ABSTRACT

A REVISION OF CARIBBEAN *ADIANTOPSIS*

by MICHAEL SHANE BARKER

*Adiantopsis* is a tropical cheilanthoid fern genus that unlike other cheilanthoid genera, is unstudied. The present work evaluated the taxonomy and relationships among Caribbean *Adiantopsis*. A total of 136 characters were examined on approximately 500 herbarium specimens. This study identified nine Caribbean *Adiantopsis* species, of which three are newly discovered. Additionally, an intriguing pattern of morphological and reticulate evolution was revealed by the analyses. *Adiantopsis* consists of three different lamina morphologies; palmate, pedate, and pinnate. The two pedate taxa are hypothesized to be fertile allotetraploid derivatives of the single palmate *A. radiata* and two different pinnate taxa. In this regard they parallel the origin of the South American *A. ×austropedata*. Thus, it appears that the pedate lamina morphologies in *Adiantopsis* are convergent, having originated multiple times via hybridization. This study provides testable hypotheses of morphological and reticulate evolution in the genus and presents a novel view of Caribbean *Adiantopsis*. 

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A REVISION OF CARIBBEAN *ADIANTOPSIS*

A Thesis

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Department of Botany

by

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This thesis is dedicated to my parents, who have always supported me in my research pursuits.
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INTRODUCTION

Adiantopsis Fée is a cheilanthoid fern genus found throughout tropical America (Tryon and Tryon, 1982) and possibly Africa (Moran and Smith, 2001). It is distinguished from other cheilanthoid genera by a combination of echinate spores, distinct pseudoindusia, adaxial carinae, and unique catenate-capitate hairs on the axes and laminae surfaces. Relative to other cheilanthoid genera, a paucity of information exists about Adiantopsis. Likely contributing to this lack of knowledge is the general rarity of Adiantopsis taxa. Many taxa are limited to narrow ecological niches, such as serpentine soils, and these taxa do not appear to disperse the great distances of other fern taxa (Tryon, 1970). Most Adiantopsis taxa occur in alkaline forests, thickets, and cliffs, but at least one species is restricted to acidic substrates. In the Caribbean, Adiantopsis is a genus primarily of calcareous forests and cliffs. Historically, the genus includes seven species, four of which occur in the Caribbean, predominantly in Cuba and Jamaica (Tryon and Tryon, 1982).

Adiantopsis has never been monographed or entirely revised. It is one of many small, overlooked tropical fern genera that have not recently or ever been examined using formal taxonomic methods. Holttum (1975) recognized this problem nearly 30 years ago, and called for “New total monographs...to reveal the kinds of groups which can be tackled by the methods of biosystematics.” One reason for studying Adiantopsis was simply to describe and enumerate the taxa present, to provide a “total monograph” and bring our knowledge of this genus up to that of more well studied genera. Such knowledge is a prerequisite for future systematic, molecular, and evolutionary research on Adiantopsis. Additionally, a complete monograph of Adiantopsis will provide data for the eventual reorganization of the polyphyletic Cheilanthes Sw. (Gastony, pers. comm.) into a natural (i.e., monophyletic) classification scheme, something that is not possible without a monographic treatment of Adiantopsis and other understudied elements of Cheilanthes.

Adiantopsis possesses a striking range of lamina morphology. The laminae may be palmate (radiate), pedate, or pinnate. This range of variation does not occur in many other fern genera, especially not one as small as Adiantopsis. However, without at least an understanding of the species present in the genus, understanding the origin of this
variation is not possible. Thus, another reason for studying *Adiantopsis* is to develop and evaluate hypotheses about the origin of these lamina morphologies.

The research presented in this thesis is a component of a larger monograph on *Adiantopsis* that is under preparation. In this thesis, a taxonomic revision of the Caribbean *Adiantopsis* taxa is presented; the Central and South American taxa will be included in the final publication of the monograph. Although this taxonomic treatment deals only with the Caribbean species, the aspects of *Adiantopsis* biology discussed in this thesis applies to the entire genus.

**Materials and Methods**

For this research, approximately 500 specimens were examined from 14 herbaria (Table 1). A total of 136 characters were scored for each species. For the most part, morphological characters were recorded without disturbing the specimen, and were collected by eye or with the aid of a dissecting microscope. The methodology for describing characters requiring special preparation are described below.

For length and width measurements, scales of the rhizome, stipe, and rachis were mounted in Hoyer’s solution (Anderson, 1954) on a microscope slide. Measurements were made on an Olympus BH-2 compound light microscope. Scales were only collected from specimens with numerous scales, so that specimens would still possess scales for future research.

Guard cell measurements were made with a compound light microscope using prepared laminar tissue. Ultimate divisions were collected from various parts of the frond to avoid any difference in guard cell length attributed to position. The collected lamina tissue was placed into a 30% w/v NaOH solution for 20 minutes to remove epicuticular wax. To decolorize the tissue, it was taken through an EtOH series of 20%, 50%, 85%, and 100%, and then backward through that series to water. The tissue was kept at each stage of the series for 10 minutes. The decolorized tissue was stained using a modification of Foster's Tannic Acid – Iron Chloride method (Johansen, 1940): decolorized tissue was placed in a 1% w/v aqueous solution of tannic acid for 10 minutes, briefly rinsed in water, and transferred to a 3% w/v aqueous solution of ferric chloride for approximately 30 minutes. The tannic acid and ferric chloride steps were repeated until
<table>
<thead>
<tr>
<th>Acronym</th>
<th>Herbarium</th>
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<tbody>
<tr>
<td>B</td>
<td>Botanischer Garten und Botanisches Museum Berlin-Dahlem, Zentraleinrichtung der Freien Universität Berlin</td>
</tr>
<tr>
<td>BM</td>
<td>The Natural History Museum, London</td>
</tr>
<tr>
<td>DUKE</td>
<td>Duke University, Durham</td>
</tr>
<tr>
<td>F</td>
<td>Field Museum of Natural History, Chicago</td>
</tr>
<tr>
<td>FI</td>
<td>Museo di Storia Naturale dell'Università, Firenze</td>
</tr>
<tr>
<td>GH</td>
<td>Gray Herbarium, Harvard University, Cambridge</td>
</tr>
<tr>
<td>L</td>
<td>Nationaal Herbarium Nederland, Leiden University branch, Leiden</td>
</tr>
<tr>
<td>MICH</td>
<td>University of Michigan, Ann Arbor</td>
</tr>
<tr>
<td>MO</td>
<td>Missouri Botanical Garden, St. Louis</td>
</tr>
<tr>
<td>MU</td>
<td>Willard Sherman Turrell Herbarium, Miami University, Oxford</td>
</tr>
<tr>
<td>NY</td>
<td>New York Botanical Garden, Bronx</td>
</tr>
<tr>
<td>P</td>
<td>Muséum National d'Histoire Naturelle, Paris</td>
</tr>
<tr>
<td>UC</td>
<td>University Herbarium, University of California, Berkeley</td>
</tr>
<tr>
<td>US</td>
<td>United States National Herbarium, Smithsonian Institution, Washington, D.C.</td>
</tr>
</tbody>
</table>

**Table 1.** List of herbaria from which *Adiantopsis* specimens were examined. Herbaria acronyms and names are reported from the online version of Index Herbariorum (http://www.nybg.org/bsci/ih/).
the cell walls were dark enough to be readily seen. Once the visibility of the cell walls was satisfactory, the tissue was mounted on slides using Hoyer's solution, and guard cell length measurements were made on an Olympus BH-2 compound light microscope.

Sporangia were collected from herbarium specimens using forceps and mounted on a slide with Hoyer's solution. Two measurements were made from collected sporangia: the number of indurated arcus cells, and their height. Data were collected on an Olympus BH-2 compound light microscope.

Spores were collected from herbarium specimens and examined using both Scanning Electron Microscopy (SEM) and light microscopy. Spores for SEM were collected from open sporangia to ensure that the spores were mature and that there were no contaminating spores from other specimens. For counting spore number per sporangium, complete intact sporangia were collected from each specimen. The closed sporangia were collected using fine forceps, and transferred to an aluminum SEM stub that was prepared with a double sided sticky tab and a drop of water. The water allowed the spores to be easily scattered over the surface of the stub, and kept the spores on the stub when breaking open intact sporangia. SEM stubs were gold-palladium sputter coated for 90 seconds at 45 milliamps. Spores were examined on a JEOL JSM-T200 SEM at various working distances, voltages, and spot sizes, depending on the stub. Pictures were taken using an attached Land camera with Polaroid Polapan 55 black and white film. For light microscopy, spores were collected with fine forceps from open sporangia. These spores were mounted on a slide with Hoyer's solution and measured on an Olympus BH-2 compound light microscope.

Data analyses were conducted using SAS (version 8) and OpenOffice.org Calc. Guard cell, arcus cell, and spore size data were compared in SAS using one way ANOVAs with Tukey-Kramer multiple pairwise comparisons ($\alpha = 0.05$) to identify significantly different values. Ranges, means, modes, and standard deviations for all quantitative characters were calculated using OpenOffice.org Calc. Box plots and histograms for select data sets were constructed using OpenOffice.org Calc.

Character terminology in this thesis generally follows Lellinger (2002). One deviation is the scoring of planar shapes; these were characterized using the “Symmetric Plane Figures” guide published by the Systematics Association Committee (1962).
Additionally, as *Adiantopsis* possesses a complex lamina architecture, terms relating to the pinnae and pinnules have been slightly modified from Lellinger (2002). In taxa that are more than bipinnately compound, the term ultimate division, which is not in Lellinger (2002), is used to describe any portion of the lamina that is not further dissected or compound, regardless of its position. Thus, an ultimate division may be a pinna, a pinnule, or a pinnulet, so long as it is not further divided. When using the term ultimate division to describe these various structures, no homology is implied. Thus, pinnae are still the primary division of the lamina, but when pinna morphology is described it only applies to pinnae that are compound themselves (*i.e.*, bipinnate and more compound species). This same logic applies to pinnules. Thus, all final divisions of the lamina are grouped under ultimate division; divisions that are themselves compound are described using standard positional terms (pinna, pinnule, etc.).

**Ecology**

*Adiantopsis* species are ecologically variable. Caribbean *Adiantopsis* frequently occur in moist, forested areas, or on moist rock walls, often in gullies or cave entrances. In South America, many species also prefer moist, forested areas, often occurring near streams or on stream banks, although some South American *Adiantopsis*, such as *A. dichotoma* Moore, do prefer exposed, rocky habitats. An alkaline substrate appears to be a requisite for most *Adiantopsis* taxa. In the Caribbean, this includes limestone, serpentine, and amphibolite substrates. *Adiantopsis radiata* appears to be able to grow in a variety of pH substrates. However, at least one South American species, *A. monticola* (Gardn.) T. Moore, prefers acidic substrates. *Adiantopsis* taxa occur from near sea level to as high as 1600 m (Tryon and Tryon, 1982).

**Morphology**

No previous description of *Adiantopsis* morphology exists. The following description is the first of its sort for the genus, but it cannot be considered comprehensive. It represents what data and patterns could be collected from herbarium specimens.

*Adiantopsis* is a genus of generally erect, small to large herbaceous ferns. Among the Caribbean species, the plants range from small (9.5 cm in *A. asplenioides*) to medium
sized ferns (to 74.0 cm in *A. parvisegmenta*); most individuals are around 20 – 40 cm tall. In South America, many taxa, such as *A. chlorophylla* and *A. × australopedata*, can exceed one and a half meters in length. Most *Adiantopsis* taxa are strict, or stiffly erect. In *A. asplenioides* and *A. paupercula*, the plants are also erect, but the stipes are not as stiff as other taxa. The major exception to this generally erect habit is *A. dichotoma*, a scandent, fractiflex South American species. Thus, Caribbean *Adiantopsis* taxa are generally smaller than their South American congeners, and less habit variation is observed.

The rhizomes of *Adiantopsis* taxa are all similar. Rhizomes range from erect, to ascending, to decumbent. It is not clear if rhizomes are distinctly subterranean or marginally surficial, but given the amount of soil on most rhizomes they appear to be at least partially buried. In this respect, no difference is observed among taxa. Rhizomes range to 5.9 cm long and 2.3 cm in diameter. Persistent, bicolorous scales densely cover the rhizomes (Figure 1); these may play some role in preventing dessication, and/or infection by fungi or bacteria. In all species, a dense tangle of fibrous roots emerge from all sides of the rhizome. Stipes also emerge from all sides of the rhizomes, suggesting an essentially radial symmetry (Figure 1). No positional relationship was observed between the stipes and the roots.

Frond axes in *Adiantopsis* are typically cheilanthoid. They are generally persistent and atropurpureous to atrocastaneous, becoming darker at senescence. These axes are characteristically carinate adaxially with a pair of golden carinae (Figure 2). Carinae are ridges of tissue raised above the surface of the axis. Tryon and Tryon (1982) used the carinae to distinguish *Adiantopsis* from *Cheilanthes*. However, characterization of *Cheilanthes* as lacking carinae is not accurate. Some *Cheilanthes*, such as *C. aemula* Maxon, *C. microphylla* (Sw.) Sw., and *C. wrightii* Hook., are adaxially bicarinate. In the bicarinate *Cheilanthes*, the carinae are usually green or pale green, approaching the color of the laminar tissue, whereas *Adiantopsis* carinae are distinctly golden, independent of lamina color. Carinae in *Cheilanthes* are typically restricted to the costae and costules, whereas in *Adiantopsis* they generally occur on all axes. Additionally, *Cheilanthes* carinae are contiguous with the laminar tissue. In *Adiantopsis*, with the exception of lamina and pinnae apices, carinae remain distinct of the laminar tissue. However, this
Figure 1. Longitudinal section of *Adiantopsis paupercula* rhizome with bicolorous scales densely covering rhizome surface, and radially attached stipes (C. Wright 964, US). Scale bar = 0.25 mm.

Figure 2. Adaxial carinae (arrows) on rachis of *A. pentagona*. (L. B. Smith 3320, A. R. Hodgdon, & F. Gonzalez, NY). Scale bar = 1.0 mm.
may be more an architectural phenomenon than a reflection of the absence of homology. Thus, the carinae of *Adiantopsis* do distinguish it from *Cheilanthes*, but only by their form, not their presence.

Of all axis characters, those associated with the stipes are the most taxonomically informative. In *Adiantopsis*, the stipes may grow to 47.0 cm long and 2.6 mm in diameter. Taxonomic differences emerge when comparing the ratio of stipe length to overall frond length. In the diffform, pinnate taxa, stipes are one third the overall frond length, whereas they are equal to or longer than the lamina in the pedate taxa. Stipes of *A. radiata* are consistently longer than the lamina, and finally in *A. paupercula* they approach equity with lamina length, being variously shorter or longer than it. There are also taxonomic differences in the extent of carinae development. In *A. paupercula*, the carinae begin in the upper half of the stipe, frequently starting just above the stipe midpoint. Carinae begin in the upper quarter of stipes in *A. pentagona* and *A. rupicola*. For *A. pedata*, carinae begin in the basal half of stipes, frequently just below the stipe midpoint. In *A. parvisegmenta*, *A. reesii*, and *A. vincentii*, carinae begin at the stipe bases or in the basal quarter of stipes. *Adiantopsis radiata* frequently lacks carinae on the stipes, but when present, they begin at the base or in the basal quarter of the stipe. Carinae are always absent on the stipes of *A. asplenioides*.

