

Systematic consideration of petiole anatomy of species of *Echinodorus* Richard (Alismataceae) from north-eastern Brazil

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Abstract

Petiole anatomy of the north-eastern Brazilian species *Echinodorus glandulosus*, *E. palaeifolius*, *E. pubescens*, *E. subalatus*, *E. lanceolatus* and *E. paniculatus* were examined. All species had petioles with an epidermis composed of tabular cells with thin walls. The chlorenchyma just below the epidermis alternates with collateral vascular bundles. The interior of the petiole is filled by aerenchyma with ample open spaces or lacunas. The lacunas are bridged at intervals by plates, or by diaphragm-like linkages. There are lactiferous ducts and groups of fibres throughout the entire length of the petiole, but more frequently in the chlorenchyma. Important taxonomic characteristics for the genus *Echinodorus* include the shape and outline of the petiole in transversal section, the presence of winged extensions, and the number of vascular bundle arcs. Exceptions occur in *E. lanceolatus* and *E. paniculatus*, whose petioles have similar anatomic patterns. A comparative chart of the petiole anatomic characteristics analyzed is presented.

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Introduction

Plants of the family Alismataceae are emergent or floating herbaceous plants inhabiting both stagnant and flowing water environments. The family comprises 11 genera and approximately 75 native species in the temperate and tropical zones (Haynes and Holm-Nielsen, 1994). *Echinodorus* and *Sagittaria* are the only neotropical genera of this family, and they demonstrate the greatest species diversity (Fasset, 1955; Rogers, 1983). *Echinodorus* has 26 species (Haynes et al., 1998),

and these occur predominantly in the South America tropics, a region considered the primary center of diversity for the genus (Haynes and Holm-Nielsen, 1989; Lot and Novelo, 1984).

The variety of petiole vascular patterns permitted Radford et al. (1974) to use these as a taxonomic characteristic. Howard (1962) developed the most complete classification system of petiole vein patterns for arboreal dicotyledonous species, taking into consideration the modifications occurring along their entire length. Based on this system, Tomlinson (1982) observed that the family Alismataceae had petiole vascular bundles arranged in arcs. According to Stant (1964), the vascular patterns in Alismataceae seem to be correlated with the size of the plant. The genera *Wisneria*, *Baldellia* and *Luronium* have simple systems with one to three

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vascular bundles, while in other genera, the vascular bundles are dispersed into one or more arcs, with a larger number of bundles.

The anatomical characteristics of the petiole were used by Erwin and Stockey (1989) to describe the fossil genus *Heleophyton* (whose discovery documents the presence of Alismataceae in the Middle Eocene in western North America). These authors note that the species *Heleophyton helobioides* Erwin and Stockey had five series of vascular bundles placed concentrically, very similar to those described by Meyer (1932, 1935) for *Echinodorus macrophyllus* (Kunth) Micheli. *H. helobioides*, however, demonstrated a larger number of vascular bundles for each series.

Populations of *Echinodorus* are frequently found in temporary lakes in north-eastern Brazil, and species identification in sympatric areas is often difficult due to their generally similar morphology. Anatomic characteristics can often be useful in distinguishing the various species. Additionally, there is a lack of knowledge concerning the biology of aquatic plants in ephemeral aquatic systems in this semi-arid region. As such, an analysis of the internal structure of these plants may contribute much to our understanding of adaptive strategies to the extremes of water availability that characterize these intermittent ecosystems.

The present work seeks to investigate the petiole anatomy of the most representative species of *Echinodorus* in north-eastern Brazil, with the object of analyzing the taxonomic characteristics most useful in defining these taxa.

Materials and methods

All plant material collected was deposited in the EAC and ICN herbaria.

