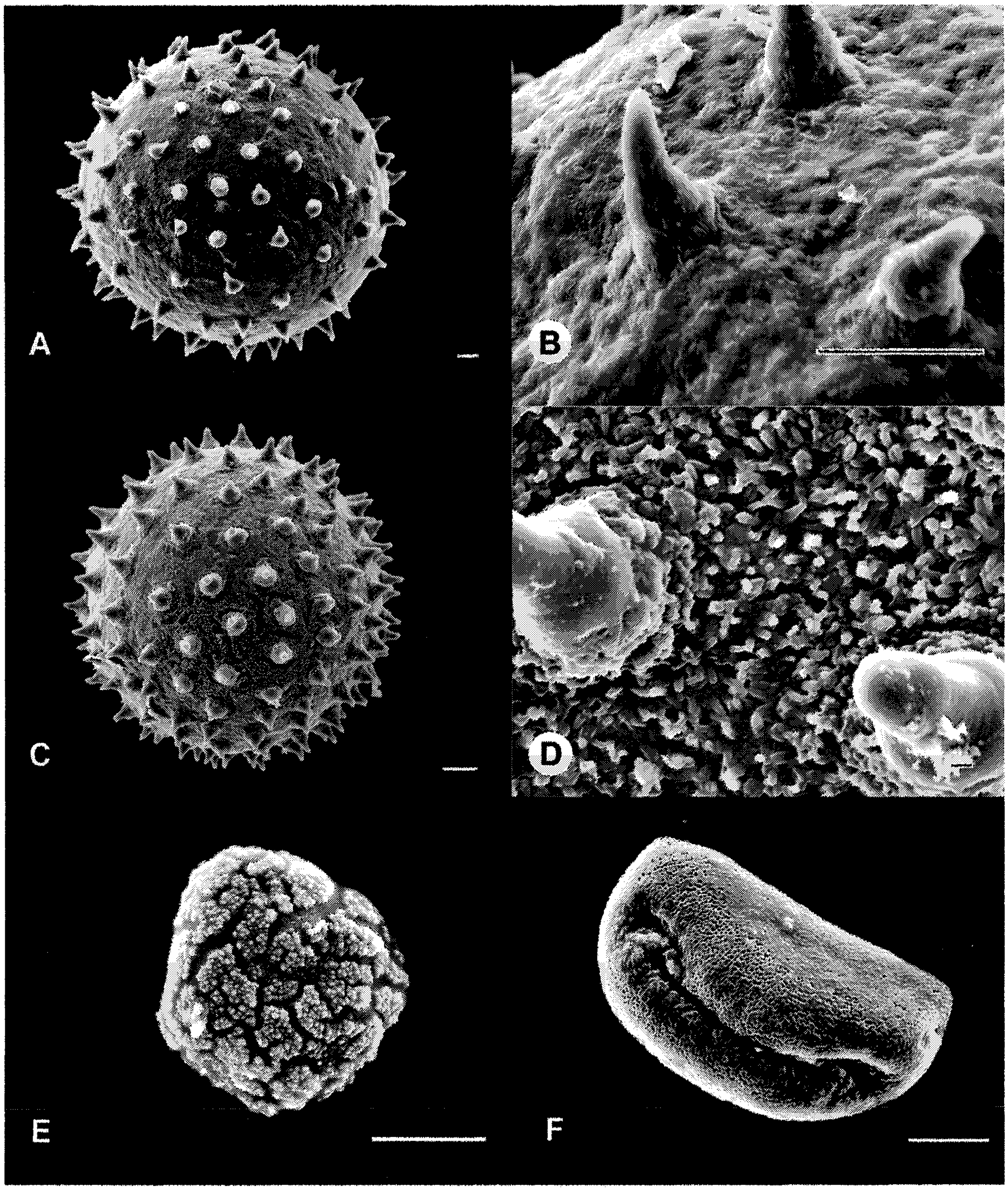
Figure 5.13. Xyridaceae Pollen. A. *Abolboda pulchella* (*L. M. Campbell 756*, NY). B. *Abolboda paniculata*, verrucate interspinal areas (*J. A. Steyermark 109328*, NY). C. *Abolboda linearifolia* (*L. M. Campbell 653*, NY). D. *Abolboda grandis* var. *rigida* (*B. Maguire 23148,* NY), baculate interspinal areas. E. *Achlyphila disticha* (*Maguire 42386*, NY). F. *Xyris anceps* (*S. K. Pell 682*, NY). Scale bars: A, C, E, F = 10 µm; B, D = represented by the ornamentation which stains differently to the inner layer (Nowicke in Steyermark 1984; pers. obs.). Pollen grains range between 62–180 µm.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The striking differences between *Xyris* and *Abolboda* pollen have been commented upon (Kuprianova 1948, Erdtman 1952, Samuelsson in Nilsson and Praglowski 1992). *Xyris* pollen is small (usually < 50 µm; see references in Appendix 5), bilaterally symmetrical, sulcate, and with fine exine ornamentation. *Achlyphila* also has small pollen grains, whereas *Aratitiyopea*, *Orectanthe*, and *Abolboda* have large grains (> 50 µm). The latter four genera have spheroidal pollen grains, large exine protuberances, and lack an obvious aperture (Erdtman 1952, Carlquist 1960, Nowicke in Steyermark 1984; Figs.5.12, 5.13). *Abolboda*, *Aratitiyopea*, and *Orectanthe* are interpreted as being omniaperturate; the exine absorbing safranin or fuchsin, and represented only by the ornamentation and the remaining wall colorless (see Nowicke in Steyermark 1984; pers. obs.). In contrast, Carlquist (1960) observed three differently staining regions in the walls of *Abolboda* and *Achlyphila* pollen and reported a thin intine. These discrepancies should be resolved by studying the wall ultrastructure using transmission electron microscopy (TEM).

Aratitiyopea.— Pollen grains are spheroidal and inaperturate (Nowicke in Steyermark 1984; Fig. 5.12A). They are ornamented with very large bacula that are often somewhat swollen distally, interspersed in a matrix of similarly shaped, finer and smaller bacula. These projections are larger near the base of the spines (Fig. 5.12B). The exine is represented by the ornamentation which stains differently than the inner layer (Nowicke in Steyermark 1984; pers. obs.). Pollen grains range between 62–180 µm.

Orectanthe.— Pollen grains are spheroidal and inaperturate (Carlquist 1960, pers. obs.; Fig. 5.12C). They are similar to baculate pollen of *Aratitiyopea*, but sculpturing is shorter and less dense. Some of the larger exine elements are constricted near the base(Fig. 5.12A). A feature unique in Xyridaceae to *Orectanthe* are ridges ('muri' of Punt) running between most of the knob-like projections (Fig. 5.12D). A thin internal layer that was found in *Abolboda* and *Achlyphila*, and interpreted as intine, was not detected in *Orectanthe*, possibly as an artifact of preservation (Carlquist 1960). Pollen grains are 140 µm–165 µm.

Abolboda.— Pollen grains are spheroidal and inaperturate (Carlquist 1960, pers. obs.; Fig. 5.13A, C). Based on exine sculpturing *Abolboda* species can be separated into two general groups: those having grains with spines and verrucate interspinal areas (the majority of species, Fig. 5.13C), and those having grains with large clavae or baculae and pila between these projections (Fig. 5.13D). The shape and size of the projection is characteristic of species, and even infraspecific taxa (Carlquist 1960, pers. obs.). Spines are conical, often with a swollen base. Pollen grains range between 62–180 µm.

Pollen morphology has been examined in only a small percentage of *Xyris* species, but appears to be more uniform in size and ornamentation than *Abolboda*. Pollen grain size may be associated with overall flower size. In general, *Abolboda* species with larger flowers and longer styles have larger pollen. Flowers with long styles have large pollen grains to meet the energy requirements for growth of a long pollen tube (Covas and Schnack 1945, Baker and Baker 1979). Pollen containing starch as an energy source, such as

Abolboda grandis Griseb. (Zona 2001), are generally larger than lipid-containing grains (Baker and Baker 1979), such as *Xyris jupicai* Rich. (Zona 2001). The type of pollen ornamentation in *Abolboda* (echinate vs. clavate/baculate) is correlated to corolla form, and is likely associated with a difference in pollinator class.

Achlyphila.— Pollen grains are spheroidal and have been considered to be inaperturate (Maguire and Wurdack 1960, Carlquist 1960; Fig. 5.11b). The pollen is clypeate (sensu Halbritter and Hesse 1995); the exine is covered with large, irregular shields of pila with narrow to wide, unornamented, recessed spaces between the shields. Pollen tubes of clypeate pollen emerge from between the shields and are either functionally omniaperturate, and have a uniformly thickened intine (Furness and Rudall 1999), or porate, with localized thickenings of intine (Chanda and Gosh 1976, Halbritter and Hesse 1995). Carlquist's (1960) illustration of sectioned *Achlyphila* pollen depicts a slightly thinner intine than the exine, but proportionally thicker than that of *Abolboda*. Pollen wall ultrastructure should be examined to better characterize the intine and probable germination sites. Dried pollen grains are 20–24 µm; alcohol preserved grains are about 32 µm (Carlquist 1960).

Xyris.— Pollen grains are elongate, elliptic, or oblong, and convex in lateral view (van Zinderen Bakker 1953, Straka and Friedrich 1984; Fig. 5.13F). There is one (Erdtman 1952, van Zinderen Bakker 1953, Sharma 1967) or two sulci (Erdtman 1952, Straka and Friedrich 1984, Cruz-Barros 2000), and Erdtman (1952) questionably lists 3-sulcate (*Xyris rupicola* Kunth). Exine ornamentation is described as finely reticulate (van Zinderen Bakker 1953, Sharma 1967, Cruz-

Barros et al. 2000) and punctate (Sharma 1967), or foveolate (Sharma 1967, Straka and Friedrich 1984). The sexine is usually thicker than nexine (except *X. schizachne* Mart.: Cruz-Barros et al. 2000), or of equal thickness (Erdtman 1952, Sharma 1967). Grains range in size from 22.5 × 37 µm (*X. wallichii* Kunth: Sharma 1967) to 34.6 × 56.4 µm (*X. umbilonis* Nilsson: van Zinderen Bakker 1953).

Examination of the pollen wall ultrastructure with TEM would clarify if pollen is better characterized as functionally monoaperturate, having a localized thickening in the intine (cf. Furness and Rudall 1999; 2000), or omniaperturate (with uniformly thin exine and thick intine, containing many cytoplasmic tubules; Thanikaimoni 1986). Nowicke's (in Steyermark 1984) interpretation of *Aratitiyopea* pollen conforms to the latter type. Germination has been found to occur in any part of the intershield region in clypeate pollen from a variety of genera (Chanda and Ghosh 1976, Halbritter and Hesse 1995). Whether this region serves as a germination site in *Achlyphila* needs investigation.

Karyology

Chromosome numbers.— Chromosome numbers are documented only for species of *Xyris* and are summarized in Table 5.2 (Fig. 5.14). Karyology has been studied in only ten percent of the species (see Appendix 4). Kral (1998) mentions *n*=8, 9, 13, and 17 for *Abolboda*, but these counts have not been documented. The base number for *Xyris* is thought to be 9 (Benko-Iseppon and Wanderley 2002) or 13 (Briggs 1966). Although Benko-Iseppon and Wanderley

Table 5.2. Summary of reported chromosome numbers in *Xyris* L.