A limited amount of data is available on the anatomy of *Adiantopsis* axes. Transverse sections of *A. radiata* stipes reveal the presence of thick walled epidermal cells, a cortical layer of sclerenchyma, and thick walled parenchyma cells (Figure 3); an endodermis surrounding the vascular bundle also appears to be present. Pneumatotrodes were also observed on all *Adiantopsis* stipes (Figures 3, 4). Bower (1923) states that pneumatotrodes, in conjunction with internal modifications of the stipe anatomy allow for gas exchange across the relatively impervious layer of sclerenchyma in the cortex. In *A. radiata*, a small airspace and thinner walled parenchyma occur below pneumatotrodes (Figure 3). However, the anatomy of axes has not been adequately explored to allow for accurate characterization of *Adiantopsis* anatomy.

Laminar axes in *Adiantopsis* are generally persistent. In most taxa, the original laminar axes position and form are retained even after the loss of ultimate divisions (Figure 5a). However, in senescent fronds of *A. rupicola* and *A. vincentii* the costae are
Figure 3. Fast green stained transverse section of an *A. radiata* stipe showing thick walled epidermal cells (EC), sclerenchyma (S), thick walled parenchyma (TP), and a pneumatothode (P). Note thin walled parenchyma (PA) associated with pneumatothode. Sectioned stipe removed from specimen growing in the Boyd Hall greenhouse, Miami University, Oxford, Ohio. Scale bar = 75 μm.

Figure 4. Surface view of pneumatothodes (arrows) on stipe of *A. pentagona* (*R. A. Howard 5387, NY*). Scale bar = 0.16 mm.
Figure 5. A. Persistent costae of *A. paupercula* (*H. A. Hespenheide 1191, US*) retaining their original position. B. Marcescent costae of *A. vincentii* (*C. V. Morton 10389, US*) curling upon themselves. Scale bars = 2.0 cm.
marcescent and curl upon themselves becoming almost circinate in appearance (Figure 5b).

In his revision of *Lindsaea*, Kramer (1957) notes that “In few fern genera such a great diversity of leaf-pattern is found as in *Lindsaea.*” If the above statement is true for *Lindsaea*, then *Adiantopsis* may have the largest diversity of lamina variation seen in any fern genus, and it is certainly the most diverse among the cheilanthoid genera. Three basic lamina architectures occur in *Adiantopsis*; palmate, pinnate, and pedate (Figure 6). The palmate architecture is observed only in *A. radiata* (Figure 6A, 12). In this species, the pinnae are born from a single point at the stipe apex, and no noticeable rachis is present. A pinnate lamina architecture occurs in *A. asplenioides*, *A. parvisegmenta*, *A. paupercula*, *A. reesii*, *A. rupicola*, and *A. vincentii* (Figure 6B). In the South American pinnate *A. dichotoma*, the lamina is fractiflex with retrorse pinnae. *Adiantopsis pedata*, *A. pentagona*, and *A. ×australopedata* are pedate (Figure 6C). As in pinnate species, the pinnae of pedate laminae are disposed along a central rachis. However, in the pedate taxa, the basal basiscopic pinnules of the first pinnae pair are considerably more developed than the other pinnules. In the pinnate and pedate taxa, the lamina lies in the same plane as the stipe and rachis. However, in palmate *A. radiata*, the lamina is geniculate to the stipe.

Overall shape of *Adiantopsis* laminae is a reflection of architecture. Palmate *Adiantopsis radiata* has an orbiculate lamina. Pinnate taxa are variously triangular to lanceolate, or linear in *A. asplenioides*. Both pedate taxa are pentagonal, as reflected in the name of *A. pentagona*. Laminae apices in the pinnate and pedate taxa are difform, with the exception of *A. paupercula*, which is conform. Pinnae of *A. radiata* are also conform.

The laminae in *Adiantopsis* range from small and simple to large and complex. *Adiantopsis asplenioides* has the smallest laminae with a maximum length of 14.5 cm and a width of 1.1 cm. It is also the simplest, with bipinnate to pinnate-pinnatifid laminae. Of the Caribbean taxa, *A. reesii* has the longest laminae at 60.0 cm, whereas the widest laminae are in *A. pentagona* at 48.2 cm wide. *Adiantopsis parvisegmenta* and *A. paupercula* may have quadripinnate laminae, and are the most compound among Caribbean *Adiantopsis* taxa. However, in South America, laminae may be pentapinnate.
as in *A. chlorophylla* and *A. dichotoma*. With the exception of *A. asplenioides*, most Caribbean *Adiantopsis* laminae are between 20 – 40 cm long and 10 – 20 cm wide.

*Adiantopsis* lamina tissues vary from papyraceous to spongiose. Papyraceous lamina tissues are found in *A. reesii* and *A. vincentii*. *Adiantopsis asplenioides* and *A. pedata* are chartaceous. *Adiantopsis rupicola* may have chartaceous to thin-spongiose tissue, whereas *A. radiata* and *A. pentagona* have thin-spongiose tissue. Finally, spongiose lamina tissue is found in *A. parvisegmenta* and *A. paupercula*.

Randomly dispersed on the adaxial lamina surface are white epidermal cells (Figure 7). These cells are hard, and probably calcified. Hydathodes are also located on the adaxial surface of the lamina tissue. In *Adiantopsis*, these hydathodes are sub-marginal on single vein tips (Figure 7), and are generally covered with a hard, amorphous, white mass. As *Adiantopsis* prefers calcareous substrates, this material appears to be a guttation product. This material, and the wall constituents of the white epidermal cells, are most likely calcium or some other mineral collected from the environment.

Guard cells are located only on the abaxial side of the laminar tissue and are anomocytic. They may be surrounded by two, three, four, or as many as five cells, even on the same ultimate division. Length differences do exist among the guard cells of different taxa (Figure 8, Table 2). The guard cells of *A. asplenioides*, *A. parvisegmenta*, *A. radiata*, *A. reesii*, *A. rupicola*, and *A. vincentii* form a group of taxa with guard cell length means centering around 45 μm. *Adiantopsis paupercula* has an average guard cell length of 61.22 μm, whereas *A. pedata* and *A. pentagona* form a group of taxa with a combined mean guard cell length of 71.47 μm. The guard cell lengths of all three groups are significantly different from each other (p<0.0001) in Tukey-Kramer pairwise comparisons.

Pinnae in *Adiantopsis* are generally triangular to fusiform. The triangular basal pinnae of the pedate taxa are strongly inequilateral, a function of the the much extended basal basiscopic pinnules. All other pinnae of the pedate taxa are more or less equilateral. In *A. parvisegmenta* and *A. paupercula*, pinnae are also somewhat inequilateral with basiscopic pinnules slightly longer than the acroscopic pinnules (Figure 5). Pinnae of *A. asplenioides* reach 6.1 mm long and 6.0 mm wide. Those of other species range to 24.1 cm long and 19.9 cm wide. Pinnae are alternate, with the exception of the subopposite
Figure 7. Adaxial view of *A. pentagona* (*J. A. Shafer 12204, NY*) ultimate division. Note white epidermal cells (W), and a sub-marginal hydathode (H). Scale bar = 0.12 mm.

Figure 8. Guard cell length differences among Caribbean *Adiantopsis*. Means are located at box centers, box ends are mean +/- one standard deviation, and bars extend to the range of cell lengths. *Adiantopsis asplenioides* to *A. vincentii* represent a putative diploid group, which differs significantly (*p* < 0.0001) from *A. paupercula* (gray) and the pedate taxa (black). *Adiantopsis paupercula* has intermediate guard cell lengths that are significantly different (*p* < 0.0001) from both the putative diploid group and the pedate taxa. The pedate taxa form a putative tetraploid group that is significantly different (*p* < 0.0001) from both the putative diploid group and *A. paupercula*. 
### Table 2: Sample sizes, means, standard deviations, and ranges for Caribbean *Adiantopsis* guard cell lengths.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>n</th>
<th>Mean (µm)</th>
<th>Standard Deviation (µm)</th>
<th>Min (µm)</th>
<th>Max (µm)</th>
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<tr>
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<td>3.53</td>
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</tr>
</tbody>
</table>

Basal pinnae of the pedate taxa. In *A. radiata*, the pinnae radiate from the stipe apex. Pinnae in *Adiantopsis* are generally ascending, but a number of taxa also have patent pinnae. In *A. parvisegmenta, A. paupercula, A. reesii, A. rupicola*, and *A. vincentii* the proximal pinnae are frequently or occasionally arcuate, with only the distal pinnae straight. This is quite different from the curling observed in senescent fronds of *A. rupicola* and *A. vincentii* (Figure 5). In these taxa, the incurved pinnae increase their curvature dramatically becoming circinate in appearance. In all other taxa, the senescent pinna axes retain their shape, whether straight or somewhat incurved.

*Adiantopsis* venation and architecture is anadromous. Pinnules are typically narrowly triangular to linear, and occasionally lanceolate. In the pinnate taxa, the basiscopic pinnules are slightly longer than the acroscopic pinnules, and may be up to 7.5 cm long and 2.5 cm wide. The basal basiscopic pinnules of the pedate taxa are much longer, and reach 15.3 cm in length. Pinnules may be patent to ascending.

*Adiantopsis* ultimate divisions are an important source of taxonomic information. For example, the ultimate divisions of *A. paupercula* are strongly articulate, with a clear enlargement and differentiation of the axis at its juncture with the lamina tissue (Figure 9). The ultimate divisions of other *Adiantopsis* taxa, while articulate with age, lack the swollen and distinct articulation point of *A. paupercula* (Figure 10). The ultimate divisions of *A. parvisegmenta* are by far the smallest of the Caribbean taxa, reaching a
maximum size of 3.5 mm long by 2.5 mm wide. The ultimate divisions of other Adiantopsis taxa generally overlap in size, with a maximum length of 13.5 mm in A. radiata and maximum width of 4.5 mm in A. paupercula. There is considerable overlap in ultimate division shapes among Caribbean Adiantopsis, with shapes ranging from oblong, to oblanceolate, lanceolate, elliptic, trullate, and rhombic. Ultimate division bases are generally cuneate and uniauriculate on the acroscopic side. The apices of A. reesii and A. pedata ultimate divisions are acute and distinctly toothed, whereas in other taxa are they are generally acute to round and entire. Adiantopsis asplenioides ultimate divisions are distinctly lobed, whereas the margins of other taxa are entire to crenulate (Figure 11). All ultimate divisions are deciduous with persistent stalks ranging from 0.1 – 6.3 mm in length.

Adiantopsis radiata possesses basal flabellate divisions, an autapomorphy for this taxon. As their name implies, these divisions are generally flabellate, and occur on the stipe apex between pinnae (Figure 12). These basal flabellate divisions appear to be homologous to ultimate divisions. The overall shape of basal pinnules and these flabellate divisions is similar (Figure 12). Additionally, the basal flabellate divisions become fertile with the other ultimate divisions. They are likely the by-product of axial compression in A. radiata, as they appear to be ultimate divisions developed within the stipe crown at a point below the stipe surface. These basal flabellate divisions are usually restricted to mature A. radiata plants with larger than average fronds and greater than five pinnae.

Adiantopsis indument consists of hairs and scales. The hairs are catenate-capitate, with well defined septa and bulbous apical cells. On the axes, they are concentrated at axis junctions, and diffuse over the intervening abaxial surface (Figure 13). They are generally appressed and may be up to ten cells long, although most are much shorter. Catenate-capitate hairs are also found on the abaxial lamina tissue. Typically, the lamina hairs are three celled, although rarely they may be two or four celled. The hairs are clavate, with an elongate basal cell, a relatively shorter middle cell, and a bulbous apical cell. In some taxa, such as A. parvisegmenta, the apical cell is very bulbous and overarches the middle cell (Figure 14A). In A. pentagona and others, the apical cell, while still bulbous, is generally elongate and does not overlap the middle cell (Figure
Figure 9. Swollen stalk apex at junction with lamina tissue (arrow) of *A. paupercula* (*C. Wright 962, UC*). Ultimate divisions are articulate and break cleanly at this swollen point. Scale bar = 1 mm.

Figure 10. Non-swollen stalk apex at junction with lamina tissue (arrow) of *A. pentagona* (*J. G. Jack 7903, US*). Ultimate divisions are articulate, but do not break cleanly from the stalk. Scale bar = 0.3 mm.
Figure 11. A. Toothed ultimate division apices of *A. reesii* (E. L. Ekman 10608, US). B. Round, entire ultimate division apices of *A. radiata* (J. A. Shafer 3777, F). C. Lobed ultimate divisions of *A. asplenioides* (Bro. Alain 1226 & Acuna, US). Scale bars = 0.5 cm.

Figure 12. Abaxial view of basal flabellate divisions of *A. radiata* (G. L. Webster 13425, MICH), indicated by arrow. The divisions are attached to the stipe apex between pinna pairs. Note similarity of shape between basal ultimate and flabellate divisions. Sori are visible on these basal flabellate divisions, and suggests they are homologous to ultimate divisions of the pinnae. Scale bar = 0.5 cm.
The basal cells are usually clear, but the middle and apical cells are quite variable, being red, gold, white, or clear, but usually the two are not the same color. While some taxonomic trends in color have been observed, they appear to be too variable to reliably differentiate taxa.

The hairs of *Adiantopsis* appear to be a synapomorphy for the genus. Tryon and Tryon (1982) stated that *Adiantopsis* is closely related to the *Cheilanthes microphylla* (Sw.) Sw. group of *Cheilanthes*. However, a number of differences between the hairs of the two groups are observed. Hairs of the *C. microphylla* group are much longer, more filamentous, and with indistinct or oblique cross walls, characteristics not associated with *Adiantopsis*. In the *C. microphylla* group, both adaxial and abaxial surfaces of the lamina and axes are covered with hairs, whereas in *Adiantopsis* the hairs are restricted to abaxial surfaces. Additionally, hairs in the *Cheilanthes* taxa are much denser than *Adiantopsis* hairs. The catenate-capitate hairs of *Adiantopsis* have not yet been observed in *Cheilanthes*.

*Adiantopsis* scales are found on the rhizome, stipe, and lamina axes. Rhizome scales are bicolorous, with persistent, black to dark brown centers and deciduous, golden or, in *A. asplenioides*, white, translucent margins (Figure 1). They densely cover the rhizome surface. These scales are generally lanceate to acicular, with truncate bases, entire to slightly repand margins, and acute, gland tipped apices. The rhizome scales of all species are quite similar and lack taxonomic value.

Stipe scales are uniformly concolorous and tan. Overall, the scales range from lanceolate to acicular, or occasionally subulate. *Adiantopsis* stipe scales are frequently biauriculate and appear pseudopeltate, but some scale bases are not auriculate and are truncate. Scale margins range from entire to slightly repand. Apices are acute to attenuate and gland tipped. In all taxa, stipe scales are deciduous, as the remnants of scale bases are often observed and the number of scales varies considerably. These scale characters possess relatively little taxonomic value. However, the stipe scales of *A. parvisegmenta*, *A. paupercula*, *A. reesii*, *A. rupicola*, and *A. vincentii* are divergent from the stipe surface, whereas *A. pedata*, *A. pentagona*, and *A. radiata* stipe scales are appressed to the stipe surface, only occasionally divergent. Stipe scales are distributed at
Figure 13. Catenate-capitate axis hair (arrow) on *A. pentagona* (*A. Gonzales 513*, BM). These hairs may be up to ten cells long. They appear to be synapomorphic for *Adiantopsis*.