Materials analyzed:

<i>Echinodorus glandulosus</i> Rataj–Ceará:	Independência, 25-VI-2003, <i>L. Q. Matias</i> 462 (EAC); Antonina, 18-V-2003, <i>L. Q. Matias</i> 421 (EAC, ICN); Parambu, 11-IV-2003, <i>L. Q. Matias</i> 375 (EAC)
<i>Echinodorus lanceolatus</i> Rataj–Ceará:	Granja, 17-VII-2003, <i>L. Q. Matias</i> 482 (EAC, ICN)
<i>Echinodorus palaefolius</i> (Nees & Martius) MacBride–Ceará:	Crato, 16-V-2003, <i>L. Q. Matias</i> 418 (EAC); Jati, 4-V-2003, <i>L. Q. Matias</i> 378 (EAC)
<i>Echinodorus paniculatus</i> Micheli–Bahia:	Iraquara, 13-V-2003, <i>L. Q. Matias</i> 407 (EAC, ICN)
<i>Echinodorus pubescens</i>	Crateús, road to Serra das Almas, 25-VI-2003, <i>L. Q. Matias</i> 461

(Martius)
Seubert–Ceará:

Echinodorus subalatus
(Martius)
Grisebach spp.
Subalatus–Bahia:

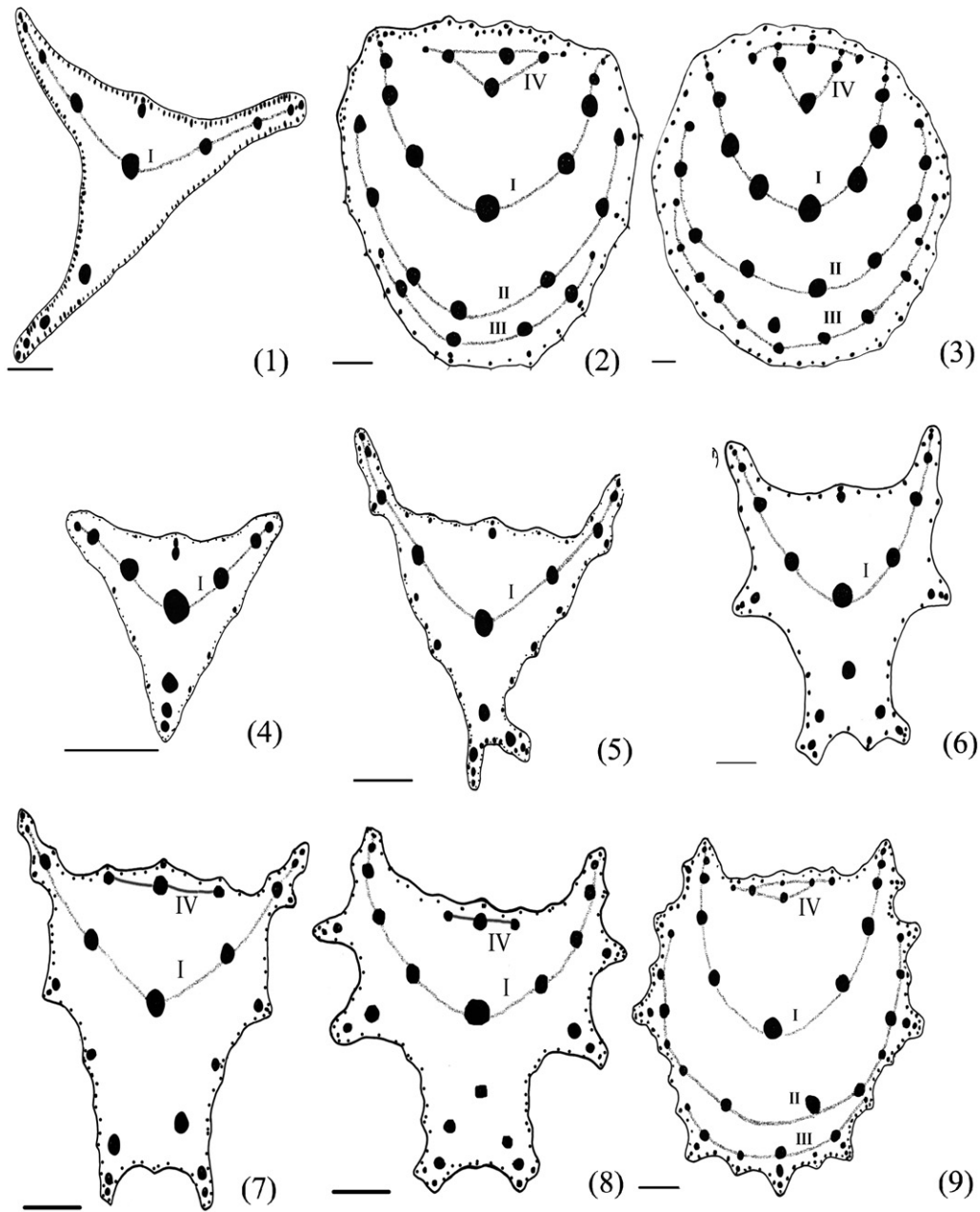
(EAC); Crateús, Xavier, 24-VI-2003, *L. Q. Matias* 443 (EAC); Aiuaba, 20-V-2003, *L. Q. Matias* 434 (EAC). Piauí: São Raimundo Nonato, Lagoa Comprida, 4-IV-2003, *L. Q. Matias* 368 (EAC 33.806) Barra, lake at border of Rio Grande, 11-V-2003, *L. Q. Matias* 400 (EAC 33.819). Ceará: Aiuaba, Estação Ecológica, Gameleira, 21-V-2003, *L. Q. Matias* 433 (EAC); Aiuaba, Estação Ecológica, Poço da Roça, 26-VI-2003, *L. Q. Matias* 469 (EAC, ICN); Caucaia, Lagamar do Cauipe, 18-VI-2003, *L. Q. Matias* 489 (EAC, ICN); Crateús, 9-VI-2003, *L. Q. Matias* 441 (EAC, ICN); Granja, 17-VI-2003, *L. Q. Matias* 481 (EAC, ICN). Rio Grande do Norte: Jardim Piranhas, 7-VI-2003, *L. Q. Matias* 437 (EAC, ICN). Paraíba: Brejo do Cruz, 10-IV-2003, *L. Q. Matias* 329 (ICN). Piauí: Caracol, 8-IV-2003, *L. Q. Matias* 371 (EAC)