Section	# taxa sampled	*n*	2*n*	Geographic region
Xyris	17	9		North America[1, 2, 3]
	2		18	North America[4]
	1		24[*]	Tropical Asia[5]
	1		32[*]	Indonesia[6]
	1		34	Africa[7]
	2		34	Tropical Asia[8]
	2		26, 50–52, 52	Australia[9]
Total taxa	**24**			
Pomatoxyris	4		26	Australia[9, 10]
	1		52, 52–54	Australia[9]
Total taxa	**7**			
Nematopus	2		26	South America[11]
	2		28	South America[11]
	2		34–46	South America[11]
	1		≈46	South America[11]
	2		52–54	South America[11]
	1		78–80	South America[11]
	1		90–92	South America[11]
	1		≈108	South America[11]
Total taxa	**12**			

[*] These counts were both for *Xyris indica* L.

[1] Kral (1966).
[2] Kral (1978).
[3] W.Lewis, Stripling, and Ross (1962).
[4] W. Lewis (1961).
[5] Ramarethianam, Dhananjayam, and Masilamani in Sharma (1972).
[6] Weinzieher (1914).
[7] Thulin (1970).
[8] Larsen (1963).
[9] Briggs (1966).
[10] J. Lewis (1980).
[11] Benko-Iseppon and Wanderley (2002).

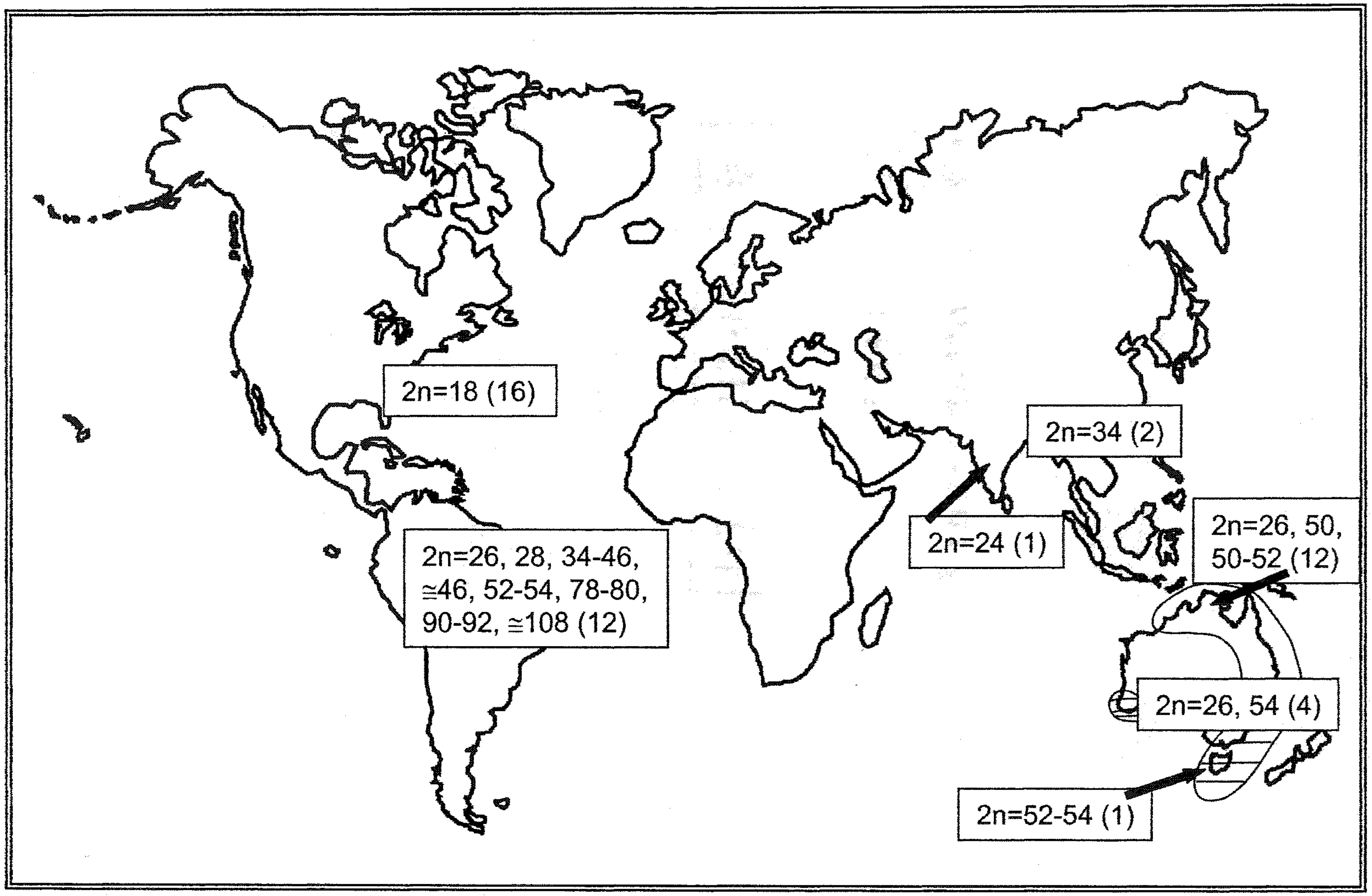

Figure 5.14. Chromosome numbers in *Xyris*. The counts are based on the number of species in parentheses. Section *Pomatoxyris* is indicated by hatching.

(2002) report all counts as 2*n*, the numbers indicate that some of the species they studied are tetraploids and that 7 and 13 may also be base numbers (Table 5.2). Larsen's (1963), generally dismissed, proposal of 17 as a third base number for *Xyris* resulting from hybridization between n =7 and n=8 species should be reconsidered in the context of additional, careful studies. The high chromosome numbers reported in species from South America were collected on Serra do Cipó, Minas Gerais State, Brazil. This is an area of high speciation and endemism in *Xyris* (Wanderley 1983, Giulietti and Pirani 1988) and Wanderley has suggested that some of the species occurring there represent a new section (Wanderley et al. 1993, pers. comm.).

Floral Phenology, Pollination, and Breeding Systems

Faden's (1992) comment that "the two outstanding features of Commelinaceae flowers that affect their reproductive biology are the lack of nectar and the brief flowering times (generally a few hours…)" could be applied equally to species of Xyridaceae. No rigorous study of breeding systems in Xyridaceae has been published, and levels of compatibility are known for only two species of *Xyris* (Ramirez and Brito 1990). Most information that has been reported on aspects of the breeding system, including what is presented here, is anecdotal or inferred. The lack of information on the basic biology of Xyridaceae can be attributed, in part, to the short longevity of individual flowers and brief seasonal flowering period in most species, and the remote localities that many members of the family occupy, all factors making detailed, long-term field studies difficult. Information on pollinators was even beyond the scope of Doust and

Conn's (1994) and Conn and Doust's (1997) comprehensive descriptions of Australian *Xyris* species, although they did include other aspects of autecology. The infra- and intergeneric variation in habitats, inflorescence structure, and floral morphology, size, and color, indicate that several classes of animals could be exploited as pollinators.

In flowers of Xyridaceae, at least two sepals are persistent firm protective structures. Blossom color—the conspicuous corolla and/or brightly colored bracts (*Aratitiyopea*)—is the main attractant for pollinators (Figure 5.4). *Orectanthe, Xyris*, and *Achlyphila* and have yellow corollas, described as "pale" (*Kral 71924*) or "dull" (Kral 1988) in the latter (except a few *Xyris* taxa with white-flowered populations and *X. filiformis* Lam. with yellow, blue, or white flowers). *Aratitiyopea* has showy magenta bracts and either white or magenta corollas. The most common corolla color in *Abolboda* is a medium blue, but varies from deep violet-blue, very pale blue, pale pinkish-blue, to pure white. In sympatric populations of *Abolboda* corolla color is often different between the species. Pollen, and the staminodial hairs present in most *Xyris* species may also be attractants, and pollen has been considered the main reward for pollinators (Kral 1983, 1998; Ramirez et al. 1990, pers. obs.). The stigmas are exserted in most species and are elaborated in *Abolboda*, *Aratitiyopea*, and *Orectanthe*. In *Abolboda* and *Aratitiyopea*, the stigma is often concolorous with the corolla, while the style is white. The flowers are nectarless (Vogel 1981 [but see Vogel 1990], Kral 1966, pers. obs.) and odorless. Pollen grain size and ornamentation is diverse in the family (see above). Pollen grain size is related to physiological factors and pollination biology. Flowers with long styles tend to have large pollen grains to meet the energy requirements for growth of a long pollen tube (Covas and Schnack 1945, Baker and Baker 1979). A directly correlated increase in size of the pollen grain with increased size in pollinator class is exhibited in other unrelated families (e.g. Polemoniaceae, Taylor and Levin 1975). As mentioned above, starchy grains are generally larger than lipid-containing grains (Baker and Baker 1979) and are less prone to desiccation (Franchi et al 1996). Pollen of *Abolboda grandis* Griseb. has been found to contain abundant starch, and the much smaller grains of *Xyris jupicai* Rich. contain little starch (Zona 2001). Both starchy grains and small grain size, which is correlated with starchlessness, are associated with amenophily and autogamy (Baker and Baker 1979).

Species of Xyridaceae usually form dense populations and often the community includes more than one species from one or more of the genera. Most inflorescences (or inflorescence unit in *Aratitiyopea*) have several to many flowers, but generally only one to three flowers are at anthesis at a time. *Orectanthe* is exceptional in this feature, having several to many simultaneously anthetic flowers. In the temperate sect. *Pomatoxyris*, flowers last at least a day and in four species longer than one day (Conn and Doust 1997). Otherwise in the taxa for which individual flower duration is known, anthesis is less than a day. Most species bloom for only a few hours, usually in the early morning. In families with both one-day long flowers and flowers lasting longer than a day, the latter occur in the temperate members (Philbrick 1985). Thus, dichogamy (protandry and protogyny) is probably not expressed in Xyridaceae, although spatial separation of reproductive organs (herkogamy) may promote outcrossing rates. Staggered daily flowering periods among species in sympatric populations may serve as a reproductive isolating mechanism and/or as a competitive strategy to partition pollinator service (Waser and Real 1979).

Floral phenology and pollination syndrome of Aratitiyopea lopezii.— *Aratitiyopea lopezii* (L. B. Sm.) Steyerm. & P. E. Berry exhibits a disjunct distribution with populations at mid- to high elevation on the Guiana Shield (ca. 0°15'–05°21'N 65°12'–70°35'W) and at mid elevation on the Ecuador/Peru border (ca. 05°14'S 78°21'W). The northern populations flower near the end of the dry and wet seasons; the present study detected a brief flowering period. Observations made in September of consecutive years on the Cerro Cuao-Sipapo populations indicate that the flowering period is probably only about two weeks. Within an inflorescence branch (paracladium), maturing seeds and anthetic flowers were found simultaneously. Flowering specimens from the Peru populations were collected in March and August.

The gestält of *Aratitiyopea* is strikingly different from the majority of other Xyridaceae, in vegetative form, inflorescence structure, and floral morphology. The inflorescence is compound, and flowers have a long floral tube with reflexed, contorted corolla lobes (Fig. 5.4). In plants growing on Cerro Cuao-Sipapo, the individual flowers were at anthesis, with pollen shed, by 700 hr and closed after noon (around 1300–1400 hr). In some flowers the anthers with pollen dehisced were touching the stigma, but there is no evidence as to whether self-fertilization occurs. As discussed above, due to temporal constraints and apparent pollinator limitations, I hypothesize that the breeding system in *Aratitiyopea* is facultative outcrossing, and in addition to possible mediated self-pollination (geitonogamy), autonomous self-pollination appears to be present. No pollinators were observed, but *Aratitiyopea* has a suite of characters consistent with ornithophily, as summarized in Table 5.3. Furthermore, one-day flowers were associated with hummingbird pollination in a study in Puerto Rico, in which all 13 hummingbird-pollinated species (11 genera, 9 families) had one-day flowers that opened before dawn (Kodric-Brown et al. 1984).