Figure 14. A. Abaxial catenate-capitate lamina hairs (arrows) on *A. parvisegmenta* (*C. V. Morton 4166*, US). Apical cells are bulbous and hang over the middle cell. B. Abaxial catenate-capitate lamina hair (arrow) on *A. pentagona* (*J. G. Jack 7903*, US). Apical cells are bulbous and elongate. Scale bars = 0.1 mm.
the base of stipes, typically to a maximum of 7.1 cm of the rhizome. However, stipe scales on some *A. reesii* specimens are distributed along the entire length of the stipe to the rachis. It is possible that stipe scales are distributed higher on the stipes of other taxa and simply not observed because of their deciduous nature. Stipe scales are conspicuously absent in *A. asplenioides*.

Distal to the stipe, scales are rarer, more easily overlooked, and are usually no more than five cells wide and eight cells long (Figure 16). They are concentrated at lamina axis junctions, and are diffusely scattered on abaxial axes surfaces. Scales are typically lanceate in overall shape, and are gland tipped. Some scales are biseriate and closely resemble axis hairs, suggesting that hairs and scales in *Adiantopsis* form a developmental and evolutionary continuum. Lamina scales are not taxonomically informative.

Venation in *Adiantopsis* is free, pseudodichotomous, and anadromous. Veins are typically obscure to occult and are generally immersed in the laminae. Veins always terminate marginally or sub-marginally in adaxial hydathodes.

*Adiantopsis* sori are marginal and consistently uninerved. Sori occur on bothacroscopic and basiscopic margins; in *A. asplenioides* they frequently occur on the interior sides of lobes. For the most part, a single, distinct pseudoindusium covers each sorus, although in *A. asplenioides*, pseudoindusia may be partially confluent across sinus bases. The generally distinct pseudoindusia distinguish *Adiantopsis* from *Cheilanthes*, in which a series of confluent pseudoindusia comprise the entire margin of an ultimate division (Tryon and Tryon, 1982). *Adiantopsis* pseudoindusia are typically lunate to quadrangular, with entire to erose margins.

Sporangia in *Adiantopsis* show a mixed development, and are generally subglobose and long stalked. The stalks are typically three cells long. However, in *A. asplenioides*, and the South American *A. monticola* and *A. reamesii*, the sporangia are globose and essentially sessile, with apparently only a single cell layer between the sporangium and receptacle. The number of indurated arcus cells shows taxonomically informative trends in *Adiantopsis*. Arcus cell numbers show narrow ranges of variation, with modes that are useful for discriminating among taxa (Figure 17). For example, *A.*
Figure 15. Concolorous stipe scales (arrow) on *A. parvisgema* (C. V. Morton 4166, US). Scale bar = 1.5 mm.

Figure 16. Axis scale at junction of rachis and costa (arrow) in *A. pentagona* (L. B. Smith 3320, A. R. Hodgdon, & F. Gonzalez, GH). Scale bar = 0.25 mm.
pedata, A. reesii, and A. vincentii have a mode of 14, A. parvisegmenta, A. paupercula, A. pentagona, and A. rupicola have a mode of 16, A. asplenioides has a mode of 11, and A. radiata has a mode of 20. Adiantopsis sporangia generally contain 64 spores, however A. asplenioides has 32 spores per sporangium.

Arcus cell sizes also differentiate taxa into two groups (Figure 18, Table 3). One group consists of the pedate taxa, with a mean arcus cell height of approximately 48 µm. All other taxa are included in the second group, with a mean arcus cell height of approximately 38 µm. These two groups were found to be significantly different from each other by Tukey-Kramer pairwise comparisons.

Adiantopsis spores are generally echinate (Figure 19). The only species to deviate from this is A. asplenioides, which has cristate spores with anastomosing strands below the muri. Among the echinate spored species, some notable differences are observed. The echinae bases of A. pedata, A. pentagona, and A. radiata are all dissected, whereas the echinae bases in other taxa are complete. Also, the echinae of A. paupercula spores are more compact relative to the echinae of other species' spores. The overall shape of Adiantopsis spores is tetrahedral-globose; this is most pronounced in A. pedata, A. pentagona, and A. radiata. Spores of A. asplenioides are globose. The laesurae are obscured by the ornamentation in all spores except A. asplenioides; its laesurae are easily observed with a dissecting microscope. Spore sizes in Adiantopsis are divided into three distinct groups all statistically different from each other, as determined by Tukey-Kramer pairwise comparisons (Figure 20, Table 4). The first group, with spore lengths averaging around 37 µm, includes A. parvisegmenta, A. paupercula, A. radiata, A. reesii, A. rupicola, and A. vincentii. Adiantopsis pedata and A. pentagona compose the second group with average spore lengths of approximately 47 µm. Finally, A. asplenioides forms a third group, with a mean spore length of 75.83 µm.

The echinate spores of Adiantopsis distinguish it from Cheilanthes. The spore ornamentation of Cheilanthes is variable, with only a few Australian species possessing echinate spores (Tryon and Tryon, 1982). Even in light of these echinate Australian Cheilanthes, Tryon and Tryon (1982) recognized Adiantopsis based primarily on the echinate spore ornamentation, as the echinate Australian Cheilanthes are easily
**Figure 17.** Frequency histograms of Adiantopsis arcus cell number. X-axis is arcus cell number, Y-axis is frequency (absolute value). A. *A. asplenioides* B. *A. parvisegmenta* C. *A. paupercula* D. *A. pedata* E. *A. pentagona* F. *A. radiata* G. *A. reesii* H. *A. rupicola* I. *A. vincentii*. 
Figure 18. Arcus cell length differences among Caribbean \textit{Adiantopsis}. Means are located at box centers, box ends are mean +/- one standard deviation, and bars extend to the range of arcus cell lengths. Y-axis is arcus cell length (\textmu m). \textit{Adiantopsis asplenioides} to \textit{A. vincentii} represent the putative diploid group (white), which is significantly different (p<0.0001) from the pedate taxa (black).

<table>
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<th>Taxon</th>
<th>n</th>
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<th>Min (\textmu m)</th>
<th>Max (\textmu m)</th>
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Table 3. Sample sizes, means, standard deviations, and ranges for Caribbean \textit{Adiantopsis} arcus cell height.
Figure 20. Spore length differences among Caribbean Adiantopsis. Means are located at box centers, box ends are mean +/- one standard deviation, and bars extend to the range of spore lengths. Adiantopsis parvisegmenta to A. vincentii represent the putative diploid group (white), which is significantly different (p<0.0001) from the pedate taxa (gray) and A. asplenioides (black). The pedate taxa form a putative tetraploid group that is significantly different (p<0.0001) from both the putative diploid group and A. asplenioides.

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<thead>
<tr>
<th>Taxon</th>
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<th>Mean (µm)</th>
<th>Standard Deviation (µm)</th>
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</table>

Table 4. Sample sizes, means, standard deviations, and ranges of Caribbean Adiantopsis spore lengths.
distinguished from *Adiantopsis* by vegetative characters. The only exception to echinate spores in Caribbean *Adiantopsis* is *A. asplenioides*. However, given its other unique characters, *A. asplenioides* most likely belongs in another genus, probably a new one. The species is retained here only until a full analysis of South American *Adiantopsis* is completed. Thus, once *A. asplenioides* is segregated from *Adiantopsis*, echinate spores will characterize the genus.

**Taxonomic Treatment**

**Taxonomic History**

In 1852, Fée erected the genus *Adiantopsis* for various species in *Adiantum*, *Cheilanthes*, and *Hypolepis* that had a distinct pseudoindusium for each sporangium. Originally, Fée included four species in *Adiantopsis*: *A. capensis* (Sw.) Fée, *A. chlorophylla* (Sw.) Fée, *A. paupercula* (Kze.) Fée, and *A. radiata* (L.) Fée. He designated *A. paupercula* as the type species for the genus. However, Christensen (1906) lectotypified the genus with *A. radiata*. This lectotypification of *Adiantopsis* seems unnecessary, as Fée clearly designated, with the term “Diagnosis”, *A. paupercula* by referencing Kunze's (1850) publication of the species. As a result, some authors (Mickel and Beitel, 1988; W3 Tropicos ver. 1.5, 2003) recognize *A. radiata* as the type, whereas others (Tryon and Tryon, 1982; Proctor, 1985) recognize *A. paupercula*. *Adiantopsis paupercula* should be recognized as the type species for the genus, as Fée unambiguously designated it the type.

Fée (1857) also published two subgenera within *Adiantopsis; Euadiantopsis* (=*Adiantopsis*) and *Cheilanthastrum* (Table 5). Although he did not provide characters for the subgenera, the list of species he included in each subgenus suggests them. *Euadiantopsis* is apparently characterized by more oblong ultimate divisions, whereas those of *Cheilanthastrum* are more elliptic to oblanceolate. Additionally, at least two of the taxa in *Euadiantopsis, A. paupercula* and *A. radiata*, have laminae architectures that are more like those found in *Adiantum* than in *Cheilanthes*. Likewise, the species placed
TABLE 5. Species included by Fée in *Adiantopsis* (1852) and his two subgenera (1857). The current placement of each species, if not *Adiantopsis*, is indicated in parentheses.

<table>
<thead>
<tr>
<th><em>Adiantopsis</em> (Fée, 1852)</th>
<th><em>Euadiantopsis</em> (Fée, 1857)</th>
<th><em>Cheilanthastrum</em> (Fée, 1857)</th>
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<td><em>A. paupercula</em></td>
<td><em>A. capensis</em> (<em>Cheilanthes</em>)</td>
</tr>
<tr>
<td><em>A. chlorophylla</em></td>
<td><em>A. pteroides</em> (<em>Cheilanthes</em>)</td>
<td><em>A. chlorophylla</em></td>
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<td><em>A. paupercula</em></td>
<td><em>A. radiata</em></td>
<td><em>A. spectabilis</em> (=<em>A. chlorophylla</em>)</td>
</tr>
<tr>
<td><em>A. radiata</em></td>
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</tr>
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</table>

Past authors have not always recognized *Adiantopsis*. For example, Hooker and Baker (1883), placed *Adiantopsis* as a subgenus within *Cheilanthes* in their *Synopsis Filicum*. However, they did use Fée's (1852) characters to recognize subgenus *Adiantopsis*. The placement of *Adiantopsis* within *Cheilanthes* is in line with their overall generic concept, which recognized a small number of large fern genera with a substantial number of included subgenera. Copeland (1947) also did not recognize *Adiantopsis*, suggesting that it was insufficiently distinct to warrant generic status; he placed it in synonymy under *Cheilanthes*.

Other authors have recognized *Adiantopsis*, but with qualification. For example, Smith (1981) suggested that if species such as *A. chlorophylla* and *A. seemannii* are included in *Adiantopsis*, the distinction between it and *Cheilanthes* disappears. Specifically, he cited the morphological similarities of these species to *C. aemula* and *C. microphylla*.

Many other researchers have recognized *Adiantopsis* as construed by Fée. Christensen (1906) recognized it in his *Index Filicum*. Maxon (1908) also recognized *Adiantopsis*, and published a useful synopsis of the Cuban taxa. Most modern tropical fern floras recognize *Adiantopsis* as distinct from *Cheilanthes* (Sehnem, 1959, 1961, 1972; Tryon and Tryon, 1982; Proctor, 1985; Mickel and Beitel, 1988; Lellinger, 1989; Proctor, 1989; Tryon *et al.*, 1990; Pacheco, 1995). In general, these researchers, and Fée, utilized a more narrowly defined generic concept than either Hooker and Baker (1883) or Copeland (1947). Only Copeland (1947) articulated problems with the recognition of
Adiantopsis, although he did not refer to a number of distinctive characters, such as spore ornamentation, adaxial carinae, and hair morphology.

Although Adiantopsis has been included in many fern floras and indices, little comprehensive research has been done at the species level. One of the most significant contributors to species level taxonomy in Adiantopsis was Sehnem. He published a series (1959, 1961, 1972) of keys and species descriptions for various floras in southeastern Brazil and the tri-border region of Argentina, Brazil, and Paraguay. In these treatments, he provides excellent keys to the species of the region, using characters that were overlooked by other pteridologists. Further, he provided some clarification to the A. chlorophylla species complex by recognizing two new species, A. perfasciculata and A. occulta. Unfortunately, most pteridologists, including Tryon and Tryon (1982) either ignored or were unaware of Sehnem's Adiantopsis research.

Tryon and Tryon (1982) were the most recent taxonomists to overview Adiantopsis. They regarded the genus as closely related to their Cheilanthes microphylla group (Cheilanthes group 1). That group and Adiantopsis share dark axes and less hair than other cheilanthoid groups. The main character used by Tryon and Tryon (1982) to distinguish Adiantopsis from Cheilanthes was the echinate spores in Adiantopsis. Additionally, they noted adaxially bicarinate lamina axes, asymmetrical and articulate ultimate divisions, and distinct indusia covering single sori as distinguishing features of Adiantopsis (Tryon and Tryon, 1982).

Tryon and Tryon (1982) recognized seven Adiantopsis species in total, including Adiantopsis paupercula, A. pedata, A. radiata, and A. reesii from the Caribbean. In their treatment, they sank A. rupicola into A. reesii, stating that it does not appear to be distinct, and considered A. asplenioides to be a juvenile form of A. paupercula. With regard to South American taxa, Tryon and Tryon (1982) did recognize one of Sehnem's species, A. minutula, but did not acknowledge his A. perfasciculata and A. occulta. It is not clear why they did not recognize these two distinctive species. Although Tryon and Tryon's (1982) treatment of Adiantopsis failed to mention some key species, they provide the only comprehensive overview of the genus.

Recent molecular work by Gastony (pers. comm.) supports the generic status of Adiantopsis. A molecular analysis with rbcL DNA sequences supports a sister
relationship between *A. radiata* and the South American *A. chlorophylla* with 23 synapomorphies and 100% bootstrap support (Gastony, pers. comm.). The analysis included representatives of all cheilanthoid genera from all geographic regions, and provides robust support that *Adiantopsis* is a distinct, monophyletic genus. Further, it refutes Smith's (1981) contention that including *A. chlorophylla* in *Adiantopsis* makes the genus indistinguishable from *Cheilanthes* because of morphological similarity to *C. aemula*. *Cheilanthes aemula* was included in Gastony's (pers. comm.) analysis, and was very distantly related to the *Adiantopsis* group. Thus, it appears any morphological similarity observed by Smith (1981) between the two taxa is likely convergent, although the taxa are morphologically distinct in this author's opinion. Future molecular research with a broader sampling of *Adiantopsis* is needed to further test this hypothesis.

**Species Concept**

In this revision of *Adiantopsis*, a morphological species concept was employed to discriminate species. Essentially, if groups of collections could be shown to be distinct morphologically they were recognized as distinct taxa; if not they were maintained as a single species. Implicit in this usage of the morphological species concept is the assumption that morphological distinctness reflects underlying genetic distinctness produced as a result of unique evolutionary histories for each species. If future research using population genetic markers that sample multiple loci across the genome, such as isozymes or inter-simple sequence repeats, does not identify partitioned genetic variation, then the species boundaries should be re-evaluated.

**Evolutionary Relationships**

Based on a comparison of morphological data obtained from Caribbean collections, a total of nine morphological species are recognized for this region. Of these nine species, seven are putative diploids and two are putative polyploids. In *Adiantopsis*, chromosome counts are only known from *A. radiata*. The counts of *n* = 30 (Walker, 1973; Smith and Foster, 1984) represent the base number for the cheilanthoid genera, and thus it is assumed that *A. radiata* is a diploid species. As material was not available to count the chromosomes of other *Adiantopsis* taxa, indirect estimates of ploidy level were
used. Barrington et al. (1986) demonstrated that guard cell and spore lengths in leptosporangiate ferns frequently correspond to ploidy level. Arcus cell size has also been correlated with ploidy level by Butters and Tryon (1948). Using these cell sizes, the ploidy levels of Adiantopsis taxa were estimated, with A. radiata serving as a reference for the diploid ploidy level (Figures 8, 18, 20; Tables 2, 3, 4). These data partition the nine species into two statistically significant groups. All pinnate taxa and A. radiata form a group of putative diploid species, whereas the two pedate taxa appear to be polyploid species, most likely tetraploids. The pedate taxa consistently possess larger cell sizes. The cell length differences between putative diploid and tetraploid Adiantopsis taxa are comparable to differences observed between diploid and tetraploid leptosporangiate ferns by Barrington et al. (1986) and Butters and Tryon (1948). Based on these data, A. pedata and A. pentagona are supported as tetraploid species, whereas all other Caribbean taxa appear to be diploid.

Two exceptions to this pattern in cell size exist. Guard cells of A. paupercula are somewhat larger than all other putative diploid taxa, but not quite as large as those of the putative tetraploid taxa (Figure 8; Table 2). Spore and arcus cell size place this species with the putative diploid taxa (Figures 18, 20; Tables 3, 4). Its not clear why its guard cells show this intermediacy. Given that its spore and arcus cell sizes are within the putative diploid range it seems probable that this is a diploid taxon, and that its guard cell lengths are influenced by other, unknown factors.

The other exception is A. asplenioides, a species with a number of unique characteristics among Caribbean Adiantopsis. Guard cell and arcus cell sizes group this taxon with other putative diploids (Figures 8, 18; Tables 2, 3). However, it has the largest spore size of all Adiantopsis taxa (Figure 20; Table 4), it is the only species with 32 spores per sporangium, and it has indurated pseudoindusia that completely and persistently cover the sori. Two hypotheses may explain these anomalous features. First, the species may be apogamous, a hypothesis supported by the reduced spore number (Evans, 1964; Klekowski, 1973). Alternatively, the spore number may be a function of a reduced number of spore mother cells, and a greater resource allocation to fewer spores. Under this hypothesis, the large spores are probably not indicative of a higher ploidy level, but rather are an adaptation for limiting spore dispersal. Barrington et al. (1986)
observed a similar pattern in *Adiantum pedatum* ssp. *calderi*, a fern that is limited to serpentine rocks. He hypothesized that the large spores may limit spore dispersal and thus prevent them from leaving the “serpentine islands” to which they are adapted. *Adiantopsis asplenioides* appears to fit Barrington's (1986) model well, as it is a serpentine species with very large spores, and based on other features appears to be a diploid. Further, the persistent and indurated pseudoindusia of *A. asplenioides* may represent an additional modification to limit spore dispersal. Thus, the reduced spore number, large spores, and indurated pseudoindusia appear to represent a suite of characters adaptive in keeping propagules within its geographically restricted edaphic niche.

*Adiantopsis pedata* and *A. pentagona* are hypothesized to be allotetraploid derivatives between *A. radiata* and two different pinnate taxa. A hybrid origin for the pedate Caribbean taxa is supported by the occurrence and morphology of the sterile hybrid *A. ×australopedata* in South America. This taxon documents that the pedate lamina morphology is of hybrid origin between *A. radiata* and a pinnate second parent (Hickey et al., 2003). Also, the dissected echinae bases on spores of *A. radiata* and the pedate taxa support *A. radiata* as one parent, as all other taxa have complete echinae bases. Additional support is evidenced by common lamina development in the two pedate taxa and *A. radiata*. The fronds of young plants, as estimated by rhizome size, are strongly ternate in both species; progressively older, larger plants of these species show increasingly complex frond development. In *A. pedata* the basal basiscopic pinnules become extended and the penultimate pinna pairs enlarge, becoming increasingly prominent. In *A. radiata* additional pinnae pairs are added to the stipe apex. This pattern of growth is only found in *A. radiata*, *A. ×australopedata*, and the pedate Caribbean taxa. The pinnate *Adiantopsis* taxa lack such ontogenetic architectural changes, and show a common architecture on both young and old plants.

*Adiantopsis reesii* is supported as the second parent of *A. pedata* on the basis of crenulate apices and generally ascending ultimate divisions. Additionally, the carinae of *A. reesii* and *A. pedata* start near the base of the stipe, and both species have a mode of 14 arcus cells. An *A. reesii × A. radiata* origin for *A. pedata* is also supported by the distributions of the taxa, as collections of *A. pedata* are currently only known from areas
where the three co-occur.

Numerous morphological comparisons support *A. rupicola* as the most likely second parent of *A. pentagona*. The overall ultimate division shape of *A. pentagona* compares most favorably with the generally trullate divisions observed in *A. rupicola*. Furthermore, the acute, and generally entire ultimate division apices, especially the terminal divisions, of *A. pentagona* reflect that character state in *A. rupicola*. The generally patent nature of *A. pentagona* ultimate divisions compare favorably with the patent disposition of the ultimate divisions in *A. rupicola*, and both *A. rupicola* and *A. pentagona* have a mode of 16 arcus cells. Finally, the carinae in *A. rupicola* and *A. pentagona* both start in the upper 1/3 to 1/4 of the stipe, a character unique to these two species.

*Adiantopsis pentagona*, however, is quite variable and there are suggestions that it may contain yet another cryptic species. Evidence for this comes from some *A. pentagona* specimens that have relatively small ultimate divisions, larger and slightly more compound laminae, and somewhat revolute fertile divisions. It should be noted, however, that all of these character states intergrade across the suite of specimens referable to *A. pentagona*, and it is not clear from this morphological analysis whether the observed variation is due to habitat/ecological differences among plants, simple genetic variation, or multiple origins with different maternal parentages (e.g., *A. rupicola* the maternal parent for some specimens, and *A. radiata* for others). Alternatively, this may be a case of cryptic allotetraploids wherein each shares a common *A. radiata* parent, but each has a different pinnate second parent. The variation in character morphology mentioned above could easily be accounted for if *A. parvisegmenta* was the second second parent of these collections. The geographic distribution of specimens does not provide any insight about the source of the morphological variation, and resolution may require molecular analyses. Future molecular studies of this group should encompass the morphological range of *A. pentagona* specimens, *A. rupicola*, *A. parvisegmenta*, and *A. vincentii*, as any could be a genetic contributor.

Based on morphology, evolutionary relationships among the diploid taxa can be hypothesized. Given its unique suite of characters, *A. asplenioides* is probably quite distantly related to all other Caribbean *Adiantopsis* taxa. No Caribbean *Adiantopsis* taxa
has the globose, sessile sporangia, indurated pseudoindusia with white to pale blue epidermal cells, ultimate division morphology, spore size, spore morphology, and spore number that \textit{A. asplenioides} possesses. \textit{Adiantopsis asplenioides}, and two South American taxa with similar characters, may best be segregated as a new genus, characterized by globose, sessile sporangia and indurated white to pale blue epidermal cells. Presently, it is not yet clear if these taxa form a monophyletic group and thus they are retained here in \textit{Adiantopsis}.

\textit{Adiantopsis paupercula} is also morphologically isolated from rest of \textit{Adiantopsis}. Its strongly articulate segments with swollen stipe apices, conform lamina apices, and compact spore echinae are distinctive. Given its overall morphological uniqueness, \textit{A. paupercula} is probably phylogenetically isolated from other \textit{Adiantopsis} taxa, but not too distant from them. If one assumes that basal \textit{Adiantopsis} taxa will be morphologically similar to \textit{Cheilanthes}, then \textit{A. paupercula} is most likely a derived species within \textit{Adiantopsis} as it does not closely resemble any \textit{Cheilanthes} taxa.

Based on its overall ultimate division shape and the nature of articulation, \textit{A. radiata} is placed near a group of pinnate taxa that includes \textit{A. parvisegmenta}, \textit{A. reesii}, \textit{A. rupicola}, and \textit{A. vincentii}. Additionally, \textit{A. radiata} putatively hybridizes with at least \textit{A. reesii} and \textit{A. rupicola}, suggesting that the taxa are not too phylogenetically distant. Furthermore, the palmate lamina architecture that distinguishes \textit{A. radiata} is likely derived from a pinnate ancestor. Preliminary anatomical data (unpubl. data) demonstrate that the lamina vasculature branches extensively within the stipe apex, despite an external appearance of a radiate origin. Ontogenetically, \textit{A. radiata} fronds increase in complexity by the successive addition of pinnae pairs, as is true for pinnate and pedate taxa. Based on these data, it is likely that the evolution of the palmate architecture from a pinnate ancestor involved a shortening of the timing and/or distance between pinna branching events. The developmental genetics behind the production of this palmate morphology may not be significantly different from that of pinnate taxa, and so \textit{A. radiata} may not be as phylogenetically distant from other \textit{Adiantopsis} as the unique palmate architecture suggests. Further anatomical research on \textit{A. radiata} and other \textit{Adiantopsis} is necessary to support and clarify this hypothesis.

\textit{Adiantopsis parvisegmenta}, \textit{A. reesii}, \textit{A. rupicola}, and \textit{A. reesii} form a group of
morphologically similar pinnate species with difform laminae apices, triangular to lanceolate laminae, and stipes that are one third the overall frond length. As the species appear to be more or less equally distinct from each, greater resolution of affinities within this group is not possible at this time. Although relationships among the species are not clear, hypotheses on their speciation are possible. Being all diploid, it is possible this group of species evolved from a common ancestor via primary divergence. This primary divergence was probably driven by a combination of geographic isolation and edaphic differences. For example, A. reesii is restricted to limestone habitats in Jamaica and Hispaniola, and does not occur on Cuba. Adiantopsis rupicola only occurs in Pinar del Rio, Cuba, on serpentine rocks and soils, whereas A. parvisegmenta and A. vincentii are both restricted to the Escambray Mountains of central Cuba on amphibolite rocks.

Adiantopsis vincentii and A. parvisegmenta may represent separate colonization events of the Escambray region, or they may be sister taxa evolving in situ. Alternatively, the character states that unite these pinnate taxa are likely to be plesiomorphies for Adiantopsis, and the species may not actually be closely related. Further research using molecular tools is needed to resolve the phylogenetic relationships among these, and other Adiantopsis taxa.

**Taxonomy**


*Rhizomes* erect to ascending, or decumbent, to 5.9 cm long, 2.3 cm in diameter; *scales* dense, overlapping, persistent, bicolored with a black to dark brown center and golden or translucent margins. *Fronds* strict to erect, to 74.0 cm long. *Stipes* persistent, atropurpureous to atrocastaneous, to 47.0 cm long, 2.6 mm in basal diameter; *carinae* when present, golden; *scales* when present, deciduous, concolorous, tan; *hairs* diffuse, rare, catenate-capitate. *Laminae* pinnate, pedate, or palmate, to 60.0 cm long, 48.2 cm wide; *laminar tissue* papyraceous, chartaceous, thin-spongiose, or spongiose, adaxially glabrous with diffuse, glossy-white epidermal cells, hydathodes marginal; *hairs* diffuse abaxially, catenate-capitate, three celled; *stoma* abaxial. *Lamina axes* persistent to marcescent, atropurpureous to atrocastaneous, grading into lamina and taking its color
and texture, adaxially bicarinate; *carinae* golden, interrupted at axis junctions, grading into lamina; *scales* when present, concentrated at rachis-costa junctions, diffuse abaxially; *hairs* concentrated at axis junctions, diffuse abaxially, catenate-capitate. *Pinnules* ascending to patent, alternate to sub-opposite. *Pinnules* anadromous, patent to ascending. *Ultimate divisions* patent to ascending, deciduous and articulate; *stalks* persistent. *Veins* free, anadromous, immersed in lamina, obscure to occult. *Sori* marginal on both acroscopic and basiscopic margins, uninerved; *pseudoindusia* distinct or occasionally confluent, lunate to quadrangular, hyaline to green or with indurated, white to pale blue epidermal cells. *Sporangia* subglobose to globose, long stalked to sessile. *Spores* 64 or 32 per sporangium, tetrahedral globose, golden to white at maturity, white to pale yellow when immature, echinate to cristate. *Chromosome number* 2n = 60.

**Range:** Found on the Caribbean Islands, central Mexico to Central America, northern South America to northern Argentina.

**Nomenclature:** Fée designated *A. paupercula* the type species by unambiguously referencing Kunze's publication of *Adiantum pauperculum*. Some authors, such as Copeland (1947), claim that *Adiantopsis* was not validly typified as Fée did not clearly designate a type species. For this reason, the genus was lectotypified by Christensen (1906) with *A. radiata*, and modern authors have variously recognized *A. paupercula* (e.g., Tryon and Tryon, 1982) or *A. radiata* (e.g., Mickel and Beitel, 1988) as the type species. Fée did, however, clearly indicate the type species, *A. paupercula* should be recognized as the type and Christensen's (1906) lectotypification should be disregarded.