Hummingbird pollination of *Aratitiyopea* would be an example of deception in which the plant has evolved features to exploit an available pollinator without the high energy expense of producing a nectar reward (Faegri and van der Pijl 1979, Stiles 1981, see Southwick 1984). In this case, the deceit attractant is the long floral tube and bright coloration, reminiscent of many nectar-producing flowers. Although animal-mediated pollination syndromes are often reliant on pollinator fidelity achieved by provision of a reward, deception has been shown to be effective in species with a brief pollination window (Faegri and van der Pijl 1979), even with intelligent pollinators (Vogel 1978, Ackerman and Mesler 1979). Mimicry by deceit (vs. mutalistic mimicry) is associated with fewer flowers produced by the mimic than by the model taxa they are imitating (Little 1983). This phenomenon may explain the low percentage of fertile individuals observed during three growing seasons on Cerro Cuao-Sipapo. The low number of duplicates per collection of herbarium specimens from other populations

Table 5.3. Floral and anthecological chacteristics of humingbird pollinaton syndrome.

Features observed in *Aratitiyopea lopezii*

Flowers stationary, seasonal, patchy in distribution[1]
Diurnal anthesis[2], mostly early morning[3], lasting less than one day[4]
Flowers solitary or loosely clustered[5]
Odorless[2]
Vivid colors[2], of long wavelenght[1], or contrasting colors[1]
Nectar guides obscure or absent[1,2]
Corolla tubular, longer than butterfly-flowers, margin absent or curved back[2]
External wall of flower hard[2]
Anthers held at same height as stigma[5]
Filaments stiff[2]
Pollen grains large, exine ornamented[6]
Ovary protected[2]

Features not observed in *Aratitiyopea lopezii*

Flowers held horizonaltly[5], or pendulous[1,2]
Copious, dilute nectar[1], peak production in early morning[3]
Nectar retained by capillarity, or otherwise protected[2]

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[1] Stiles (1981).
[2] Faegri and van der Pijl (1979).
[3] Proctor et al. (1996).
[4] Primack (1985).
[5] Endress (1994).
[6] Ferguson and Skvarla (1982).

indicates consistent low rates of flower production.

It has long been considered that in ornithophilous pollination syndromes, a close correlation exists between bill and floral tube lengths (Proctor et al. 1996) reflecting a close coadaptation of bird and plant species. While there are examples to support this theory, Temeles et al. (2002) found that hummingbirds may be more opportunistic than previously thought, foraging in flowers with floral tubes longer or shorter than their bill length. In their study, the width of the floral tube opening was a more significant dimension; flowers with wider opening facilitated visits by both long- and short-billed hummingbirds. Thus, flowers of *Aratitiyopea* may accommodate visits by a number of gregarious hummingbird species that are visiting flowers with a variety of morphologies.

Co-occurring plant species that function in concert to exploit resources are termed guilds (Simberloff and Dayan 1991, Endress 1994). Hummingbirds require a year-round supply of nutrients (Stiles 1978, 1981), and guilds are often described for hummingbird-pollinated communities in which staggered flowering is an adaptive strategy (e.g. Stiles 1977, Murray et al. 1987, Kraemer et al. 1993, García-Franco et al. 2001). On Cerro Cuao-Sipapo, *Aratitiyopea* occurs in a Bromeliaceae-Rapateaceae community. In September 2001 flowering along with *Aratitiyopea lopezii* were taxa reported to be hummingbird pollinated (Givnish et al. 2000, Smith 1974): Rapateaceae (*Kunhardtia rhodantha* Maguire and *Stegolepis* spp.), and Bromeliaceae (*Navia mima* L. B. Sm. and *Brewcaria* sp.), while many other Bromeliaceae were sterile.

The southern populations of *Aratitiyopea* occur in the Cordillera del Cóndor in Ecuador and Peru, which is physiognomically similar to the Guayana region, although geologically it is much younger (Foster and Beltran 1997). Several Guayana disjunct species or sibling species occur there (Müller 1973, Foster and Beltran 1997, G. A. Romero-González, pers. com.). The avifaunas of the Venezuelan Guayana (Meyer de Schauensee and Phelps 1978) and the Cordillera del Cóndor, Ecuador and Peru (Parker 1997, Schulenberg and Wust 1997) have in common twelve species and an additional five genera represented by different species of Trochilidae.

Floral phenology and pollination syndromes in Orectanthe, Abolboda, Achlyphila, *and* Xyris.—Descriptions of Xyridaceae pollination syndromes involve Hymenoptera (Kral 1966, 1983;Vogel 1981; Renner 1989; pers. obs.) including buzz-pollination (Renner in Kral 1998); Diptera (Kral 2000, pers. obs.); birds (Vogel 1981, Kral 1998, O. Huber, pers. comm.); Coleoptera (pers. obs.) and wind (Kral 2000). During the course of my field studies surprisingly few pollinators were observed, even in large *Abolboda-Xyris* communities with many open flowers. All taxa produce several to many fertile seeds (Kral 1966, Ramirez and Brito 1990, Kraus et al. 1994, pers. obs.) and, generally, all fruits develop. Even if pollinators are not limited, automatic self-pollination is likely a part of the breeding system for at least some species, due to the very brief flowering periods and concomitant high seed set. Mediated self pollination (geitonogamy) is likely to occur in inflorescences with several flowers open (Lloyd and Schoen 1992), but pollen competition results in varying success of self pollen grains

(Stephenson and Bertin 1983, Wilson and Burley 1983). Ramirez and Brito (1990) conducted controlled breeding system studies in a tropical savanna that included two species of *Xyris*, and found different levels of self compatibility in the two. Although they characterized one of the species as questionably nonautagomous, exclosed inflorescences did produce seed, albeit fewer than in flowers with controlled pollination. Natural pollination is not necessarily invoked by only one means, and seed set could be maximized with a combination of pollination strategies. In neotropical Xyridaceae, flowering is dependent on available water (pers. obs., *V. A. Funk 6261*; MO, US [*Abolboda ciliata* Maguire & Wurdack]). In communities with constant moisture some species of Xyridaceae are fertile at most times. In both constantly wet and seasonally dry regions, two main phenological patterns are expressed, in which some species have a very brief flowering period of a few days to about two weeks, and other species have a longer flowering for one to about three months. These patterns are also present in the temperate species (Kral 1966, Conn and Doust 1997).

Andrenid, bombid (Kral 1966), anthophorid (Kral 1998), and halictid bees (Wall et al. 2002) are reported pollinators of *Xyris* species, and I have observed stingless (non-trigonid) bees, *Bombus*, *Centris*, *Xylocopa*, and syrphid flies on *Xyris*, as well as beetles eating the pollen. The flower (excluding the inconspicuous calyx) is polysymmetric except in a few section *Pomatoxyris* species, in which the androecium is twisted away from the centrally located style (Conn and Doust 1997). The corolla, androecium, and gynoecium are a uniform yellow color. Most *Xyris* species have antesepalous staminodia that are usually distally enlarged, are typically bifurcate, and usually have penicillate, moniliform, hairs. Within a flower, the hairs are uniform, and often abundant, either exceeding the length of the anthers and forming a conspicuous component of the floral display, or located below the anthers, filling the throat of the corolla. Although implicated in secondary pollen presentation (Vogel 1990), this has not been observed (Yeo 1993, pers. obs.), and their precise function is not yet known (Yeo 1993). Hairs of this type have been interpreted as mimicking abundant pollen in Commelinaceae pollen flowers (Vogel 1978, see also Lunau 2000). In addition to being a visual attractant, the hairs increase the surface area of the flower and may serve as insect footholds or to direct their movements, or in pollen collection for either animal or wind mediated pollination (Faden 1992, Endress 1994).

Kral (2000) suggested wind as a main pollination vector, an important mode in open habitats (Proctor 1978, Endress 1994) such as the meadows and savannas in which *Xyris* occur. The branched style with three exserted stigmas could be advantageous to wind-borne pollen capture. The conspicuous, brightly colored corolla is contrary to the anemophilous pollination syndrome as it was initially perceived (see Faegri and van der Pijl 1979); however, species in other families with fully developed corollas are wind pollinated (e.g. Asteraceae). North American species of *Xyris* produce small amounts of pollen (Kral 1983). A large pollen load to allow for unsuccessful pollination is usually associated with anemophilous pollination, but wind pollination has been shown not to be as haphazard as originally thought (Honig et al. 1992). Small, smooth grains, as reported for some species of *Xyris*, are considered advantageous in wind pollination (Wodehouse 1959, Bolick 1990), whereas reticulate sculpturing, found in other *Xyris* species is associated with melittophily (Ferguson and Skvarla 1982, Ruiz and Xena de Enrech 1997).

Because individual flowers of the majority of *Xyris* species have such a short anthesis, I hypothesize that most species are facultative outcrossers, and that the presence of latrorse anther dehiscence in some species (vs. extrorse dehiscence) may indicate a trend toward autonomous self pollination (Wyatt 1983). Pollination is probably effected by either bees and flies, and possibly wind. Flowers pollinated by a variety of insects ('generalists' flowers) require only the basic modifications for entomophily (Proctor 1978) and the trends toward morphological and biological specializations in *Xyris* flowers, such as the staminodial hairs, enantiomorphy, and floral duration may be adaptations for specific pollinators. It would be interesting to investigate if species with specialization for pollinator specificity have a longer anthesis than species with a more generalized flower, and if they have evolved in areas where insects are a limited resource.

Achlyphila disticha is an understory plant of high-elevation cloud forests and is narrowly endemic. Plants flower in the morning (*Kral 71924*) and flowering herbarium specimens were collected in December and February. The yellow, dish-like flowers are slightly monosymmetric and have latrorsely dehiscing anthers that may be versatile (Maguire and Wurdack 1960, but see Kral 1992). The latter two characters are associated with pollination by large animals

(Endress 1994), including butterflies, although nectar, the typical reward associated with psychophily, does not appear to be present. Bees are common in the habitat (Renner 1989) and may be attracted to the corolla, anthers and pollen (see Lunau 2000), and rewarded with pollen.

Nothing is known about pollination in *Abolboda* other than floral traits that can be utilized to infer possible syndromes. Corollas range from less than 1 cm to over 2 cm diameter and are salverform and oriented more or less horizontally, to cucullate-porrect and held vertically. With respect to the orientation of the stamens or the style, some species are monosymmetric while others are polysymmetric. The branched and papillate stigma, often conspicuously colored, and possibly the pollen may be attractants. *Abolboda* floral features are most consistent with melittophily, and the range of morphologies (Fig. 5.4) indicates that several insects may be pollinators.

Amongst Xyridaceae *Orectanthe sceptrum* (Oliv.) Maguire has the most robust flowers in terms of size, with the broadest diameter and the widest corolla tube (8–9 mm). The flower is monosymmetric and the corolla is arched. The porrect corolla is yellow; the exserted stigma that appears to be yellow, is highly branched and plumose. *Orectanthe* is reported to be hummingbird pollinated (Kral 1998; O. Huber, pers. comm.) and according to O. Huber (pers. comm.) the birds often tear the corolla. This predation may explain the evolution of the thickened corolla tube in *Orectanthe*, while all other Xyrids have a uniformly textured corolla. The floral morphology is consistent with melittophily and pollination may be effected by large bees foraging for pollen (see van der Pijl

1954a, b). Flower duration has not been reported for *Orectanthe*, but appears to be less than a day. Herbarium specimen data indicates two main flowering periods in *Orectanthe*: near the end of the dry season (January–February) and near the end of the rainy season (September–October). However, a few specimens were collected out of these ranges, and it is possible that historically *Orectanthe* flowered for much of the year. In the present study a much briefer flowering period was detected in populations of *Orectanthe sceptrum* subsp. *sceptrum* in the Gran Sabana, Bolívar State, Venezuela. Flowering occurred for about two weeks in September, and no winter flowering was observed, although plants at higher elevation are known to flower in February (Brunner 1999; F. Michelangeli, pers. comm.) and may flower more continuously. Changes in floral phenology can be attributed to recent regional climatic fluctuations changes associated with El Niño and global warming, and the dwindling populations due to local human activities.