**Characters:** *Adiantopsis* is distinguished from *Cheilanthes* by the following combination of characters: echinate spore ornamentation (excluding *A. asplenioides*); separate and distinct pseudoindusia, each covering a single sors; an adaxial pair of golden carinae that occur on all lamina axes and generally on stipes, and which are distinct in color and position from lamina tissue; and finally catenate-capitate hairs with distinct, transverse septae and bulbous apical cells, these distributed diffusely on abaxial surfaces of axes and lamina tissue, although often concentrated at axis junctions.
**KEY TO THE SPECIES AND DESCRIPTIONS**

1.) Lamina palmate.................................................................................................................. *A. radiata*

1.) Lamina pedate or pinnate

2.) Lamina pinnate

3.) Pseudoindusia indurated with whitened to pale blue cells; sporangia sessile; lamina once pinnate to bipinnate; ultimate divisions deeply lobed........................................................................................................... *A. asplenioioides*

3.) Pseudoindusia not indurated, hyaline to green; sporangia stalked; lamina bipinnate or more compound; ultimate divisions entire to crenulate

4.) Lamina apex conform; ultimate divisions with stalk swollen at juncture with lamina tissue.................................................................................. *A. paupercula*

4.) Lamina apex difform; ultimate divisions without stalk swollen at juncture with lamina tissue

5.) Lamina quadripinnate; ultimate divisions less than 3.5 mm long and 2.5 mm wide; fertile segments strongly revolute................................................................. *A. parvisegmenta*

5.) Lamina tripinnate or less compound; ultimate divisions more than 3.5 mm long and 2.5 mm wide; fertile segments more or less flat

6.) Carinae beginning in upper quarter of stipe; lamina tissue thin-spongiose to chartaceous; mode of 16 indurated arcus cells.......................... *A. rupicola*

6.) Carinae beginning in lower half or quarter of stipe; lamina tissue papyraceous; mode of 14 indurated arcus cells

7.) Apices of ultimate divisions crenulate; rachis basal diameter 1.1-[1.33]-1.5 mm; ultimate divisions ascending; lamina axes persistent, the costae straight, Jamaica and Hispaniola.................................................. *A. reesii*
7.) Apices of ultimate divisions entire; rachis basal diameter 0.6-[0.88]-1.2 mm; ultimate divisions patent to slightly ascending; lamina axes marcescent, the costae curling acroscopically, Cuba .......................................................... A. vincentii

2.) Lamina pedate

8.) Apices of ultimate divisions crenulate; carinae beginning in basal half of stipe; mode of 14 annulus cells; ultimate division stalks 0.1-[0.33]-0.6 mm long; ultimate divisions slightly ascending; basal basiscopic pinnules 2.2-[3.6]-5.1 times longer than basal acroscopic pinnule; Jamaica and Hispaniola................................................................. A. pedata

8.) Apices of ultimate divisions acute to round; carinae beginning in apical half of stipe; mode of 16 annulus cells; ultimate division stalks 0.9-[3.50]-6.3 mm long; ultimate divisions more or less patent; basal basiscopic pinnules 1.8-[5.6]-13.1 times longer than basal acroscopic division; Cuba................................................................. A. pentagona


Rhizome erect, stiff, to 1.5 cm long, 0.3-[0.62]-0.8 cm in diameter; scales dense, overlapping, persistent, bicolorous with an atrocastaneous center and ephemeral translucent margins, acicular to lanceate (subulate), basifixed, 1.60-[3.14]-5.20 mm long, 0.12-[0.28]-0.55 mm wide, bases truncate, margins entire to slightly repand, apices attenuate, gland tipped. Fronds aggregated, erect, 9.5-[12.45]-18.5 cm long. Stipes persistent, atrocastaneous to castaneous, not bicarinate, shorter than lamina, 1.5-[2.52]-4.0 cm long, 0.2-[0.34]-0.6 mm in basal diameter; scales absent; hairs diffuse, rare, catenate-capitate or rarely ciliform. Laminae bipinnate to pinnate-pinnatifid, linear,
drying dull green, 8.0-[9.93]-14.5 cm long, 0.5-[0.83]-1.1 cm wide, apex confluent, long attenuate; *lamina tissue* chartaceous, adaxially glabrous, with diffuse, glossy-white epidermal cells, hydathodes marginal in sinuses, surrounded by prominent white to pale blue epidermal cells; *hairs* diffuse abaxially, catenate-capitate, three-celled, basal cell elongate, clear or white, middle cell short, tan or clear, apical cell elongate-bulbous, clear, white, or golden; *stoma* abaxial, guard cells 45.64-[52.42]-57.05 μm long. *Lamina axes* persistent, atrocastaneous to castaneous, grading into lamina and taking its color and texture, adaxially bicarinate; *rachis* 0.2-[0.32]-0.5 mm in basal diameter; *carinae* colored as axis or golden, interrupted at axis junctions, grading into lamina; *scales* absent; *hairs* concentrated at axis junctions, diffuse abaxially, catenate-capitate. *Pinnae* patent to slightly ascending, 16-[17.6]-20 pairs, alternate, sub-opposite basally, articulate, deciduous, widely rhombiform, obovate, to oblong, usually auriculate acroscopically, to 2.7-[4.45]-6.3 mm long, 1.7-[3.76]-6.0 mm wide, bases cuneate, margins deeply 2 – 6 lobed, apices round to acute. *Pinnules* of basal pinnae anadromous, patent, widely rhombic to obovate, to 2.6-[3.12]-4.1 mm long, 1.5-[2.17]-3.1 cm wide, bases cuneate, margins deeply 2 – 3 lobed, apices round to acute; *stalks* persistent, not swollen at junction with lamina tissue, 0.1-[0.22]-0.4 mm long. *Veins* free, anadromous, immersed in lamina, obscure to occult. *Sori* marginal on both acroscopic and basiscopic margins, frequently on sides of sinuses, uninerved; *pseudoindusia* distinct or confluent across sinuses, reniform to sub-reniform, white to pale blue, occasionally hyaline, 0.50-[0.57]-0.78 mm long, 0.36-[0.42]-0.50 mm wide, margin entire to slightly erose. *Sporangia* globose, sessile on receptacle, arcus of 11-[13]-15 indurated cells, these 30.97-[34.98]-39.12 μm tall. *Spores* 32 per sporangium, tetrahedral-globose, white to pale yellow (both mature and immature), 58.68-[75.83]-88.02 μm in diameter, cristate with anastomosing strands below the muri, laesura not obscured by ornamentation. *Chromosome number* unknown.

**Distribution:** A rare endemic of Pinar del Río, and an unknown site in eastern Cuba.

**Habitat:** Restricted to moist, serpentine soils or rocks. Found on serpentine mogotes of Pinar del Río.
FIGURE 21. A. Adiantopsis asplenioides (Bro. Alain 1226 & Acuna, US). Scale bar = 3.0 cm. B. Lobed ultimate divisions with indurated pseudoindusia. Scale bar = 0.5 cm.
Figure 22. Distribution of some Cuban Adiantopsis. Adiantopsis asplenioides and A. rupicola occur in the province of Pinar del Río, indicated by black dots. Adiantopsis parvisegmenta and A. vincentii occur in the Escambray Mountains, indicated by stars.

Notes: This species is morphologically similar to the Brasilian A. monticola. The atropurpureous axes, shorter fronds, and oblong ultimate divisions distinguish it from A. asplenioides. Both A. asplenioides and A. monticola appear to be allied with the Bolivian and Paraguayan A. reamesii. All three taxa have sessile, globose sporangia, deeply lobed margins, white to pale yellow spores, and prominent white or blue cells surrounding the hydathodes. These three taxa may constitute a new genus, especially if molecular data sets support them as a monophyletic group separate from other Adiantopsis taxa.

Adiantopsis asplenioides is unique among Caribbean Adiantopsis in having 32, very large spores per sporangium, and indurated pseudoindusia. Although it has the largest spores, this species is likely a diploid, as guard and arcus cell sizes place it among other putative diploid taxa. It is more likely that this suite of characters are adaptations to restrict spore distribution to the serpentine substrates on which it occurs. Alternatively,
the species may be apogamous, a common cause of reduced spore number.

*Adiantopsis asplenioides* is an extremely rare species. There are few collections of this taxon, and it is geographically restricted to serpentine substrates in Pinar del Río, Cuba. This species is most likely still extant in Cuba, and protected within the confines of Valley de Viñales and other national parks.


*Rhizome* ascending to decumbent, stiff, to 2.5 cm long, 1.2-[1.87]-2.3 cm in diameter; *scales* dense, overlapping, persistent, bicolorous with a black to dark brown center and ephemeral golden margins, lanceate to acicular, basifixed, 4.50-[5.44]-6.00 mm long, 0.33-[0.41]-0.50 mm wide, bases truncate, margins entire to slightly repand, apices acute, gland tipped. *Fronds* aggregated, strict, 54.0-[64.32]-74.0 cm long. *Stipes* persistent, atrocastaneous, bicarinate adaxially, shorter than lamina, 15.5-[20.85]-28.3 cm long, 1.6-[1.88]-2.3 mm in basal diameter; *carinae* golden, beginning at stipe base or in the basal ¼ of stipe and continuing into rachis; *scales* extending 1.3-[2.87]-3.35 cm up the stipe, deciduous, divergent, concolorous, tan, lanceolate to acicular (subulate), pseudopeltate to basifixed, 3.40-[4.01]-4.63 mm long, 0.30-[0.37]-0.48 mm wide, bases biauriculate to truncate, margins entire to slightly repand, apices acute, gland tipped; *hairs* diffuse, rare, catenate-capitate. *Laminae* quadripinnate, triangular to lanceate, drying dull green, 26.3-[36.68]-45.7 cm long, 6.5-[19.25]-28.0 cm wide, apex pinnatifid, confluent, cuneate to acute; *lamina tissue* spongiose, adaxially glabrous, with diffuse,
glossy-white epidermal cells, hydathodes marginal; hairs diffuse abaxially, catenate-capitate, three-celled, basal cell elongate, clear or white, middle cell short, tan or clear, apical cell bulbous, clear, white, or golden; stoma abaxial, guard cells 32.60-[45.50]-58.68 μm long. Lamina axes persistent, atrocastaneous, grading into lamina and taking its color and texture, adaxially bicarinate; rachis 1.7-[1.90]-2.3 mm in basal diameter; carinae golden, interrupted at axis junctions, grading into lamina; scales concentrated at rachis-costa junctions, diffuse abaxially, deciduous, appressed to patent, concolorous, tan, basifixed, narrowly triangular, 0.65-[0.84]-1.10 mm long and 0.02-[0.05]-0.10 mm wide, base truncate, margins entire, apex acute, gland tipped; hairs concentrated at axis junctions, diffuse abaxially, catenate-capitate. Pinnae ascending, 26-[36]-45 pairs, alternate, frequently incurved in basal half of lamina, straight distally, triangular to narrowly triangular, inequilateral, to 8.5-[13.06]-16.5 cm long, 3.3-[8.66]-12.5 cm wide, apices acute to cuneate, confluent. Pinnules anadromous, patent to slightly ascending, narrowly triangular, to 1.5-[4.26]-7.5 cm long, 0.5-[1.43]-2.5 cm wide, basiscopic pinnules slightly larger than acroscopic pinnules, apices attenuate to cuneate, confluent. Ultimate divisions patent to slightly ascending, articulate, ovate, elliptic to oblong, 1.9-[2.72]-3.5 mm long, 1.2-[1.53]-2.5 mm wide, bases cuneate, frequently uniauriculate acroscopically, margins entire, apices round to acute; terminal divisions equivalent to other divisions; stalks persistent, not swollen at junction with lamina tissue, 0.2-[0.36]-0.5 mm long. Veins free, anadromous, immersed in lamina, occult. Sori marginal on both acroscopic and basiscopic margins, uninerved; pseudoindusia distinct, lunate to quadrangular, green to white, becoming hyaline distally, occasionally black maculate, 0.50-[0.58]-0.72 mm long, 0.22-[0.35]-0.48 mm wide, margin erose to slightly erose. Sporangia subglobose, long stalked, arcus of (12)-14-[17]-25 indurated cells, these 32.60-[40.78]-48.90 μm tall. Spores 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 34.23-[40.59]-47.27 μm in diameter, echinate, with complete echinae bases, laesura obscured by ornamentation. Chromosome number unknown.

Figure 23. A. *Adiantopsis parvisegmenta* (C.V. Morton 4166, US). Scale bar = 3 cm. B. Small, revolute ultimate divisions of *A. parvisegmenta*. Scale bar = 0.15 cm.
Habitat: Occurring on rocks, most likely amphibolite, at approximately 800 meters altitude.

Notes: As its name implies, *A. parvisegmenta* is easily distinguished from most other pinnate taxa by its small ultimate divisions or segments. However, it may be confused with *A. vincentii*, as the ultimate division sizes of the two taxa overlap. Three characters can be used to reliably distinguish the two species. *Adiantopsis parvisegmenta* has a spongiose lamina in contrast to the papyraceous lamina of *A. vincentii*. The fertile ultimate divisions of *A. parvisegmenta* are strongly revolute, whereas those of *A. vincentii* are more or less flat. Finally, *A. parvisegmenta* is quadripinnate with a generally broader lamina than *A. vincentii*, which is tripinnate and generally narrower.

*Adiantopsis parvisegmenta* is most likely a diploid species, based on arcus cell, guard cell, and spore sizes. This species is implicated in the parentage of the pedate *A. pentagona*, at least in part. Some elements within the putative allotetraploid *A. pentagona* have small ultimate divisions that are strongly revolute when fertile, two characters that may be inherited from an *A. parvisegmenta* parent. However, because these collections intergrade morphologically with other *A. pentagona* collections, no clear boundary can be made solely on morphological data. Resolution of the parentage of these collections will likely be obtained only with molecular data.

Like other *Adiantopsis* taxa, *A. parvisegmenta* is known from very few collections and from one small geographic region. It is confined to the Escambray Mountains of central Cuba. These mountains are composed of an amphibolite rock, and this species appears to be confined to this substrate, as it is not found outside of the region. The species lies within the Trinidad and Valley de los Ingenios National Park and World Heritage site, which should afford it some protection.

It is not clear in which modern Cuban provinces this species occurs. Collections were made prior to the break up of Las Villas province into Villa Clara, Cienfuegos, and Sancti Spiritus. All three provinces include portions of the Escambray Mountains (sometimes referred to as the Trinidad Mountains by collectors), and collection data is not detailed enough to be identify the corresponding modern province. However, the species probably occurs throughout this mountain range, and thus may be found in any of the
three provinces. For the purposes of the specimens examined list, all species are stated to have been collected in Las Villas.

It should be noted that specimens of *A. parvisegmenta* were frequently determined as *A. reesii*. In folders at US, Proctor noted that these collections were not *A. reesii*, and he was correct. Thus, Cuban material determined as *A. reesii* may be *A. parvisegmenta*, *A. rupicola*, or *A. vincentii*, as these species were frequently included under *A. reesii* by past researchers.