Dispersal.— The minute to small seeds have no features that suggest means other than passive dispersal by wind and or water. Kral (1966) has observed abundant germination in natural populations of temperate *Xyris* species, indicating that seeds are retained in the population. Dormancy is not required (Kral 1996, pers. obs.), and *Xyris* seeds have longevity (Kral 1996) and high germination rates (Kraus et al. 1994). Germinated seeds of *Aratitiyopea lopezii* were found on wet leaf surfaces below flowers and fruits (pers. obs).

Fossil History

Relative to other angiosperms, monocotyledons are poorly represented in the Cretaceous fossil record, when they are believed to have evolved (Herendeen and Crane 1995; Gandolfo et al. 2000). This may be due to an historic relative diversity comparable to the modern flora (monocots representing 22% of extant angiosperm species; Herendeen and Crane 1995) and that the structures of wind- or insect-pollinated herbaceous plants do not fossilize well (Herendeen and Crane 1995). Mai (1985) reports *Xyris*, probably a seed, from Miocene (ca. 5–20 MYA) northern European wetlands without additional information.

A fossil from the Deccan Intertrappean collected in Mohgaonkalan, M.P., India (22°1'N, 79°11'E; Jain 1964) has been related to *Achlyphila* (Patil 1979). The Deccan Traps are the remains of volcanic activity from the Masstrichian (ca. 65 MYA; Shukla et al. 2001) and are implicated in the mass extinctions observed in the fossil record from the Cretaceous-Tertiary boundary (Courtillot et al. 1988). The Intertrappean materials are primarily cherty limestone and shale. The fossil ascribed to Xyridaceae consists of a vegetative axis with roots and a root-opposed bud (Patil 1979). The flattened axis is about 4–6 times the diameter of *Achlyphila disticha* Maguire & Wurdack. The association with Xyridaceae is questionable as none of the anatomical features described for the fossil are unique to Xyridaceae and no synapomorphies for extant Xyridaceae were presented. Furthermore, the vascular bundles appear to be collateral, rather than concentric (amphivasal) as found in Xyridaceae.

Economic Uses

The family has limited economic use, and it is mostly on a local level. In South America some Xyridaceae infructescences are harvested as dried flowers (Kraus et al. 1994, Giulietti et al. 1996, pers. obs.; see Conservation Status, below). Species of other regionally significant families, Eriocaulaceae (Burman 1991, Giulietti et al. 1996, pers. obs.) and Rapateaceae, are similarly used (Schultes 1954, pers. obs.). The two *Xyris* species naturalized in Hawaii are cultivated for use in dried flower arrangements (Wagner et al. 1990). In Indonesia leaves are woven into mats (Dahlgren et al. 1985) and temple figures (Mabberley 1997). A few *Xyris* species are cultivated ornamentals (Mabberley 1997, Simmons and Conn 1998) and others are used as aquaria plants (Lawrence 1955). Kral (1992) remarked that *Aratitiyopea* "should be cultivated, as it is without question...the most beautiful of the Xyridaceae"; however this will probably not be realized due to the high ambient moisture requirement.

Mucilage from *Xyris* species has been used topically for skin problems (Piso 1648, Seubert 1855, Beumée 1917, Castellanos 1945, Kahn and Ara 1991). *Xyris semifuscata* Bojer ex Baker contains Danthron (1,8-Dihydroxyanthraquinone), a cathartic, in the leaves and stems (Buckingham 1994). Leaves of *Orectanthe* are reported to be used locally as a headache remedy (*J. A. Steyermark 58615*, GH, VEN). The seeds may be dietarily important for wild fowl in North America (Kral 1960, 1966)

Conservation Status

The family is of conservation interest because some taxa are localized and occur in habitats that are threatened by human activities. For example, illegal gold mining activities have caused habitat loss on Cerro de la Neblina on the Venezuela/Brazil border, the only known locality of *Achlyphila disticha* Maguire & Wurdack, two species of *Abolboda*, and four *Xyris* taxa.

Infructescences of several Xyridaceae species are harvested from wild populations for use as dried flowers, a practice that is threatening extirpation or extinction of species in the campos rupestre of Brazil (Burman 1991, Giulietti, et al. 1996). Removing infructescences can lower local seed banks. In the Gran Sabana region of Bolívar state, Venezuela dried *Orectanthe* infructescences are sometimes gathered even though most populations occur on protected land (pers. obs.). Plants are often damaged or even removed during the process, which is of concern because the Gran Sabana populations are already being diminished by intentional burning by indigenous groups (pers. obs.).

In Restionaceae sand-binding roots persist long after the aerial portion of the plant dies, and are considered important substrate stabilizers in fragile, erosion-prone habitats (Pate and Meney 1999) The ecological attributes of sand-binding roots remain to be investigated in Xyridaceae.

The *IUCN Red List* treatment for Xyridaceae (Walter and Gillett 1997) is in need of revision, for example the western hemisphere appears to be largely overlooked as only one species is included. A worldwide monograph of *Xyris* would aid in determining conservation recommendations (cf. Kirschner and Kaplan 2002).

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APPENDIX 1. CHARACTER LIST FOR CLADISITC ANALYSIS.

Details of the data matrix and analysis are presented as follows: Character states are enumerated for each character followed by the individual consistency indices (C.I.) and retention indices (R.I.).

0. Duration: 0 annual, 1 perennial. C.I. = 0.20; R.I. = 0.
1. Habit: 0 plants caulescent. 1 acaulescent.[uninformative].
2. Internodes: 0 condensed, 1 elongate. C.I.= 0.2; R.I. = 0.
3. Phyllotaxy: 0 ranked, 1 spiraled. C.I. = 0.33.; R.I. = 0.87.
4. Leaf morphology: 0 unifacial, 1 bifacial. C.I. = 0.5; R.I. = 0.93.
5. Leaf polymorphism: 0 monomorphic, 1 dimorphic. C.I. = 0.25; R.I. = 0.5.
6. Proportion of epidermis in leaf cross section: 0 shallow, 1 deep. C.I. =0.55; R.I. = 0.66.
7. Hypodermis: 0 absent, 1 present. C.I. = 0.6; R.I. = 0.61.
8. 'Ligule' (see Chapter 4): 0 absent, 1 present. C.I. = 0.25; R.I. = 0.66.
9. Peduncle: 0 a scape, 1 not a scape. C.I. = 0.25; R.I. = 0.
10. Peduncle: 0 glabrous, 1 pubescent. C.I. = 0.5; R.I. =1.0.
11. Inflorescence prophyll: 0 open, 1 closed. C.I. = 1.0; R.I.= 1.0
12. Prophyll: 0 with a lamina, 1 sheath only. C.I. = 0.5; R.I. = 0.66.
13. Peduncle: 0 unribbed, 1 ribbed. C.I. = 1.0; R.I. = 1.0.
14. Scape: 0 noncarinate, 1 carinate. C.I. = 0.5; R.I. = 0.5.
15. Scape sulcate: 0 absent, 1 present. C.I. = 0.5; R.I. = 0.75.
16. Scape bracts: 0 absent , 1 present. C.I. = 0.5; R.I. = 0.93.
17. Number of scape nodes: 0 one, 1 two, 2 many. C.I. = 0.66; R.I. = 0.5.
18. Bract type: 0 cataphyll, 1 foliose. C.I. = 0.5; R.I. = 0.
19. Flower duration: 0 < day, 1 at least one day. C.I. = 1.0; R.I. = 1.0.
20. Inflorescence: 0 simple, 1 compound. C.I. = 0.25; R.I. = 0.0.
21. Pedicel: 0 absent, 1 present. C.I. = 0.5; R.I. = 0.93.
22. Inflorescence bracts: 0 absent, 1 present. C.I. = 0.5; R.I. = 0.94.
23. Involucrum: 0 absent, 1 present. C.I. = 0.5; R.I. = 0.80.
24. Receptacle: 0 glabrous, 1 pubescent. C.I. = 1.0; R.I. = 1.0.
25. Number of flowers per branch: 0 numerous, 1 few (2–6), 2 one. C.I. = 0.28; R. I. = 0.73.
26. Flower size: 0 minute (< 0.5 cm), 1 small to medium (0.5–2.5 cm), 2 large (>3cm). C.I. = 1.0; R.I. = 1.0
27. Floral expression: 0 monoclinous, 1 diclinous. C.I. = 1.0; R.I. = 1.0.
28. Sepal aestivation: 0 valvate, 1 imbricate. C.I. =1.0; R.I. = 1.0.
29. Sepals: 0 monomorphic, 1 dimorphic. C.I. = 0.33; R.I. = 0.60.
30. Median sepal: 0 abaxial, 1 adaxial. C.I. = 1.0; R.I. = 1.0.
31. Number of sepals caducous/aborting: 0 zero, 1 one. C.I. = 0.5; R.I. = 0.83.
32. Corolla fusion: 0 choripetalous, 1 sympetalous. C.I. = 0.5; R.I. = 0.93.
33. Petals clawed: 0 present, 1 absent. C.I. = 0.33; R.I. = 0.
34. Corolla symmetry: 0 monosymmetric, 1 polysymmetric. C.I. = 0.25; R.I. = 0.57.

35. Corolla shape: 0 salverform, 1 porrect, 2 dish, 3 infundibular. C.I. = 0.5; R.I. = 0.66.
36. Petal midvein: 0 absent, 1 present. C.I. = 0.5; R.I. = 0.93.
37. Androecium: 0 uniseriate, 1 biseriate. C.I. = 0.11; R.I. = 0.52.
38. Outer androecium: 0 stamens, 1 staminodia. C.I. = 1.0; R.I. = 1.0.
39.Staminodia type: 0 filamentous, 1 distally enlarged. C.I. = 1.0; R.I. = 1.0
40. Staminodia branching: 0 unbranched, 1 bifurcate, 2 multifurcate. C.I. = 0.5; R.I = 0.77
41. Staminodia adnation: 0 absent, 1 to adjacent corolla lobes. C.I. = 1.0; R.I. = 1.0
42. Inner androecium: 0 hypogenous, 1 epipetalous. C.I. = 0.33; R.I. = 0.80.
43. Connective apex: 0 not sunken, 1 sunken. C.I. = 0.50; R.I. = 0.71.
44. Anther attachment: 0 basifixed, 1 dorsifixed. C.I. = 0.5 ; R.I. = 0.9.
45. Anther dehiscence: 0 latrorse, 1 extrorse, 2 introrse. C.I. =; 0.50, R.I. = 0.85.
46. Pollen shape: 0 spherical, 1 oblong. C.I. = 0.5; R.I. = 0.93.
47. Pollen aperture: 0 inaperturate, 1 sulcate, 2 spiral. C.I. = 1.0; R.I. = 1.0
48. Exine sculpturing 0 echinate (> 1 um but < 3 um), 1 spinose (sensu Erdtman : > 3 um), 2 clavate/baculate, 3 foveolate, 4 reticulate. C.I. = 1.0; R.I. = 1.0.
49. Exine 2° features: 0 spinules (< 1 um), 1 verrucae, 2 pila. C.I. = 0.66; R.I. = 0.75.
50. Placentae: 0 intruded into the locule, 1 not intruded. C.I. =0.5; R. I. = 0.9.
51. Ovule attachment: 0 distal only, 1 throughout the carpel, 2 proximal only. C.I. = 1.0; R. I. = 1.0
52. Ovules per carpel: 0 > one, 1 one. C.I. = 1.0; R.I. = 1.0.
53. Ovule arrangement: 0 biseriate, 1 multiseriate. C.I. = 1.0; R.I. = 1.0.
54. Ovule orientation: 0 anatropous, 1 orthotropous. C.I. = 0.5; R.I. = 0.94.
55. Ovary apex shape: 0 rounded, 1 three-lobed, 2 crested. C.I. = 0.33; R.I. = 0.8.
56. Ovary apex: 0 smooth, 1 tuberculate. C.I. = 0.28 R.I. = 0.76.
57. Style sunken: 0 absent, 1 present. C.I. = 0.33; R.I. = 0.88.
58. Gynoecium appendages: 0 absent, 1 present. C.I. = 0.33; R.I. = 0.89.
59. Appendage location: 0 style, 1 ovary. C.I. = 1.0; R.I. = 1.0.
60. Appendage size: 0 unequal, 1 uniform. C.I. = 1.0; R.I. = 1.0.
61. Appendages horned: 0 absent, 1 present. C.I. = 0.53; R.I. = 0.
62. Number of appendages pendulous: 0 zero, 1 one, 2 two, 3 three. C.I. = 0.4; R.I. = 0.25
63. Style: 0 hollow, 1 solid. C.I. = 0.5; R.I. = 0.83
64. Style: 0 straight, 1 curved (arcuate). C.I. = 0.5; R.I. = 0.88.
65. Style branching: 0 simple, 1 short-branched (stigma), 2 long-branched (stylodia). C.I. = 0.5; R.I. = 0.88
66. Stylar branches: 0 simple, 1 compound. C.I. = 0.5; R.I. = 0.93
67. Fruit: 0 fully dehiscent, 1 apically indehiscent. C.I. = 0.5; R.I. = 0.87.
68. Seed shape: 0 spherical, 1 prismatic, 2 oblong. C.I. = .066; R.I. = 0.95.
69. Pollen color: 0 yellow, 1 white. C.I. = 0.5; R.I. = 0.66.
70. Anthophore: 0 absent, 1 present. [uninformative].

APPENDIX 2. LIST OF SYNONYMY OF *ABOLBODA* HUMB. & BONPL.

As reference for Appendix 3 and application of published names, currently accepted taxa circumscribed now in the genus *Abolboda* are listed alphabetically. Accepted taxa appear in bold italics and synonyms are listed in plain roman. According to article 29 of the International Code of Botanical Nomenclature (Greuter et al., 2000), the nomenclatorial innovation proposed here, indicated with an asterisk, will not be validly published until it appears in an appropriate botanical journal. The effective publication is planned for December 2004 in Brittonia.

Abolboda abbreviata Malme
Abolboda acaulis Maguire
Abolboda acaulis Maguire var. ***acaulis***
Abolboda acaulis Maguire **var. *scaposa*** Kral
Abolboda acicularis Idrobo & L. B. Sm.
Abolboda acicularis Idrobo & L. B. Sm. var. acicularis = ***A. acicularis*** Idrobo & L. B. Sm.
Abolboda acicularis Idrobo & L. B. Sm. var. granularis Maguire = ***A. granularis*** (Maguire) L. M. Campbell*
Abolboda americana (Aubl.) A. Cast. = ***A. americana*** (Aubl.) Malme ex Lanj.
Abolboda americana (Aubl.) Malme ex Lanj.
Abolboda americana (Aubl.) Malme ex Lanj. var. imberbis (H.B.K.) Maguire = ***A. americana*** (Aubl.) Malme ex Lanj.
Abolboda? aubletii Kunth = ***A. americana*** (Aubl.) Malme ex Lanj.
Abolboda bella Maguire
Abolboda brasiliensis A. Cast. = ***A. pulchella*** Humb. & Bonpl.
Abolboda brasiliensis Kunth = ***A. pulchella*** Humb. & Bonpl.
Abolboda chapadensis Hoehne = ***A. poarchon*** Seub. **var. *poarchon***
Abolboda chapadensis Hoehne var. chapadensis = ***A. poarchon*** Seub. **var. *poarchon***
Abolboda chapadensis Hoehne var. pauciflora Hoehne = ***A. poarchon*** Seub. **var. *poarchon***
Abolboda ciliata Maguire & Wurdack
Abolboda dunstervillei Maguire ex Kral
Abolboda ebracteata Maguire & Wurdack
Abolboda ebracteata Maguire **var. *ebracteata***
Abolboda ebracteata Maguire **var. *brevifolia*** Maguire
Abolboda egleri L. B. Sm. & Downs
Abolboda excelsa Malme = ***A. macrostachya*** Spruce ex Malme **var. *robustior*** Steyerm.
Abolboda gleasonii Steyerm. = ***A. grandis*** Griseb. **var. *rigidia*** Malme
Abolboda glomerata Maguire = ***A. ×glomerata*** Maguire (*pro sp.*)
Abolboda gracilis Huber = ***A. pulchella*** Humb. & Bonpl.
Abolboda grandis Griseb.
Abolboda grandis Griseb. fm. angustifolia Miq. = ***A. grandis*** Griseb. **var. *grandis***

Abolboda grandis Griseb. **var.** ***grandis***

Abolboda grandis Griseb. var. guayanensis Maguire = ***A. grandis*** Griseb. **var.** ***rigidia*** Malme

Abolboda grandis Griseb. var. minor Spruce ex Malme = ***A. grandis*** Griseb. **var.** ***grandis***

Abolboda grandis Griseb. **var.** ***rigidia*** Malme

Abolboda granularis (Maguire) L. M. Campbell*

Abolboda imberbis H.B.K. = ***A. americana*** (Aubl.) Malme ex Lanj.

Abolboda inermis Link = ***A. americana*** (Aubl.) Malme ex Lanj.

Abolboda killipii Lasser

Abolboda linearifolia Maguire

Abolboda longifolia Malme = ***A. pulchella*** Humb. & Bonpl.

Abolboda macrostachya Spruce ex Malme

Abolboda macrostachya Spruce ex Malme var. angustior Maguire = ***A. macrostachya*** Spruce ex Malme **var.** ***macrostachya***

Abolboda macrostachya Spruce ex Malme **var.** ***macrostachya***

Abolboda macrostachya Spruce ex Malme **var.** ***robustior*** Steyerm.

Abolboda minima Maguire = ***A. killipii*** Lasser

Abolboda neblinae Maguire

Abolboda paniculata Maguire

Abolboda pervaginata Malme = ***A. grandis*** Griseb. **var.** ***rigidia*** Malme

Abolboda poarchon Seub.

Abolboda poarchon Seub. var. exaltata = ***A. poarchon*** Seub. **var.** ***poarchon***

Abolboda poarchon Seub. **var.** ***intermedia*** (L. B. Sm. & Downs) Kral

Abolboda poarchon var. pauciflora (Hoehne) Hoehne = ***A. poarchon*** Seub. **var.** ***poarchon***

Abolboda poarchon Seub. **var.** ***poarchon***

Abolboda poeppigii Kunth = ***A. americana*** (Aubl.) Malme ex Lanj.

Abolboda psammophila Maguire = ***A. killipii*** Lasser

Abolboda ptaritepuiana Steyerm. = ***Orectanthe ptaritepuiana*** (Steyerm.) Maguire

Abolboda pulchella Humb. & Bonpl.

Abolboda pulchella Humb. & Bonpl. var. intermedia L. B. Sm. & Downs = ***A. poarchon*** Seub. **var.** ***intermedia*** (L. B. Sm. & Downs) Kral

Abolboda pulchella Humb. & Bonpl. var. longifolia (Malme) L. B. Sm. = ***A. pulchella*** Humb. & Bonpl.

Abolboda rigida Gleason = ***A. macrostachya*** Spruce ex Malme **var.** ***robustior*** Steyerm.

Abolboda rigida (Malme) Steyerm. = ***A. grandis*** Griseb. **var.** ***rigida*** Malme

Abolboda scabrida Kral

Abolboda sceptrum Oliv. ex Thurn = ***Orectanthe sceptrum*** (Oliv.) Maguire

Abolboda schultesii Idrobo & L. B. Sm. = ***A. sprucei*** Malme

Abolboda sprucei Malme

Abolboda uniflora Maguire

Abolboda vaginata (Spreng.) Nilsson = ***A. pulchella*** Humb. & Bonpl. (Xyris vaginata Nilsson)

Abolboda* ×*glomerata Maguire (*pro sp.*)

Chloerum gramineum Willd. ex Kunth = ***A. americana*** (Aubl.) Malme ex Lanj.
Chloerum imberbe Willd. ex Steud. = ***A. americana*** (Aubl.) Malme ex Lanj.
(Chloerum imberbe Willd. ex Steud)

Jupica caerulea Raf. 'cerulea' = ***A. americana*** (Aubl.) Malme ex Lanj.
Jupica cerulea Raf. = ***A. americana*** (Aubl.) Malme ex Lanj.

Poarchon caerulea Mart. ex Seub. 'coerulea' = ***A. poarchon*** Seub. **var. *poarchon***
Poarchon coerulea Mart. ex Seub. = ***A. poarchon*** Seub. **var. *poarchon***

Xyris americana Aubl. = ***A. americana*** (Aubl.) Malme ex Lanj.
Xyris caerulea Lam. = ***A. americana*** (Aubl.) Malme ex Lanj.
Xyris vaginata Spreng. = ***A. pulchella*** Humb. & Bonpl.

Literature Cited

Greuter, W., J. McNeil, F. R. Barrie, H. M. Burdet, V. Demoulin, T. S. Filqueiras, D. Nicolson, P. C. Silva, J. E. Skog, and D. L. Hawksworth, eds. 2000. *The International Code of Botanical Nomenclature (St. Louis Code)*. Koeltz Scientific Books, Konigstein, Germany.

APPENDIX 3. TAXONOMIC TREATEMENT OF XYRIDACEAE, EXCLUDING SPECIES OF *XYRIS*

According to Article 29 of the *International Code of Botanical Nomenclature* ([*ICBN*] Greuter et al., 2000), the nomenclatorial innovations proposed here, indicated with an asterisk, will not be validly published until they appear in an appropriate botanical journal. The effective publication is planned for 2004 in Brittonia.

Xyridaceae C. Agardh

Xyridaceae C. Agardh, *Aphor. Bot.* 158. 1823., 'Xyrideae', *nom. conserv.* Type genus: *Xyris* Gronov. ex L.

Abolbodaceae (Suess. & Beyerle) Nakai, Ord. Fam. Trib. Nov. 221. 1943. Abolbodoideae Suess. & Beyerle, Bot. Jahrb. 67: 139. 1935. Type genus: *Abolboda* Humb. & Bonpl.

Aratitiyopea Steyerm. & P. E. Berry

Aratitiyopea Steyerm. & P. E. Berry, Ann. Missouri Bot. Gard. 71: 297. 1984. Type species: *Aratitiyopea lopezii* (L. B. Sm.) Steyerm. & P. E. Berry

1. *Aratitiyopea lopezii* (L. B. Sm.) Steyerm. & P. E. Berry, Ann. Missouri Bot. Gard. 71: 297. 1984. Basionym: *Navia lopezii* L. B. Sm., Bot. Mus. Leafl. 15: 40. 1951. Type: Brazil. Amazonas: Cerro Dimití, upper Río Negro basin, on rocks, ca. 300 m, 12–19 May 1948, *R. E. Schultes & F. López 9956* (Holotype: US; Isotypes: GH; US, 2 sheets).

Note: Although Schultes (1954: 195) cites the authorship as 'L. B. Sm. ex R. E. Schultes', it is clear from the introduction (Schultes 1951: 33) and the protolog that Smith provided the description.