**Rhizome** decumbent to erect, stiff, to 5.9 cm long, 0.3-[0.64]-1.1 cm in diameter; **scales** dense, overlapping, persistent, bicolorous with a black to dark brown center and ephemeral golden margins, lanceate to acicular, basifixed, 3.61-[7.47]-13.93 mm long, 0.30-[0.52]-0.87 mm wide, bases truncate, margins entire, apices attenuate, gland tipped. **Fronds** aggregated, erect, 12.5-[32.61]-65.5 cm long. **Stipes** persistent, atropurpureous to atrocastaneous, bicarinate adaxially, longer than or equal (shorter) to lamina, 8.5-[17.56]-35.5 cm long, 0.4-[1.09]-2.3 mm in basal diameter; **carinae** golden, beginning near midpoint of stipe and continuing into rachis; **scales** extending 1.4-[3.28]-6.4 cm up the stipe, deciduous, divergent, concolorous, tan, lanceate, pseudopeltate to basifixed, 3.2-[6.58]-9.5 mm long, 1.2-[4.00]-5.2 mm wide, bases biauriculate to truncate, margins
entire, apices attenuate, gland tipped; *hairs* diffuse, catenate-capitate. *Laminae* tripinnate, bipinnate, to quadripinnate, triangular, drying green to brown, 9.5-[15.89]-30.0 cm long, 4.5-[9.29]-19.0 cm wide, apex pinnate, attenuate; *lamina tissue* spongiose, adaxially glabrous with diffuse, glossy-white epidermal cells, hydathodes marginal; *hairs* diffuse abaxially, catenate-capitate, three-celled, basal cell elongate, clear or white, middle cell short, clear, red, or golden, apical cell bulbous, clear, red, or golden; *stoma* abaxial, guard cells 48.90-[61.22]-68.46 μm long. *Lamina axes* persistent, atropurpulaceous to atrocastaneous, not grading into lamina at apices, adaxially bicarinate; *rachis* 0.5-[0.73]-1.4 mm in basal diameter; *carinae* golden, interrupted at axis junctions, not grading into lamina; *scales* absent; *hairs* concentrated at axis junctions, diffuse abaxially, catenate-capitate. *Pinnae* ascending to patent, 21-[24]-33 pairs, alternate, occasionally incurved in basal half of lamina, straight distally, linear to narrowly triangular, to 3.1-[6.13]-12.4 cm long, 0.9-[2.89]-7.4 cm wide, apices acute to cuneate, conform. *Pinnules* anadromous, slightly ascending to patent, linear, basal pinnules 1.1-[2.39]-6.0 cm long, 0.5-[0.76]-1.0 cm wide, basiscopic pinnules slightly larger than acroscopic pinnules, apices cuneate to acute, conform. *Ultimate divisions* slightly ascending to patent, strongly articulate, flabellate, rhombiform, to oblong, 3.2-[5.1]-8.0 mm long, 2.5-[3.4]-4.5 mm wide, bases acute, truncated, margins entire, apices round to acute; *terminal divisions* as others; *stalks* persistent, swollen at junction with lamina tissue, 2.4-[3.5]-4.8 mm long. *Veins* free, flabellate, immersed in lamina, occult to obscure. *Sori* marginal on both acroscopic and basiscopic margins, uninerved; *pseudoindusia* distinct, lunate, hyaline, occasionally black maculate, 8.0-[8.53]-9.0 mm long, 2.4-[4.07]-6.0 mm wide, margin erose. *Sporangia* subglobose, long stalked, arcus of 14-[17]-20 indurated cells, these 35.86-[40.59]-47.27 μm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 35.86-[41.40]-45.64 μm in diameter, echinate, echinae compact with complete bases, laesura obscured by ornamentation. *Chromosome number* unknown.

**Distribution:** Found on the islands of Cuba, Jamaica, and Puerto Rico.

**Habitat:** Shaded, rocky limestone or serpentine slopes and cliffs.
Figure 24. A. *Adiantopsis paupercula* (W. R. Maxon 4239, US). Scale bar = 3 cm. B. Ultimate divisions of *A. paupercula*. Scale bar = 0.5 cm.
FIGURE 25. Distribution of *A. paupercula* on Cuba, Jamaica, and Puerto Rico.

**Notes:** *Adiantopsis paupercula* is one of the more distinctive *Adiantopsis* species. The strongly articulate, flabellate to rhombiform ultimate divisions with a swelling at the junction of the stalk and lamina tissue distinguish this species from other *Adiantopsis*. It is likely a diploid species, as its arcus cell and spore sizes place it within a diploid group of taxa. However, its guard cell sizes are larger than other putative diploids, and it is not clear why.

*Adiantopsis paupercula* is the most widespread endemic Caribbean *Adiantopsis*. This is probably because the species can occur on both limestone and serpentine substrates, whereas other endemic Caribbean *Adiantopsis* appear to be more restricted. It should be noted that on a recent collecting trip to Puerto Rico *A. paupercula* was not found, and it may no longer be on the island, as it was previously only known from one collection. However, it probably still occurs on Cuba and Jamaica. In Cuba, some of its habitat is protected by the Alejandro de Humboldt National Park and World Heritage site.

Cuban collections of *A. paupercula* were collected in the province of Oriente prior to its break up into Las Tunas, Granma, Holguín, Santiago de Cuba and Guantánamo. For some collections, it could not be determined what modern province they are located,
and Oriente is indicated as the province of collection.


**Portland:** East slope of the John Crow Mts., ca. 2.5 miles southwest of Ecclesdown, elevation 2000-3000 ft. in pockets of jagged limestone crags, April 4, 1951, *G. R. Proctor 5729* (MO). **St. Ann:** Douglas Castle District, ca. 2 mi. NW of Mason River Savanna, small dissected limestone knob, densely wooded, Jan. 6, 1967, *A. M. Evans 2349* (BM).


*Rhizome* erect to decumbent, stiff, to 3.0 cm long, 0.6-[0.93]-1.4 cm in diameter; *scales* dense, overlapping, persistent, bicolorous with a black to dark brown center and ephemeral, golden margins, lanceate, basifixed, 3.50-[4.13]-4.75 mm long, 0.43-[0.44]-0.45 mm wide, bases truncate, margins entire, apices acute, gland tipped. *Fronds* aggregated, strict, 21.7-[27.18]-32.3 cm long. *Stipes* persistent, atropurpureous to atrocastaneous, bicarinate adaxially, longer than or equal to lamina, 11.3-[16.05]-19.0 cm long, 0.8-[1.06]-1.3 mm in basal diameter; *carinae* golden, beginning at stipe base or in the basal ½ of stipe and continuing into rachis; *scales* extending 2.3-[2.96]-3.4 cm up the stipe, deciduous, appressed, concolorous, tan, lanceolate, pseudopeltate, 3.50-[3.75]-4.00 mm long, 0.53-[0.56]-0.58 mm wide, bases biauriculate, margins entire to slightly repand, apices acute, gland tipped; *hairs* diffuse, rare, catenate-capitate. *Laminae* pedate, tripinnate to rarely quadripinnate basally, abruptly bipinnate above, broadly deltate-pentagonal, drying yellow-green, green, dark green to brown, 8.5-[12.78]-19.4 cm long,
9.4-[17.08]-25.7 cm wide, apex attenuate; lamina tissue chartaceous, adaxially glabrous with diffuse, glossy-white epidermal cells, hydathodes marginal; hairs diffuse abaxially, catenate-capitate, three-celled, basal cell elongate and clear, middle cell frequently short and red, golden red, golden, or white apical cell bulbous and clear, white, or golden; stoma abaxial, guard cells 53.79-[65.86]-78.24 μm long. Lamina axes persistent, atropurpureous to atrocastaneous, grading into lamina and taking its color and texture, adaxially bicarinate; rachis 0.4-[0.64]-1.0 mm in basal diameter; carinae golden, interrupted at axis junctions, grading into lamina; scales concentrated at rachis-costa junctions, diffuse abaxially, deciduous, appressed to patent, concolorous, tan, linear, basifixed, 0.45-[.67]-0.88 mm long and 0.02-[0.04]-0.07 mm wide, base truncate, margins entire, apex acute, gland tipped; hairs concentrated at axis junctions, diffuse abaxially, catenate-capitate. Pinnae ascending to patent, 21-[24.8]-28 pairs, basal pinnae opposite to sub-opposite, straight, triangular, inequilateral, to 4.7-[8.54]-12.9 cm long, 1.7-[3.23]-6.0 cm wide, apices attenuate to acute, confluent; penultimate pinnae opposite to sub-opposite, narrowly fusiform to linear, abruptly shorter, 2.5-[4.58]-7.1 cm long; distal pinnae alternate, quickly reduced in length. Pinnules anadromous, patent to slightly ascending, linear, apices attenuate to cuneate, confluent; basal basiscopic pinnules of basal pinnae narrowly triangular to fusiform, much extended, 1.0-[3.50]-5.6 cm long, 2.2-[3.6]-5.1 times longer than basal acroscopic pinnule, basal acroscopic pinnule 0.5-[0.89]-1.3 cm long, distal pinnules of first pinnae equivalent, abruptly shorter than basal basiscopic pinnule. Ultimate divisions ascending, dimidiate, articulate, oblanceolate, narrowly elliptic, to narrowly oblong, 4.0-[6.10]-9.0 mm long, 1.4-[2.20]-3.5 mm wide, bases cuneate, uniauriculate acroscopically, margins entire proximally, apices round to acute, crenulate; terminal divisions narrowly trullate to narrowly elliptic, bases acute to cuneate, margins entire proximally, apices acute to cuneate, crenulate; stalks persistent, not swollen at junction with lamina tissue, 0.10-[0.33]-0.60 mm long. Veins free, anadromous, immersed in lamina, occult to obscure. Sori marginal on both acroscopic and basiscopic margins, uninerved; pseudoindusia distinct, lunate to quadrangular, green to white, occasionally black maculate, hyaline distally, 0.60-[0.72]-0.84 mm long, 0.30-[0.43]-0.56 mm wide, margin slightly erose. Sporangia subglobose, long stalked, arcus of 13-[14]-15(-20) indurated cells, these 40.75-[48.80]-55.42 μm tall. Spores 64 per
sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 38.31-[45.50]-54.61 μm in diameter, densely echinate, echinae bases dissected, laesura obscured by ornamentation. *Chromosome number* unknown.

**Distribution:** A rare fern known only from the Dominican Republic and Jamaica.

**Habitat:** Terrestrial in humus on wooded hillsides scattered with limestone rocks; 2500 – 3100 ft. altitude.

**Notes:** *Adiantopsis pedata* formerly included plants from Cuba. However, the Cuban material, recognized here as *A. pentagona*, is clearly distinct. Carinae beginning in the basal half of the stipes, generally ascending ultimate divisions with crenulate apices, and a mode of 14 arcus cells distinguish *A. pedata* from *A. pentagona*. *Adiantopsis pentagona* has carinae beginning in the apical half of the stipes, patent or slightly ascending ultimate divisions, entire or only slightly crenulate ultimate division apices, and a mode of 16 arcus cells. Both Caribbean taxa may be confused with the South American *A. × australopedata* Hickey, Barker, & Ponce, which is a sterile hybrid that occurs in the tri-border region of Argentina, Brazil, and Paraguay. The aborted spores, crenulate margins, and generally much larger frond size distinguish *A. × australopedata* from the Caribbean taxa (Hickey *et al.*, 2003).

*Adiantopsis pedata* appears to be a tetraploid derivative of *A. radiata* and *A. reesii*. Arcus cell, guard cell, and spore sizes strongly suggest that it is tetraploid. Its pedate morphology suggests that it is a hybrid taxon, with *A. radiata* as one parent (Hickey *et al.*, 2003). Also shared with *A. radiata* are spore echinae that are basally dissected, and a common pattern of lamina development. With *A. reesii*, *A. pedata* shares distinctly toothed ultimate division apices and carinae beginning in the lower half of the stipe. Based on all these data, *A. pedata* is supported as a tetraploid derivative of *A. radiata* and *A. reesii*. Future cytological research needs to be conducted to confirm its ploidy level, and future molecular research should examine the parentage of *A. pedata*.

*Adiantopsis pedata* is a rare plant that probably still exists today. Although no recent collections have been made, it occurs in very rural areas that have little economic
FIGURE 26.  A. *Adiantopsis pedata* (*Wm. Harris 10878*, GH). Scale bar = 3 cm. B. Ultimate divisions of *A. pedata* with toothed apices. Scale bar = 0.75 cm.
development, such as the Cockpit Country of Jamaica. Given that ecotourism is becoming an industry in this part of Jamaica, the habitat of *A. pedata* is likely to be preserved and the species may still be found there if collections are sought.

**Specimens Examined:** **Dominican Republic.** **Monte Cristi:** Cordillera Central, Monción, at a brook, c. 400 m, very rare, 30 May 1929, *E. L. Ekman 12693* (B, BM, US-2).


**Adiantopsis pentagona** Barker and Hickey, *ined.* **TYPE:** Cuba, Santa Clara Province, vicinity of Sopapo, Buenos Aires, Trinidad Mountains, shaded limestone cliff, 4 August 1936, *L. B. Smith 3320, A. R. Hodgdon, & F. Gonzalez* (holotype GH!;
Rhizome erect to decumbent, stiff, to 3.8 cm long, 0.5-[1.29]-1.8 cm in diameter; scales dense, overlapping, persistent, bicolorous with a black to dark brown center and ephemeral, golden margins, acicular to lanceate, basifixed, 2.13-[4.75]-7.58 mm long, 0.08-[0.51]-0.88 mm wide, bases truncate, margins repand to entire, apices acute, gland tipped. Fronds aggregated, strict, 33.2-[47.55]-72.1 cm long. Stipes persistent, atropurpureous to atrocastaneous, bicarinate adaxially, longer than or equal to lamina, 17.1-[26.53]-44.0 cm long, 0.8-[1.39]-2.1 mm in basal diameter; carinae golden, beginning in the upper ½ (½) of stipe and continuing into rachis; scales extending 2.0-[2.58]-3.7 cm up the stipe, deciduous, appressed, concolorous, tan, acicular to lanceate (subulate), pseudopeltate, 1.05-[3.89]-6.38 mm long, 0.13-[0.50]-0.83 mm wide, bases biauriculate, margins entire to slightly repand, apices acute, gland tipped; hairs diffuse, rare, catenate-capitate. Laminae pedate, tripinnate to quadripinnate basally, abruptly bipinnate above, broadly deltate-pentagonal, drying brown, dark green, green to yellow green, 14.7-[20.38]-28.1 cm long, 12.8-[29.87]-48.2 cm wide, apex long attenuate; lamina tissue thin-spongiose, adaxially glabrous with diffuse, glossy-white epidermal cells, hydathodes marginal; hairs diffuse abaxially, catenate-capitate, three-celled, basal cell elongate and clear, middle cell frequently short and white, golden, golden red, or red, apical cell bulbous and clear, white, or golden; stoma abaxial, guard cells 48.90-[67.51]-83.13 μm long. Lamina axes persistent, atropurpureous to atrocastaneous, grading into lamina and taking its color and texture, adaxially bicarinate; rachis 0.5-[0.80]-1.3 mm in basal diameter; carinae golden, interrupted at axis junctions, grading into lamina; scales concentrated at rachis-costa junctions, diffuse abaxially, deciduous, appressed to patent, concolorous, tan, lanceate to linear, basifixed, 0.77-[1.11]-1.45 mm long, 0.08-[0.10]-0.17 mm wide, base truncate, margins entire, apex gland tipped; hairs concentrated at axis junctions, diffuse abaxially, catenate-capitate. Pinnae patent to ascending, 28-[35.3]-40 pairs, basal pinnae opposite to sub-opposite, straight, triangular, inequilateral, to 6.4-[14.93]-24.1 cm long, 2.8-[10.41]-19.9 cm wide, apices attenuate to acute, confluent; penultimate pinnae sub-opposite, linear, abruptly shorter, 1.4-[7.62]-14.2 cm long; distal pinnae alternate, quickly reduced in length. Pinnules anadromous, patent to
slightly ascending, linear to narrowly lanceate, apices cuneate to attenuate, confluent; *basal basiscopic pinnules* of basal pinnae fusiform to narrowly triangular, much extended, 1.8-[8.41]-15.3 cm long, 1.8-[5.6]-13.1 times longer than basal acroscopic pinnule/segment, basal acroscopic pinnule or segment 0.4-[1.87]-5.8 cm long, distal pinnules of first pinnae equivalent, abruptly shorter than basal basiscopic pinnule.