1a. *Aratitiyopea lopezii* (L. B. Sm.) Steyerm. & P. E. Berry

1b. *Aratitiyopea lopezii* (L. B. Sm.) Steyerm. & P. E. Berry var. *colombiana* (L. B. Sm.) Steyerm. & P. E. Berry, Ann. Missouri Bot. Gard. 71: 299. 1984. Basionym: *Navia lopezii* L. B. Sm. var. *colombiana* L. B. Sm., Bot. Mus. Leafl. 16: 195. 1954. Type: Colombia. Vaupés: Río Kananarí, Cerro Isibukuri, on cliff in shade, 250–700 m, 4 August 1951, *R. E. Schultes & I. Cabrera 13342* (Holotype: US; Isotype: COL).

Note: A specimen cited at GH (Kral 1992), has not been located.

Orectanthe Maguire

Orectanthe Maguire, Mem. New York Bot. Gard. 10(1): 2. 1958.Type species: *Orectanthe sceptrum* (Oliv. ex Thurn) Maguire

1. *Orectanthe sceptrum* (Oliv. ex Thurn) Maguire, Mem. New York Bot. Gard. 10(1): 2. 1958. Basionym: *Abolboda sceptrum* Oliv. ex Thurn, Timehri 5: 208. 1886. Type: Guyana: Roraima summit, *E. F. im Thurn 312* (Holotype: K, Isotypes: K, US).

   Orectanthe sceptrum (Oliv. ex Thurn) Maguire subsp. *occidentalis* Maguire, Mem. New York Bot. Gard. 10(1): 5. 1958. Type: Venezuela. Amazonas: Cerro Huachamacari, southeast escarpment, 1900 m, *B. Maguire, R. S. Cowan, & J. J. Wurdack 30140* (Holotype: NY).

2. *Orectanthe ptaritepuiana* (Steyerm.) Maguire, Mem. New York Bot. Gard. 10(1): 5. 1958. Basionym: *Abolboda ptaritepuiana* Steyerm., Fieldiana, Bot. 28: 104. 1951. Type: Venezuela. Bolívar: Ptari-tepui, *Bonnetia roraima* forest, south-west facing shoulder, 2000–2200 m, *J. A. Steyermark 59760* (Holotype: F; Isotypes: GH, VEN).

Note: These two taxa have overlapping distributions, and exhibit morphological intergradation. *Orectanthe ptaritepuiana* appears to be variant expressing several adaptations to high-elevation tepui scrub vegetation. Due to the inaccessibility of where it occurs only herbarium material was available for study, and Maguire (1958) and Kral (1992) are followed here pending additional field work.

Abolboda Humb. & Bonpl.

Abolboda Humb. & Bonpl., *Pl. Aequinoct.* 2: 25, pl. 114. 1813. Type species: *Abolboda pulchella* Humb. & Bonpl.

Chloerum Willd. ex Link, *Jahrb. Gewächsk.* 1, pt. 3: 74. 1820, *nom. inval.* Type species: *Abolboda inermis* Link, *Jahrb. Gewächsk.* 1, pt. 3: 74. 1820, *nom. inval.*

Jupica Raf., *Fl. Tellur.* 2: 15. 1836 [1837]. Type species: *Jupica caerulea* Raf., '*cerulea*'.

Note: *Jupica* Raf. is formed from the Brazilian colloquial name, 'Iupicai' for *Xyris* species (Piso 1648). *Jupica caerulea* Raf. is a superfluous name for *Xyris americana* Aubl. (= *Abolboda americana* (Aubl.) Malme ex Lanj.).

Poarchon Mart. ex Seub., *pro syn.*, in Mart. *Fl. Bras.* 3: 1. 223. 1855. Type species: *Poarchon caerulea* Mart. ex Seub., '*coerulea*'

1. *Abolboda abbreviata* Malme, Ark. Bot. 19(13): 5. 1924. Type: Brazil. Pará: Campos de Ariamba, *A. Ducke 11895* (Lectotype: S; Isolectotypes: K; MG, *n.v.*; NY; RB, *n.v.*; U, *n.v.*; US, 2 sheets. Lectotypified by Kral, 1992).

2. *Abolboda acaulis* Maguire, Bull. Torrey Bot. Cl. 75: 191. 1948. Type: Guyana. Kaieteur Plateau, 30 April 1944, *B. Maguire & D. B. Fanshawe 23096* (Holotype: NY; Isotypes BR; F, *n.v.*; GH, K, MO, NY, S, US, VEN).

2a. *Abolboda acaulis* Maguire var. *acaulis*

2b. *Abolboda acaulis* Maguire var. *scaposa* Kral, Ann. Missouri Bot. Gard. 79: 825. 1992. Type: Venezuela. Bolívar: sandy seeps around rocks at edge of rapateaceous savanna by road, ca. 1.5 km E of Kavanayén, ca. 1200 m, 27 July 1983, *R. Kral & A. C. González 70537* (Holotype: VEN; Isotypes: F, GH, K, MO, NY).

Note: A specimen cited at VEN (Kral 1992), has not been located.

3. *Aboloda acicularis* Idrobo & L. B. Sm., Caldasia 6 (29): 250. 1954. Type: Colombia. Vaupés: Yapoboda, 10 December 1943, *P. H. Allen 3150* (Holotype: US; Isotypes: COL, MO, NY).

4. *Abolboda americana* (Aubl.) Malme ex Lanj., Recueil Trav. Bot. Neerl. 34: 492. 1937. Basionym: *Xyris americana* Aubl., *Hist. Pl. Guiane* 3: 40. 1775. *Xyris caerulea* Lam., *Tabl. Encycl.* 1: 132. 1791, t. 36, f. 1, *nom. superfl. Abolboda? aubletii* Kunth, *Enum. Pl.* 4: 28. 1843, *nom. superfl.* (*nec. syn. Xyris jupicai* Rich.). *Jupica caerulea* Raf., '*cerulea*', *Fl. Tellur.* 2: 15. 1836 [1837]. *Abolboda americana* (Aubl.) A. Cast., *Gen. Sp. Pl. Argent.* 3: 47.1945, *nom. superfl.*, *nom. illegit.* Type: French Guiana. 'Habitat in locis paludosis, praefertim *Macouria*, florebat Decembri, 1775', *J. B. C. Aublet s.n.* (Lectotype: P; Isolectotype: BM. Lectotypified by Kral, 1992).

Abolboda imberbis H.B.K., Nov. Gen. Sp. 6: 256. 1815 [1816]. *Abolboda inermis* Link, *Jahrb. Gewächsk.* 3, pt. 1: 74. 1833, *nom. inval. Chloerum imberbe* Willd. ex Steud., *Nomencl. Bot.* ed. 2, 1: 2. 1840, *pro syn. Chloerum gramineum* Willd. ex Kunth, *Enum. Pl.* 4: 27. 1843, *pro syn. Abolboda americana* (Aubl.) Malme ex Lanj. var. *imberbis* (H.B.K.) Maguire, Bull. Torrey Bot. Cl. 75: 193. 1948. Type: Venezuela. Amazonas: 'crescit in arenosis Guayanae ad flumen Atabapo, ♃, Floret Majo', *F. A. Humboldt & A. Bonpland 1099* (Type: B-W, Willdenow #1068).

Note: Link's epithet *inermis* ('unarmed') is probably a transcription mistake and should have been *imberbe* ('unbearded'), referring to the lack of bearded staminodes typical of most *Xyris* species. Although Link applied the epithet to *Abolboda* he referred the entity to the new genus *Chloerum*.

Abolboda poeppigii Kunth, Enum. Pl. 4: 27. 1843. Type: Brazil. 'Rio Pará. Poeppig in herb. Lucaeano' Lectotype: *E. F. Poeppig 2993*, B; F; G, n.v. (photograph: NY); M, P; S. Lectotypified by Kral, 1992).

Note: The collection Kunth cited had an original identification of *Abolboda imberbis*. Lanjouw (1937) cited a possible Poeppig collection (*s.n.*, B) given to Kunth by Lucae. A. F. T. Lucae's herbarium at KIEL (see de Candolle 1880, Stafleu and Cowan 1981: 179) has been destroyed (H. Usinger, pers. comm.; see also Stafleu and Cowan 1981: 179); however a specimen from GOET bearing a *Universitatis Kiliensis* label matches the type data. Possible type material is being sought from B, LE, and W, where other 'important' sets of Poeppig's collections are reported as being housed (Stafleu and Cowan 1983: 310). Kral (1992) cited the type collection as *E. F. Poeppig 2993*, with specimens at B, F, M, P, and a photograph at NY.

5. *Abolboda bella* Maguire, Mem. New York Bot. Gard. 10(1): 15. 1958. Type: Venezuela. Amazonas: Yapacana Savanna III, 125 m, 17 March 1953, *B. Maguire & J. J. Wurdack 34514* (Holotype: NY; Isotypes: NY, S, US, VEN).

6. *Abolboda ciliata* Maguire & Wurdack, Mem. New York Bot. Gard. 10(1): 17. 1958. Type: Venezuela. Amazonas, Cerro de la Neblina, in boggy open cumbre savanna, 5 km west Cumbre Camp, 1900 m, 6 January 1954, *B. Maguire, J. J. Wurdack & G. S. Bunting 37132* (Holotype: NY; Isotypes: NY, US, VEN).

7. *Abolboda dunstervillei* Maguire ex Kral, Ann. Missouri Bot. Gard. 79: 851. 1992. Type: Venezuela. Amazonas: summit of Cerro Avispa, Río Siapa, 1°30'N, 65°51'W, 5 December 1972, *G. C. K. & E. Dunsterville s.n.* (Holotype: NY; Isotype: VEN).

8. *Abolboda ebracteata* Maguire & Wurdack, Mem. New York Bot. Gard. 10(1): 17. 1958. Type: Venezuela. Amazonas: Yapacana Savanna III, 125 m, 31 December 1950, *B. Maguire, R. S. Cowan, & J. J. Wurdack 30469* (Holotype: NY; Isotypes: NY, S, US, VEN).

8a. *Abolboda ebracteata* Magurie & Wurdack var. *ebracteata*

8b. *Abolboda ebracteata* Maguire & Wurdack var. *brevifolia* Maguire, Mem. New York Bot. Gard. 10(5): 8. 1964. Type: Venezuela. Amazonas: Sabana de

Moyo, right hand bank of Río Orinoco, 10 km above mouth of Río Ventuari, 125 m, 31 July 1959, *J. J. Wurdack & L. S. Adderley 43689* (Holotype: NY; Isotypes: GH; M; NY; S; US; VDB, *n.v.*).

9. *Abolboda egleri* L. B. Sm. & Downs, Proc. Biol. Soc. Wash. 73: 258. 1960. Type: Brazil. Pará: Ererreri, Rio Cururú, region of the upper Rio Tapajós, 8 February 1960, *W. A. Egler & Raimundo 1271* (Holotype: US; Isotypes: MG; NY, 2 sheets).

10. *Abolboda* ×*glomerata* Maguire (*pro sp.*), Mem. New York Bot. Gard. 10(1): 14. 1958. Type: Venezuela. Amazonas: Sabana Venado, left bank Caño Pimichín, affluent Río Guainía, 140 m, 14 April 1953, *B. Maguire & J. J. Wurdack 35593* (Holotype: NY; Isotypes: US, VEN).

Note: This entity is a delicately-leaved rhizomatous *Abolboda* with a congested, branched inflorescence that appears to produce only bracts and sepals (Maguire 1958, Kral 1992, pers. obs.). At the time of his revision, Kral (1992) knew of only specimens from the type locality; however, there is another similarly sterile collection (*J. A. Steyermark et al. 113831*, VEN) from approximately 740 km north-northeast of the type locality. Kral interpreted this *Abolboda* as a sterile hybrid, and proposed *A. linearifolia* and *A. macrostachya* var. *macrostachya* as putative parents. *Abolboda linearifolia* is known from only a few localities, but is proximate to both populations of *A.* ×*glomerata*, which is morphologically more similar to *A. grandis* than *A. macrostachya*.

11. *Abolboda grandis* Griseb., Linnaea 21: 281. 1848. Type: Surinam: 'In arenosis prope Joden-Savanna (Cordonpad), fl Novembri', *H. A. Kegel 1131* (Holotype: GOET).

11a. *Abolboda grandis* Griseb. var. *grandis*

Abolboda grandis Griseb. var. *minor* Spruce ex Malme, Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26, Afd. 3(19): 14. 1901. Type: Brazil: 'Provincia Rio Negro (nunc Alto Amazonas) prope Bara s. Manaos, July 1851', *R. Spruce 1654* (Holotype: K; Types: BM, BR, NY, S [fragment]).

Abolboda grandis Griseb. forma *angustifolia* Miq., *Stirp. Surinam. Select.* 218. 1851. Type: *F. W. Hostmann 1319* (Holotype: GOET; Isotype: GH).

11b. *Abolboda grandis* Griseb. var. *rigida* Malme, Bull. Torrey Bot. Club 58: 326. 1931. (*Abolboda grandis* 'Miq.' var. *rigida* Malme). Type: Venezuela. Amazonas: [Cerro Duida] Brocchinia Hills, 4500 ft., *G. H. H. Tate 586* (Holotype: NY; Isotypes: F, NY, S [fragment]).

Abolboda rigida (Malme) Steyerm., Fieldiana, Bot. 28: 105. 1951, *non Abolboda rigida* Gleason, 1929. *Abolboda gleasonii* Steyerm., Fieldiana, Bot. 28: 820. 1957, *nom. nov.*

Abolboda pervaginata Malme, Ark. Bot. 25A (12): 16. 1933. Type: Brazil. Pará: 'Campos de Ariamba, in regione medii fluminis Trombetas, in uliginosis frequentissime, 12 April 1910', *A. Ducke 11352* [MG #18967] (Lectotype: S; Isolectotypes: G, *n.v.* (photograph: NY); K; MG; RB, *n.v.*; S; US. Lectotypified by Kral, 1992).

Abolboda grandis var. *guayanensis* Maguire, Mem. New York Bot. Gard. 10(1): 8. 1958. Type: Venezuela. Amazonas: Cerro Sipapo, Campo Grande, 1500 m, 8 December 1948, *B. Maguire & L. Politi 27561* (Holotype: NY; Isotypes: NY, S, US, VEN).

12. *Abolboda granularis* (Maguire) L. M. Campbell, *stat. et comb. nov.** *Abolboda acicularis* var. *granularis* Maguire, Mem. New York Bot. Gard. 10(1): 17. 1958. Type: Venezuela. Amazonas: Sabana Venado, left bank Caño Pimichín, above Puerto Pimichín, 140 m, 23 November 1953, *B. Maguire, J. J. Wurdack & G. S. Bunting 36341* (Holotype: NY; Isotypes: S, US, VEN).

13. *Abolboda killipii* Lasser, Bol. Soc. Venez. Ci. Nat. 9 (59): 178. 1944. Type: Venezuela. Bolívar: sabanas fangosas cerca del Río Tonoro, Alto Paragua, 20 August 1943, *F. Cardona 832* (Holotype: VEN; Isotypes: F, NY, US).

Abolboda psammophila Maguire, Bull. Torrey Bot. Club 75: 193. 1948. Type: Surinam. West side of railway, Zanderij II, 3 June 1944, *B. Maguire & G. Stahel 23667* (Holotype: NY; Isotypes: A, NY, U, *n.v.*).

Abolboda minima Maguire, Mem. New York Bot. Gard. 10(5): 7. 1964. Type: Venezuela. Amazonas: Río Atabapo, Sabana Manacal, 15 km above Guarinumo, 125–140 m, 12 June 1959, *J. J. Wurdack & L. S. Adderley 42977* (Holotype: NY; Isotypes: GH, NY, S, US, VEN).

14. *Abolboda linearifolia* Maguire, Mem. New York Bot. Gard. 10(1): 14. 1958. Type: Venezuela. Amazonas: Yapacana Savanna III, 125 m, 31 December 1950, *B. Maguire, R. S. Cowan, & J. J. Wurdack 30468* (Holotype: NY; Isotypes: F, M, NY, S, US, VEN).

15. *Abolboda macrostachya* Spruce ex Malme, Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26, Afd. 3(19): 15. 1901. Type: Venezuela. Amazonas: 'prope Esmeralda, ad flumen Orenoco, 18 December 1853', *R. Spruce 3229* (Lectotype: S, Isolectotypes: BM; BR; GOET; K, 2 sheets; NY; P, *n.v.*; S (fragment); W, *n.v.* (photographs: F, MO). Lectotypified by Kral, 1992.).

Note: The lectotype is a fragment ('ex orig.') including fruit parts, seeds, and a peduncle bract or part of a leaf.

15a. *Abolboda macrostachya* Spruce ex Malme var. *macrostachya*

Abolboda macrostachya Spruce ex Malme var. *angustior* Maguire, Mem. New York Bot. Gard. 10(1): 10. 1958. Type: Venezuela. Amazonas: Caño Pimichín, aff. Río Guainía, Sabana Venado, 140 m, 23 November 1953, *B. Maguire, J. J. Wurdack & G. S. Bunting 36342* (Holotype: NY; Isotypes: GH, M, NY, S, US, VEN).

15b. *Abolboda macrostachya* Spruce ex Malme var. *robustior* Steyerm., Fieldiana, Bot. 28: 104. 1951. Type: Venezuela. Bolívar: Gran Sabana, between Mission of Santa Teresita de Kavanayén, northwest to Río Karuai, on large mesa, 1220 m, 26 October 1944, *J. A. Steyermark 59349* (Holotype: F, 2 sheets).

Note: A specimen cited at VEN (Kral 1992), has not been located.

Abolboda rigida Gleason, Bull. Torrey Bot. Cl. 56: 16. 1929. Type: British Guiana, *R. H. Schomburgk 146.S* (Lectotype: K, right-hand element. Lectotypified by Kral, 1992).

Note: The protolog cites the collection number as *146.5.* Robert Schomburgk's '.S' collection series denotes single plant collections, and the letter is often mistaken for the number five (Romero-González and Campbell 2001, van Dam 2002).

Abolboda excelsa Malme, Ark. Bot. 25A (12): 16. 1933. Type: Venezuela: Bolívar: Río Cuquenan [Kukenán], in paludibus ad Quewewoda, February 1910, *E. Ule 8545.* (Lectotype: K; Isolectotypes: L, *n.v.*; MG; S (fragment). Lectotypified by Kral, 1992).

Note: The type of *A. excelsa* (*E. Ule 8545*) was referred to *A. macrostachya* Spruce ex Malme by Malme in 1914. This reference was subsequently listed in a format similar to synonymy (Malme 1933), resulting in an erroneous author citation for the latter species as Malme ex Pilger, 1914 non Spruce ex Malme, 1901.

16. *Abolboda neblinae* Maguire, Mem. New York Bot. Gard. 17: 80. 1967. Type: Venezuela. Bolívar: Cerro de la Neblina, 2 km east of Boundary Marker No. 4, 1 November 1965, *B. Maguire, J. M. Pires & C. K. Maguire 60523* (Holotype: NY; Isotypes: F; GH; K; M; NY; UB, *n.v.*; US; VEN).

Note: The type-set specimen labels say Brazil and include C. K. Maguire as a collector, but the protolog specifies Venezuela and lists Nilo T. Silva rather than C. K. Maguire.

17. *Abolboda paniculata* Maguire, Mem. New York Bot. Gard. 10(1): 10. 1958. Type: Venezuela. Amazonas: Cerro Parú, 2000 m, 10 February 1951, *R. S. Cowan & J. J. Wurdack 31387* (Holotype: NY; Isotypes: US, VEN).

18. *Abolboda poarchon* Seub., *Fl. Bras.* 3(1): 223. 1855. *Poarchon caerulea* Mart. ex Seub., *pro syn.*, *Fl. Bras.* 3(1): 223. 1855, '*coerulea*'. Type: Brazil. Minas Gerais: 'campis ascensus Chapado do Paranán', *C. Martius 1728* (Lectotype: M, *n.v.* Lectotypified by Kral, 1992. Syntype: Brazil. Goías. *G. Gardner 3486*, F, G (2 sheets), GH, K (3 sheets), NY).

18a. *Abolboda poarchon* Seub. var. *poarchon*

Abolboda chapadensis Hoehne, *Com. Lin. Telegr., Bot.* 11. 1915. Type: Brazil. Matto Grosso: 'In pratis paludosis in montis Chapada, prope fluminem Taquara-ussú; floret mense Martio'. *F. C. Hoehne 3597* (Lectotype: R, *n.v.* (photograph: US); Isolectotype: SP, *n.v.*; Syntypes: *F. C. Hoehne 3597,* R, *n.v.*; SP, *n.v.*; *3598*; R, *n.v.*; SP, *n.v.* Lectotypified by Kral, 1992).

Abolboda chapadensis Hoehne var. *pauciflora* Hoehne, *Com. Lin. Telegr., Bot.* 12. 1915. *A. poarchon* Seub. var. *pauciflora* (Hoehne) Hoehne, *Ind. Bibliogr. Com Rondon.* 144. 1951. Type: Brazil. Matto Grosso: 'In pratis inundatis prope Coxim; floret mense Junio'. *F. C. Hoehne 3595* (Lectotype: R, *n.v.* (photograph: US); Isolectotype: SP, *n.v.*; Syntype: *F. C. Hoehne 3596*: R, *n.v.*; SP, *n.v.* Lectotypified by Kral, 1992).

Note: The text of *Commissão de Linhas Telegáphicas Estratégicas de Matto Grosso ao Amazonas (Annexo n. 5, Historia Natural, Botanica)* cites collections by number only, and the collectors' names are listed on pages 6–7. See also a separate index published later (Hoehne, 1951). Kral (1992: 859) cited the collector as com Rondon. According to Stafleu and Cowan (1979) Hoehne's type specimens are at SP.

Abolboda poarchon Seub. var. *exaltata* Maguire ex Malme, *pro syn.*, Mem. New York Bot. Gard. 10(1): 15. 1958. Type: not designated.

Note: This name was based on *A. Glaziou 22233* (S).

18b. *Abolboda poarchon* Seub. var. *intermedia* (L. B. Sm. & Downs) Kral, Ann. Missouri Bot. Gard. 79: 860.1992. Basionym: *Abolboda pulchella* Humb. & Bonpl. var. *intermedia* L. B. Sm. & Downs, Arq. Bot. Estado São Paulo, n.s., Vol. 4 (2): 26. 1966. Type: Brazil. Minas Gerais: Carandaí–Brejão, 28 November 1946, *A. P. Duarte 682* (Holotype: US; Isotype: RB, *n.v.*).

19. *Abolboda pulchella* Humb. & Bonpl., *Pl. Aequinoct.* 2: 110, pl. 114. 1813. Type: Venezuela. Amazonas: 'Habitat in locis humidis, prope Maypures, ad Orinocum'. *F. A. Humboldt & A. Bonpland 1114* (Lectotype: B-W #1067).

Note: Kral (1992) suggested the plate for a lectotype, but did not designate it according to the *International Code of Botanical Nomenclature* (Greuter, et al. 2000). The *Herbarium Humboldt, Bonpland et Kunth* [microform] (1968, see also Burns-Balogh 1988) does not include a specimen of *Abolboda*, and no specimen was found by staff at P.