*Ultimate divisions* patent to slightly ascending, dimidiate, articulate, narrowly oblong, oblanceolate, lanceolate, to narrowly elliptic, 6.1-[8.14]-11.1 mm long, 2.5-[3.14]-4.2 mm wide, bases cuneate, frequently uniauriculate acroscopically, margins entire to slightly crenulate, apices round to acute; *terminal segments* narrowly trullate, narrowly oblong, to narrowly elliptic, bases acute to cuneate, margins entire to slightly crenulate, apices acute to round; *stalks* persistent, not swollen at junction with lamina tissue, 0.9-[3.50]-6.3 mm long. *Veins* free, anadromous, immersed in lamina, occult to obscure. *Sori* marginal on both acroscopic and basiscopic margins, uninerved; *psuedoindusia* distinct, lunate to quadrangular, hyaline with a brown or black area proximally where hydathode terminates, occasionally black maculate, 0.35-[0.72]-1.10 mm long, 0.20-[0.43]-0.60 mm wide, margin entire to slightly erose. *Sporangia* subglobose, long stalked, arcus of 14-[16]-22 indurated cells, these 40.75-[48.66]-58.68 μm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 40.75-[49.17]-58.90 μm in diameter, densely echinate, echinae bases dissected, laesura obscured by ornamentation. *Chromosome number* unknown.

**Distribution:** A Cuban endemic found in the province of Pinar del Río, and the Escambray Mountains of Cienfuegos, Sancti Spiritus, and Villa Clara.

**Habitat:** Moist, shaded limestone or amphibolite soils, rocks, cliffs, and cave entrances. If in soil, generally found on slopes scattered with limestone or amphibolite rocks.

**Notes:** *Adiantopsis pentagona* is named for the overall pentagonal outline of the lamina. *Adiantopsis pedata* and *A. ×australopedata* Hickey, Barker, & Ponce also have pentagonal lamina outlines, and may be confused with *A. pentagona*. Carine beginning in the basal half of the stipes, distinctly crenulate ultimate division apices, generally
Figure 28. A. Adiantopsis pentagona (L. B. Smith 3320 et al., US). Scale bar = 3 cm. B. Ultimate divisions of A. pentagona without toothed apices. Scale bar = 0.75 cm.
ascending ultimate divisions, and mode of 14 arcus cells, distinguish *A. pedata* from *A. pentagona*, which has carinae beginning in the apical half of the stipe, entire or slightly crenulate ultimate division apices, patent to slightly ascending ultimate divisions, and a mode of 16 arcus cells. *Adiantopsis ×australopedata*, a hybrid distributed in the tri-border region of Argentina, Brazil, and Paraguay, may be distinguished from the Caribbean species by its aborted spores, crenulate margins, and generally larger laminae.

*Adiantopsis pentagona* appears to be the tetraploid derivative of *A. radiata* and *A. rupicola*. The large spores, guard cells, and arcus cells relative to putative diploid taxa, such as *A. radiata* and *A. rupicola*, suggest that *A. pentagona* is a tetraploid. Its pedate morphology suggests that it is a hybrid taxon, with *A. radiata* as one parent (Hickey *et al.*, 2003). Also shared with *A. radiata* are spore echinae that are basally dissected, and a common pattern of lamina development. With *A. rupicola*, *A. pentagona* shares carinae beginning in the apical half of the stipes, and the overall ultimate division shapes agrees most favorably with *A. rupicola*. The type of *A. pentagona*, Smith 3320 *et al.*, was selected in part because its morphology supports an allotetraploid origin clearly involving *A. radiata* and *A. rupicola*. However, some collections of *A. pentagona*, with relatively small ultimate divisions that are revolute when fertile, suggest that *A. parvisegmenta* may be the parent of another cryptic species. This putative cryptic species is included in *A. pentagona* as the available data do not clearly differentiate it. Future molecular research should encompass the morphological range of *A. pentagona*, and include *A. rupicola*, *A. parvisegmenta*, and *A. vincentii*, to evaluate if cryptic elements are included.

*Adiantopsis pentagona* is most likely still found in Cuba. In Pinar del Río, it is most likely protected within the boundaries of Valley de Viñales National Park, and by the Trinidad and Valley de los Ingenios National Park in the Escambray Mountains.

It is not clear in which Cuban provinces this species currently occurs. Collections were made prior to the break up of Las Villas province into Villa Clara, Cienfuegos, and Sancti Spíritus. All three provinces include portions of the Escambray Mountains (sometimes referred to as the Trinidad Mountains by collectors), and collection data is not always detailed enough to be identify the corresponding modern province. However, the species probably occurs throughout this mountain range, and thus may be found in any of the three provinces. For the purposes of the specimens examined list, specimens which
could not be placed in a modern province are indicated as occurring in Las Villas.


TYPE: Brasil, Estado de São Paulo, Iguape, A. C. Brade s.n. (holotype RB?).

Adiantopsis alata Prantl, Gartenfl. 32:99. t.1115. 1883. TYPE: Unknown (holotype HBG?).

Rhizome erect, stiff, to 3.3 cm long, 0.5-[0.72]-0.9 cm in diameter; scales dense, overlapping, persistent, bicolorous with a black to dark brown center and ephemeral, golden margins, lanceolate to acicular, pseudopeltate to basifixed, 3.75-[3.94]-4.43 mm long, 0.41-[0.51]-0.58 mm wide, bases cordate to truncate, margins repand, apices acute to acuminate, gland tipped. Fronds aggregated, strict, 19.7-[32.2]-62.3 cm long. Stipes persistent, atropurpureous to atrocastaneous, rarely bincarinate adaxially, longer than lamina, 10.5-[20.48]-47.0, 0.8-[1.29]-2.0 mm in basal diameter; carinae when present, golden, beginning at stipe base and continuing into lamina; scales extending 0.2-[1.79]-3.5 cm up the stipe, deciduous, appressed, bicolorous with a broad castaneous or tan center and golden margins, or concolorous and tan, lanceolate, pseudopeltate, 3.00-[3.96]-5.50 mm long, 0.45-[0.58]-0.75 mm wide, bases biauriculate, margins repand, apices acute, gland tipped; hairs diffuse, rare, catenate-capitate. Laminae palmate, radially bipinnate, orbiculate, geniculate, drying olive-green, dark green, black, to yellow green, 10.2-[15.2]-26.3 cm long, 4.4-[14.3]-25.8 cm wide; lamina tissue thin-spongiose, adaxially glabrous with diffuse, glossy-white epidermal cells, hydathodes marginal; hairs diffuse abaxially, catenate-capitate, three-celled, basal cell elongate and clear, middle cell frequently short and golden or red, apical cell bulbous and clear or white; stoma abaxial, guard cells 35.86-[49.77]-63.57 μm long. Lamina axes persistent, atropurpureous to atrocastaneous, grading into lamina and taking its color and texture, adaxially bincarinate; carinae golden, interrupted at axis junctions, grading into lamina
apically; scales absent; hairs concentrated at axis junctions, diffuse abaxially, catenate-capitate. *Pinnae* spreading radially from stipe apex, 3-9, straight, linear to narrowly fusiform, apices acute, conform; central pinna to 9.2-[11.74]-15.3 cm long, 1.4-[1.89]-2.7 cm wide; basal pinna to 2.6-[5.33]-9.2 cm long, 1.0-[1.44]-2.2 cm wide; *basal flabellate segments* frequently attached to the stipe apex with one segment between two pinnae, these often fertile. *Pinnules* patent to ascending, dimidiate, articulate, oblong to narrowly oblong, 6.0-[9.3]-13.5 mm long, 2.1-[2.8]-3.7 mm wide, bases cuneate to acute, margins entire to crenulate, apices round to acute; *terminal segments* lanceolate, oblanceolate to oblong, bases acute to cuneate, margins entire to crenulate, apices acute to round; *stalks* persistent, not swollen at junction with lamina tissue, 1.0-[3.3]-6.0 mm long. *Veins* free, anadromous, immersed in lamina, obscure to occult. *Sori* marginal on both acroscopic and basiscopic margins, uninerved; *pseudoindusia* distinct, lunate to quadrangular, hyaline with a brown or black area proximally where hydathode terminates, occasionally black maculate, 4.00-[5.89]-8.40 mm long, 2.20-[3.48]-5.60 mm wide, margin entire to slightly erose. *Sporangia* subglobose, long stalked, arcus of 16-[20]-27 indurated cells, these 30.97-[39.05]-46.46 μm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 34.23-[39.94]-47.27 μm in diameter, densely echinate, echinae bases dissected, laesura obscured by ornamentation. *Chromosome number* n=30.

**Distribution:** Widespread in tropical America from the Caribbean Islands and Mexico, south to Argentina.

**Habitat:** Moist, calcareous or serpentine, rocky, wooded slopes. Also on limestone cliffs and walls.

**Notes:** *Adiantopsis radiata* is the most distinctive *Adiantopsis* species, as it is the only palmate species. As the name implies, the pinnae radiate outward from a single point at the stipe apex. Young *A. radiata* may be confused with young *A. pedata* and *A. pentagona* because all three taxa share a similar ternate juvenile form. The most reliable character to distinguish these taxa, even in many juvenile specimens, is arcus cell
Figure 29. A. *Adiantopsis radiata* (G. R. Proctor 29256, F). Scale bar = 3 cm. B. Ultimate divisions of *A. radiata*. Scale bar = 0.75 cm.
Adiantopsis radiata has a mode of 20 arcus cells, whereas A. pedata possesses a mode of 14 and A. pentagona has a mode of 16. Also, the stipes of A. radiata are typically lacking carinae, whereas both A. pedata and A. pentagona stipes are always adaxially bicarinate. Another character that is useful for distinguishing A. radiata and A. pedata is ultimate division shape and orientation. The ultimate divisions of A. radiata are usually oblong with round apices and are generally patent. Adiantopsis pedata ultimate divisions are more frequently oblanceolate with a distinctly toothed apex and are ascending.

The two A. radiata synonyms are minor variations of A. radiata. Brade's A. radiata f. bifurcata is an abnormal plant with a pinna that is bifurcated at the apex. Adiantopsis alata is a form of A. radiata that is adaxially bicarinate along the stipe. Although most A. radiata specimens lack carinae on the stipe, there is a full gradation from those without to those with carinae. There are no other characters that separate the two taxa, and thus they are treated here as conspecific.

Adiantopsis radiata is implicated in an interesting pattern of reticulate and morphological evolution. The species apparently hybridizes with different pinnate taxa to produce pedate derivatives. In the Caribbean, these hybrid derived pedate taxa are A. pedata and A. pentagona, and in South America A. × australopedata (Hickey et al., 2003).

Adiantopsis radiata is by far the most common and widely distributed Adiantopsis species. It occurs throughout the Neotropics from the Caribbean to northern Argentina. The species is even cultivated for its distinctive lamina morphology.

It is not clear what modern province Cuban collections are located. Oriente is indicated as the province, although this province no longer exists.


Jamaica. Clarendon: Peckham Woods, wooded limestone hillside, in soil, c. 2500 ft., March 10, 1954, G. R. Proctor 8445 (MO); Peckham Woodland, in woodland 2500-2800 ft alt., February 3, 1910, Wm. Harris 10860 (F); Summit area of Crofts Mountain, 2500-2650 ft., in dense moist woodland sloping into a limestone sinkhole,

Unknown Parish: 1886, J.P. 390 (MO); Wm. Harris 9163(MO).


Rhizome decumbent to ascending, stiff, to 2.8 cm long, 0.6-[0.74]-0.8 cm in diameter; scales dense, overlapping, persistent, bicolorous with a black to dark brown center and ephemeral golden margins, lanceate to acicular, basifixed, 4.05-[4.74]-5.50 mm long, 0.52-[0.57]-0.61 mm wide, bases truncate, margins slightly repand, apices acute, gland tipped. Fronds aggregated, strict, 17.1-[34.54]-60.0 cm long. Stipes persistent, atrocastaneous, bicarinate adaxially, much shorter than lamina, 2.2-[8.98]-22.0 cm long, 1.0-[1.51]-2.6 mm in basal diameter; carinae golden, beginning at stipe base or in the basal ¼ of stipe and continuing into rachis; scales extending 1.9-[2.74]-4.2 cm up the stipe or to the rachis, deciduous, divergent, concolorous, tan, lanceate to acicular (subulate), pseudopeltate, 1.25-[3.95]-5.75 mm long, 0.20-[0.55]-0.74 mm wide, bases cordate, margins entire to slightly repand, apices acute, gland tipped; hairs diffuse, rare, catenate-capitate. Laminae tripinnate, lanceolate to narrowly triangular, drying dull green, 5.0-[25.57]-53.0 cm long, 5.5-[10.40]-14.6 cm wide, apex pinnatifid, attenuate to acuminate; lamina tissue papyraceous, adaxially glabrous with diffuse, glossy-white epidermal cells, hydathodes marginal; hairs diffuse abaxially, catenate-capitate, three-celled, basal cell elongate and clear, middle cell frequently short and clear, brown, or red, apical cell bulbous and frequently covering middle cell, white, clear, or golden; stoma abaxial, sunken, guard cells 32.60-[44.34]-53.79 μm long. Lamina axes persistent, atrocastaneous, grading into lamina and taking its color and texture, adaxially biconcave; rachis 1.1-[1.33]-1.5 mm in basal diameter; carinae golden, interrupted at axis junctions, grading into lamina; scales concentrated at rachis-costa junctions, diffuse abaxially, deciduous, appressed to patent, concolorous, tan, narrowly rhombic to lanceolate, basifixed, 0.70-[1.05]-1.60 mm long and 0.05-[0.11]-0.19 mm wide, base acute, margins entire, apex acute, gland tipped; hairs concentrated at axis junctions, diffuse abaxially, catenate-capitate. Pinnae ascending, 23-[31.8]-55 pairs, alternate, slightly incurved in basal half of lamina, straight distally, narrowly triangular to linear, to 5.7-[6.60]-8.2 cm
long, 1.8-[2.58]-3.7 cm wide, apices cuneate to acuminate, confluent. *Pinnules* anadromous, ascending to slightly ascending, narrowly triangular to narrowly lanceate, to 1.2-[1.56]-2.3 cm long and 0.7-[0.98]-1.10 cm wide, basiscopic pinnules slightly larger than acroscopic pinnules, apices obtuse to acute, confluent. *Ultimate divisions* ascending, articulate, narrowly oblong, oblanceolate, to nearly flabellate, 3.4-[5.3]-9.1 mm long, 1.2-[2.1]-3.8 mm wide, bases cuneate, margins entire to crenulate proximally, crenulate distally, apices round, acuminate to acute; *terminal divisions* narrowly trullate to narrowly oblong, bases acute to cuneate, margins entire to crenulate proximally, crenulate distally, apices cuneate to acute; *stalks* persistent, not swollen at junction with lamina tissue, 0.3-[0.44]-0.6 mm long. *Veins* free, anadromous, impressed to immersed in lamina, prominent. *Sori* marginal, on both acroscopic and basiscopic margins, uninerved; *pseudoindusia* distinct, lunate to quadrangular, green to white, becoming hyaline distally, occasionally black maculate, 0.44-[0.61]-0.92 mm long, 0.30-[0.37]-0.44 mm wide, margin erose to entire. *Sporangia* subglobose, long stalked, arcus of 9-[14]-17(-23) indurated cells, these 21.19-[36.34]-48.90 μm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 30.97-[36.34]-44.83 μm in diameter, echinate, echinae bases complete, laesura obscured by ornamentation. *Chromosome number* unknown.