Xyris vaginata Spreng., *Syst. Veg.* 182. 1825. *Abolboda vaginata* (Spreng.) Nilsson, Bih. Kongl. Svenska Vetensk.-Akad. 24 (14): 63. 1891. *Abolboda brasiliensis* Kunth, *Enum. Pl.* 4: 26. 1843. *Abolboda brasiliensis* A. Cast., *nom. superfl.*, *nom. illegit. Gen. Sp. Pl. Argent.* 3: 47. 1945. Type: 'Brasilia meridionalis, inter Minas et St. Paulo', *F. W. Sello* (Lectotype: BR, Isolectotypes: G, HAL; K, 2 sheets; L, *n.v.*; S. Lectotype based on *A. brasiliensis* Kunth, Kral 1992).

Note: Nilsson cited one collection when forming the combination *Abolboda vaginata*: 'Inter Minas et São Paulo in arenosis palustribus camporum Araraquara, *G. Gardner 4824*'. Kral (1992: 846) proposed *G. Gardner 4024* as a lectotype (Goiás: 'marsh Lima de Natividade, July 1840', [Lectotype: K; Isolectotype: NY]); however that collection would be a neotype as the Gardner specimen was collected after 1825. Sprengel's name was probably based on a Sello collection, also the type of *A. brasiliensis* Kunth. The HAL, K, S, specimens have the collection number *223*.

Abolboda longifolia Malme, Bih. Kongl. Svenska Vetensk.-Akad. Handl. 22, Afd. 3 (2): 20. 1896. *Abolboda pulchella* Humb. & Bonpl. var. *longifolia* (Malme) L. B. Sm. & Downs, Arq. Bot. Estado São Paulo 4(2): 26. 1966. Type: Brazil. Matto Grosso: inter São Jeronymo et Cuyabá, prope Arecá, 200–300 m, 17 February 1894, *G. O. A. Malme 1402* (Lectotype: S; Isolectotypes: G, S. Lectotypified by Kral, 1992).

Abolboda gracilis Huber, Bol. Mus. Paraense Hist. Nat. 5: 323. 1909. Type: Brazil: Campos do Ariramba, 22 August 1906, *A. Ducke 8074* (Lectotype: MG. Lectotypified by Kral, 1992).

20. *Abolboda scabrida* Kral, Ann. Missouri Bot. Gard. 76: 975. 1989. (*non* Ann. Missouri Bot. Gard. 79: 1992). Type: Venezuela. Amazonas: Dept. Río Negro, Cerro Aracamuni, summit, Proa Camp, 01°32'N, 65°49'W, 1400 m, 28 October 1987, *R. Liesner & G. Carnevali 22598* (Holotype: VEN; Isotypes: MO; NY, 2 sheets; VDB, *n.v.*).

21. *Abolboda sprucei* Malme, Ark. Bot. 25A (12): 17. 1933. Type: Venezuela. Amazonas: 'ad flumen Guainía v. Río Negro, supra ostium fluminis Casiquari', 1884, *R. Spruce 3546* (Lectotype: K; Isolectotypes: BR; K, 2 sheets; P; S. Lectotypified by Kral, 1992).

    Abolboda schultesii Idrobo & L. B. Sm., Caldasia 6 (29): 246. 1954. Type: *R. E. Schultes, R. E. D. Baker, & I. Cabrera 18177* (Holotype: COL, *n.v.*; Isotypes: GH; US, 2 sheets).

22. *Abolboda uniflora* Maguire, Mem. New York Bot. Gard. 10(1): 12. 1958. Type: Venezuela. Amazonas: Cerro Duida, Brocchinia Hills, 1700–1980 m, 1 September 1944, *J. A. Steyermark 58169* (Holotype: F; Isotype: NY, 2 sheets).

Excluded Name

'*Albolboa*' Hieron. is listed by Airy Shaw in Willis (1966) but not found in Hieronymous publications at NY. The name may be from an index or list, perhaps at K.

Achlyphila Maguire & Wurdack

Achlyphila Maguire & Wurdack, Mem. New York Bot. Gard. 10(2): 12. 1960.Type species: *Achlyphila disticha* Maguire

1. *Achlyphila disticha* Maguire & Wurdack, Mem. New York Bot. Gard. 10(2): 12. 1960. Type: Venezuela. Amazonas: Cerro de la Neblina, upper Cañon [sic] Grande Basin, 2000 m, 14 December 1957, *B. Maguire, J. J. Wurdack, & C. K. Maguire 42402* (Holotype: NY; Isotypes: F, GH, K, NY, US, VEN).

Xyris Gronov. ex L.

Xyris Gronov. ex L., *Gen. Pl.* 5 ed. 25. 1754.Type species: *Xyris indica* L.

Xyroides A. Thouars., *Gen. Nov. Madagasc.* 4. 1806, *nom. superfl.* Type species: none designated.

Xyris Adans., *Fam. Pl.* 2: 220. 1763. *Kotsjiletti* Adans., *Fam. Pl.* 2: 60. 1763., *nom. superfl.* Type species: none designated

Note: *Kotsjiletti* was based on van Rheede's (1689: 139, t. 71) *Kotsjiletti-pullu* for *Xyris indica* L.

Ramotha Raf., *Fl. Tellur.* 2: 15. 1836 [1837]., *nom. superfl.* Type species: none designated.

Note: *Ramotha* is based on Hermann's (1726) 'Ranmotha'.

Synoliga Raf., *Fl. Tellur.* 2: 15. 1836 [1837]. Type species: *Xyris subulata* Ruiz & Pav., designated here.*

Xuris Raf., *Fl. Tellur.* 2: 14. 1836 [1837]., *nom. illegit.* Type species: none designated.

Note: Rafinesque intended to correct Linneaus's *Xyris*, Greek for *Iris*, however, he explicitly excluded the type species of *Xyris* L. Thus, according to Article 53.3 of the *ICBN Xuris* Raf. is to be treated as a later homonym.

Schismaxon Steud., Bot. Zeit. 14: 391. 1856, *nom. nud.* Type species: *Schismaxon distichioides* Steud., *nom. nud.*

Note: According to Heimerl (1906) *W. Lechler 2598* (W) was identified as *Schismaxon distychioides* Steud., and matches the plate of *X. subulata* Ruiz & Pav. var. *macrotona* Nilsson (Nilsson 1892: t. 2, f. 4).

Xyris L. section *Xyris*

Xyris L. section *Pomatoxyris* Endl., *Gen. Pl.* 124. 1836.Type species: *Xyris operculata* Labill.

Xyris L. section *Nematopus* Seub., *Fl. Bras.* 3(1): 211. 1855.Type species: 'Tab. 28. Diagramma.'

Note: Plate 28 includes two sect. *Nematopus* species, *X. consanguinea* Kunth and *X. hystrix* Seub., and neither is specified as the source for the accompanying floral diagram. According to Article 10.1 (*ICBN*), the type of a genus subdivision is the type of a species name, thus section *Nematopus* Seub. needs to be lectotypified accordingly.

Excluded Name

Xyris L. section *Australoxyris* P. Royen, Blumea 7: 478. 1954.Type species: *Xyris nigromucronata* P. Royen

Note: *Xyris nigromucronata* P. Royen = *Borya nitida* Labill. (Liliaceae)

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APPENDIX 4. PUBLISHED ACCOUNTS OF XYRIDACEAE POLLEN MORPHOLOGY.

Species	Reference
Abolboda acaulis Maguire	Carlquist 1960
Abolboda acicularis Idrobo & L. B. Sm. *var. acicularis*	Carlquist 1960
Abolboda bella Maguire	Carlquist 1960
Abolboda ebracteata Maguire & Wurdack	Carlquist 1960
Abolboda grandis Griseb. *var. guayanensis* Maguire	Carlquist 1960
Abolboda linearifolia Maguire	Carlquist 1960
Abolboda macrostachya Spruce ex Malme *var. macrostachya*	Carlquist 1960
also as *A. macrostachya* var. *angustior* Maguire	Carlquist 1960
Abolboda macrostachya Spruce ex Malme *var. robustior* Steyerm.	Carlquist 1960
Abolboda poarchon Seub.	Kuprianova 1948, Erdtman 1952
Abolboda pulchella Humb. & Bonpl.	Erdtman 1952
Abolboda sprucei Malme	Carlquist 1960
Achlyphila disticha Maguire	Carlquist 1960, Maguire and Wurdack1960
Aratitiyopea lopezii (L. B. Sm.) Steyerm. & P.E. Berry	Nowicke in Steyermark 1984
Orectanthe ptaritepuiana (Steyerm.) Maguire	Carlquist 1960
Orectanthe sceptrum (Oliv. ex Thurn) Maguire	Malme 1933, Carlquist 1960
Xyris anceps Lam.	Straka and Friedrich 1984
Xyris capensis Thunb.	Erdtman 1952, Sharma 1967
Xyris caroliniana Walter	Erdtman 1952
Xyris formosa Hayata	Huang 1972
Xyris frondosa Maguire & L. B. Sm.	Salgado-Labouriau and Villar de Seoane 1992
Xyris humilis Kunth	Straka and Friedrich 1984

Xyris jupicai Rich.	Cruz-Barros 2000
Xyris pauciflora Willd.	Govindapa 1956
Xyris rupicola Kunth	Erdtman 1952
Xyris savanensis Miq.	Cruz-Barros 2000
Xyris schizachne Mart.	Cruz-Barros 2000
Xyris smalliana Nash	Erdtman 1952
Xyris teres Nilsson	Cruz-Barros 2000
Xyris tortula Mart.	Cruz-Barros 2000
Xyris umbilonis Nilsson	van Zinderen Bakker 1953
Xyris wallichii Kunth	Sharma 1967
Xyris sp. (‘*alpestris*’)	Kuprianova 1948
Xyris sp. (‘*eriantha*’)	Kuprianova 1948

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APPENDIX 5. *XYRIS* TAXA EXAMINED FOR CHROMOSOME NUMBER.

Taxon	Reference
X. ambigua Beyer ex Kunth	3
X. archeri L. B. Sm. & Downs	1
X. asperula Mart.	1
X. baldwiniana Schult.	3
X. bialata Malme	1
X. bracteata R. Br. (as *X. gracilis* R. Br. subsp. *laxa* O. Evans)	2
X. brevifolia Michx.	3
X. capensis Thunb.	10
X. capensis Thunb. var. *schoenoides* (Mart.) L. A. Nilsson	5
X. caroliniana Walt.	3
X. complanta R. Br.	5
X. diamantinae Malme	1
X. difformis Chapm.	7
X. difformis Chapm. var. *curtissii* (Malme) Kral	3
X. difformis Chapm. var. *difformis*	3
X. difformis Chapm. var. *floridana* Kral	3
X. drummondii Malme	3
X. ellottii Chapm.	3,8
X. fimbriata Elliott	3
X. flabelliformis Chapm.	3
X. gracilis R. Br. subsp. *gracilis*	2
X. gracilis subsp. *gracilis-laxa* integrade	2
X. indica L.	9,11
X. iridifolia Chapm.	3
X. itatiayensis (Malme) Wand. & M. G. Sajo	1
X. jolyi Wand. & T. M. Cerati	1
X. juncea R. Br.	2
X. laxifolia Mart.	1
X. longiscapa L. A. Nilsson	1
X. itatiayensis (Malme) Wand. & M. G. Sajo	1
X. mello-barretoi L. B. Sm. & Downs	1
X. muelleri Malme	2, 6
X. operculata Labill.	2
X. pilosa Kunth	1
X. platylepis Chapm.	7
X. serotina Chapm.	3
X. smalliana Nash	3
X. stricta Chapm.	3
X. tasmanica (D.I. Morris) A. N. Doust & B. J. Conn	2
X. tennesseensis Kral	4

X. torta J. E. Smith	7, 8
X. tortula Mart.	1
X. sp.	5

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