**Distribution:** A rare endemic of Hispaniola and Jamaica.

**Habitat:** Shaded limestone cliffs and slopes, to 900 meters altitude.

**Notes:** *Adiantopsis reesii* is distinctive in its toothed ultimate division apices which distinguish it from other pinnate *Adiantopsis*. Further, the ultimate divisions of *A. reesii* are rather elongate compared to other pinnate taxa such as *A. rupicola*, *A. parvisegmenta*, and *A. vincentii*.

*Adiantopsis reesii* is a putative diploid, as evidenced by the sizes of its guard cells, spores, and arcus cells. This species appears to be one diploid parent, along with *A. radiata*, of the putative tetraploid *A. pedata*. The distinctly toothed apices and ascending ultimate divisions of *A. reesii* are evident in *A. pedata*. Future molecular research should
examine this hypothesized relationship.

Like many other Adiantopsis species, *A. reesii* is known from only a few collections. The species appears to be rare, and it occurs only on limestone areas of Jamaica and Hispaniola. However, the species is probably still extant, as it occurs in rural areas with little economic development. Additionally, ecotourism in the Cockpit Country of Jamaica may protect its habitat from economic development.


![Figure 31. Distribution of *A. reesii*.](image)

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Figure 32. A. *Adiantopsis reesii* (E. L. Ekman 9987, F). Scale bar = 3 cm. B. Ultimate divisions of *A. reesii* with toothed apices. Scale bar = 0.25 cm.

Rhizome ascending to decumbent, stiff, to 2.2 cm long, 0.6-[0.88]-1.2 cm in diameter; scales dense, overlapping, persistent, bicolorous with a black to center and ephemeral golden margins, acicular to linear, basifixed, 1.60-[2.70]-3.60 mm long, 0.30-[0.32]-0.36 mm wide, bases truncate, margins slightly repand, apices acute, gland tipped. Fronds aggregated, strict, 23.5-[33.24]-50.2 cm long. Stipes persistent, atropurpureous to atrocastaneous, occasionally bicarinate adaxially, shorter than lamina, 4.0-[10.95]-17.5 cm long, 0.6-[1.21]-1.7 mm in basal diameter; carinae when present golden, beginning in upper ¼ of stipe and continuing into rachis; scales extending 1.9-[4.04]-7.1 cm up the stipe, deciduous, divergent, concolorous, tan, acicular to lanceate, pseudopeltate to basifixed, 1.00-[3.57]-6.64 mm long, 0.06-[0.25]-0.70 mm wide, bases biauriculate to truncate, margins slightly repand to entire, apices attenuate, gland tipped; hairs diffuse, catenate-capitate. Laminae tripinnate, narrowly triangular to lanceate, drying dull green to brown, 11.0-[22.17]-39.5 cm long, 4.2-[9.53]-17.5 cm wide, apex pinnatifid, attenuate; laminae tissue thin-spongiose to chartaceous, adaxially glabrous with diffuse, glossy-white epidermal cells, hydathodes marginal; hairs diffuse abaxially, catenate-capitate, three-celled, basal cell elongate, clear or white, middle cell short, tan or clear, apical cell bulbous, clear, white, or golden; stoma abaxial, guard cells 42.38-[49.75]-57.05 μm long. Lamina axes marcescent with costae curling acroscopically, atropurpureous to atrocastaneous, grading into lamina and taking its color and texture, adaxially bicarinate; rachis 0.6-[0.94]-1.5 mm in basal diameter; carinae golden, interrupted at axis junctions, grading into lamina; scales concentrated at rachis-costa junctions, diffuse abaxially, deciduous, appressed to patent, concolorous, tan, narrowly lanceolate, basifixed, 0.67-[1.04]-1.12 mm long and 0.08-[0.11]-0.16 mm wide, base acute, margins entire, apex attenuate, gland tipped; hairs concentrated at axis junctions, diffuse abaxially, catenate-capitate. Pinnae ascending, 21-[22.3]-24 pairs, alternate, frequently incurved in basal half of lamina, straight distally, narrowly triangular, to 3.2-[8.13]-16.0 cm long, 0.9-
[2.70]-5.5 cm wide, apices acute to attenuate, confluent. **Pinnules** anadromous, patent to slightly ascending, narrowly triangular to linear, basal pinnules 0.7-[2.04]-3.9 cm long, 0.5-[0.99]-1.5 cm wide, basiscopic pinnules slightly larger than acroscopic pinnules, apices acute, confluent. **Ultimate divisions** slightly ascending to patent, articulate, oblong to trullate, 3.8-[6.43]-9.5 mm long, 2.0-[3.17]-5.5 mm wide, bases acute to cuneate, frequently uniauriculate acroscopically, margins entire, apices acute to round; terminal divisions trullate to narrowly trullate, bases acute to cuneate, margins entire, apices acute to cuneate; **stalks** persistent, not swollen at junction with lamina tissue, 0.1-[0.22]-0.5 mm long. **Veins** free, anadromous, immersed in lamina, occult to obscure. **Sori** marginal on both acroscopic and basiscopic margins, uninerved; **pseudoindusia** distinct, lunate to quadrangular, green to white, becoming hyaline distally, occasionally black maculate, 0.42-[0.57]-0.70 mm long, 0.30-[0.33]-0.40 mm wide, margin erose to slightly erose. **Sporangia** subglobose, long stalked, arcus of 12-[16]-21 indurated cells, these 32.6-[37.16]-42.38 μm tall. **Spores** 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 34.23-[37.75]-40.75 μm in diameter, echinate, echinae bases complete, laesura obscured by ornamentation. **Chromosome number** unknown.

**Distribution**: Endemic to the province of Pinar del Rio, Cuba.

**Habitat**: Shaded, rocky limestone slopes, or on shaded limestone cliffs.

**Notes**: *Adiantopsis rupicola* may be confused with *A. vincentii*. The carinae of *A. rupicola* begin in the apical quarter of the stipes, whereas the carinae of *A. vincentii* begin in the basal half of the stipes. Also, *A. rupicola* has a mode of 16 arcus cells, whereas *A. vincentii* has a mode of 14. The generally smaller, obovate to oblong ultimate divisions and lanceate to lanceolate lamina of *A. vincentii* also distinguish it from *A. rupicola* which has generally larger ultimate segments that are trullate to oblong and a narrowly triangular to lanceate lamina. Additionally, *A. vincentii* appears to be hemidimorphic with smaller sterile fronds, whereas *A. rupicola* shows no signs of dimorphism.

Guard cell, spore, and arcus cell sizes place *A. rupicola* in a group of putative...
Figure 33. A. Adiantopsis rupicola (Britton 7497 et al., US). Scale bar = 3 cm. B. Ultimate divisions of A. rupicola. Scale bar = 0.75 cm.
diploid species. This species is most likely a parent, along with *A. radiata*, of the putative tetraploid *A. pentagona*. The overall ultimate division shape of *A. pentagona* resembles the generally trullate divisions of *A. rupicola* more than those of any other extant, pinnate species. Additionally, carinae beginning in the upper half of the stipes is unique to these two species. However, *A. rupicola* may not be the parent of all elements of *A. pentagona*. Some specimens of *A. pentagona* have a tendency towards relatively larger and slightly more compound laminae, and smaller ultimate divisions, suggesting an *A. parvisegmenta* parentage for these collections.

*Adiantopsis rupicola* is frequently spelled incorrectly as *A. rupincola*. Tryon and Tryon (1982) consistently use this incorrect spelling, and some specimens are determined with it. However, Maxon (1908) published the species as *A. rupicola*, and on subsequent determinations used that spelling. Therefore, rupicola does not appear to be an orthographic error and should be used.

Similar to other *Adiantopsis* taxa, *A. rupicola* is known from few collections. It is a rare species, endemic to Pinar del Río, Cuba. Although there are no recent collections of *A. rupicola*, it probably still occurs there, and is likely protected within the boundaries of Valley de Viñales National Park.


*Rhizome* erect to repent, stiff, to 2.7 cm long, 0.5-[1.07]-1.5 cm in diameter; *scales* dense, overlapping, persistent, bicolorous with a black to dark brown center and ephemeral golden margins, narrowly lanceate to acicular, basifixed, 2.60-[3.21]-5.68 mm long, 0.20-[0.34]-0.44 mm wide, bases truncate, margins entire to slightly repand, apices attenuate to cuneate, gland tipped. *Fronds* aggregated, strict, 13.2-[22.88]-36.5 cm long. *Stipes* persistent, atropurpureous to atrocastaneous, bicarinate adaxially, shorter than lamina, 2.9-[7.53]-13.8 cm long, 0.7-[1.39]-1.8 mm in basal diameter; *carinae* golden, beginning in basal $\frac{1}{2}$ of stipe and continuing into rachis; *scales* extending 1.5-[2.13]-3.4 cm up the stipe, deciduous, divergent, concolorous, tan, narrowly lanceate to acicular, pseudopeltate, 0.70-[2.23]-2.80 mm long, 0.06-[0.32]-0.46 mm wide, bases biauriculate to truncate, margins slightly repand to entire, apices attenuate, gland tipped; *hairs* diffuse, catenate-capitate. *Laminae* tripinnate, lanceate to lanceolate, drying green to brown, 12.2-[19.17]-28.5 cm long, 4.2-[6.23]-10.5 cm wide, apex pinnatifid, attenuate; *lamina tissue* papyraceous, adaxially glabrous with diffuse, glossy-white epidermal cells, hydathodes marginal; *hairs* diffuse abaxially, catenate-capitate, three-celled, basal cell elongate, clear or white, middle cell short, tan or clear, apical cell bulbous, clear, white, or golden; *stoma* abaxial, guard cells 40.75-[45.84]-53.79 μm long. *Lamina axes* marcescent with costae curling acroscopically, atropurpureous to atrocastaneous, grading into lamina and taking its color and texture, adaxially bicarinate; *rachis* 0.6-[0.88]-1.2 mm in basal diameter; *carinae* golden, interrupted at axis junctions, grading into lamina; *scales* concentrated at rachis-costa junctions, diffuse adaxially, deciduous, patent to appressed, concolorous, tan, linear, biseriate, basifixed, 0.62-[0.84]-1.24 mm long and 0.02-[0.036]-0.04 mm wide, base cuneate to truncate, margins entire, apex attenuate, gland tipped; *hairs* concentrated at axis junctions, diffuse abaxially, catenate-capitate. *Pinnae* ascending to patent, 23-[28]-32 pairs, alternate to sub-opposite, frequently incurved in basal half of lamina, straight distally, narrowly triangular to linear, slightly inequilateral, to 2.3-[4.24]-7.8 cm long, 0.7-[1.19]-1.8 cm wide, apices attenuate,
confluent. *Pinnules* anadromous, patent to slightly ascending, narrowly triangular to linear, basal pinnules 0.6-[1.07]-1.7 cm long, 0.3-[0.56]-1.0 cm wide, basiscopic pinnules slightly larger than acroscopic pinnules, apices cuneate to acute, confluent. *Ultimate divisions* patent to slightly ascending, articulate, obovate, oblong to elliptic, 2.7-[4.28]-6.0 mm long, 1.7-[2.48]-3.6 mm wide, bases cuneate, margins entire, apices round to acute; *terminal divisions* trullate to rhombic, bases cuneate to acute, margins entire, apices acute to round; *stalks* persistent, not swollen at junction with lamina tissue, 0.1-[0.23]-0.5 mm long. *Veins* free, anadromous, immersed in lamina, obscure to occult. *Sori* marginal on both acroscopic and basiscopic margins, uninerved; *pseudoindusia* false, distinct, lunate to quadrangular, green to white, becoming hyaline distally, occasionally black maculate, 0.46-[0.59]-0.70 mm long, 0.40-[0.43]-0.50 mm wide, margin slightly erose to entire. *Sporangia* subglobose, long stalked, arcus of 12-[14]-16 indurated cells, these 32.60-[38.01]-52.16 μm tall. *Spores* 64 per sporangium, tetrahedral-globose, golden at maturity, white to pale yellow when immature, 32.60-[38.16]-44.01 μm in diameter, echinate, echinae bases complete, laesura obscured by ornamentation. *Chromosome number* unknown.

**Distribution:** A rare endemic in the Escambray mountains of Cienfuegos, Sancti Spiritus, and Villa Clara Provinces, Cuba.

**Habitat:** Unknown.

**Notes:** *Adiantopsis vincentii* is named in honor of Michael A. Vincent, curator of the Willard Sherman Turrell Herbarium (MU) at Miami University, Oxford, Ohio. Dr. Vincent has continued to expand the collection at MU, and has raised the Institution's standing in the world of botany through his activities as curator. Further, he has spent a significant amount of time dealing with the research loans, and through these activities facilitates the research of many at Miami University.

*Adiantopsis vincentii* is most likely to be confused with either *A. rupicola* or *A. parvisegmenta*. The generally smaller, obovate to oblong ultimate divisions and lanceate to lanceolate lamina of *A. vincentii* distinguish it from *A. rupicola* which has generally
Figure 34. A. *Adiantopsis vincentii* (C. V. Morton 10389, US). Scale bar = 3 cm. B. Ultimate divisions of *A. vincentii*. Scale bar = 0.5 cm.
larger ultimate segments that are trullate to oblong and a narrowly triangular to lanceate lamina. *Adiantopsis vincentii* may be distinguished from *A. parvisegmenta* by three characters. The lamina of *A. vincentii* is papyraceous whereas the lamina of *A. parvisegmenta* is spongiose. *Adiantopsis vincentii* is tripinnate with a generally narrower lamina than the quadripinnate and broader lamina of *A. parvisegmenta*. Also, the fertile segments of *A. vincentii* are more or less flat whereas the fertile segments of *A. parvisegmenta* are strongly revolute.

Based on the sizes of guard cells, spores, and arcus cells, *A. vincentii* is placed with a putative diploid group of species. *Adiantopsis vincentii* is also the only hemidimorphic Caribbean *Adiantopsis*. On herbarium specimens with large rhizomes, and thus presumed to be mature plants, the fertility of the fronds is strongly correlated with frond size. The smallest fronds are consistently sterile, with a gradual increase in the number of sori and sporangia on progressively larger fronds. This pattern is not evident on specimens of other *Adiantopsis* taxa, and may serve as a useful character for recognizing the species if it can be confirmed to be unique.

Presently, *A. vincentii* is not convincingly implicated in any patterns of reticulate evolution in *Adiantopsis*. However, it is possible that some elements of *A. pentagona* may have an *A. vincentii* parentage although no explicit hypothesis is presented. Future molecular studies should include *A. vincentii* as the range of ultimate division variation in *A. pentagona* includes the character states that would likely be inherited from an *A. vincentii* parent.

*Adiantopsis vincentii* is known from the old Cuban province of Las Villas, as are *A. parvisegmenta* and *A. pentagona*. All specimens of *A. vincentii* are listed under Las Villas, as the label data is insufficient to identify it to its modern province.

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