Fragments of the petiole were taken from its distal end, approximately 10 cm from the leaf base. Fragments were fixed in 50% FAA (Johansen, 1940), washed in 50% ethanol and stored in 70% ethanol. The petiole fragments were embedded in Jung historesin (Feder and O'Brien, 1968) and sectioned with a Leica 2065 microtome at 5 µm. The transversal sections were stained with 0.12% toluidin blue in borax, and 0.05% aqueous fuchsin (Junqueira, 1990) and mounted in Entellan. Observations, interpretations, and drawings were performed using an optical microscope (Dialux 20EB) with a *camara lucida* attachment. Micrometric scales were projected under the same optical conditions.

Results

The petioles of *Echinodorus* had the following cross-sectional forms: triangular with three-winged extensions in *E. paniculatus* and *E. lanceolatus* (Fig. 1); semicircular in *E. pubescens* (Fig. 2); circular in *E. glandulosus* (Fig. 3); semicircular to polygonal in *E. palaefolius* (Figs. 7–9, respectively); and triangular to hexagonal in *E. subalatus* (Figs. 4, 6–10).

The surface of the petiole is smooth in *E. lanceolatus* and *E. paniculatus* (Fig. 1); slightly irregular in *E. pubescens* (Fig. 2) and *E. glandulosus* (Fig. 3); and has prominent ridges in *E. palaefolius* (Figs. 8 and 9). The petiole surface of *E. subalatus*, on the other hand, shows a great degree of intra-population variability,



Figs. 1–9. Diagrams of transverse sections of *Echinodorus*. (1) *E. paniculatus* and *E. lanceolatus*, bar = 1.20 mm; (2) *E. pubescens*, bar = 0.63 mm; (3) *E. glandulosus*, bar = 1.15 mm; (4–6) *E. subalatus*, bar = 0.63 mm; (7–9) *E. palaefolius*, bar = 1 mm.

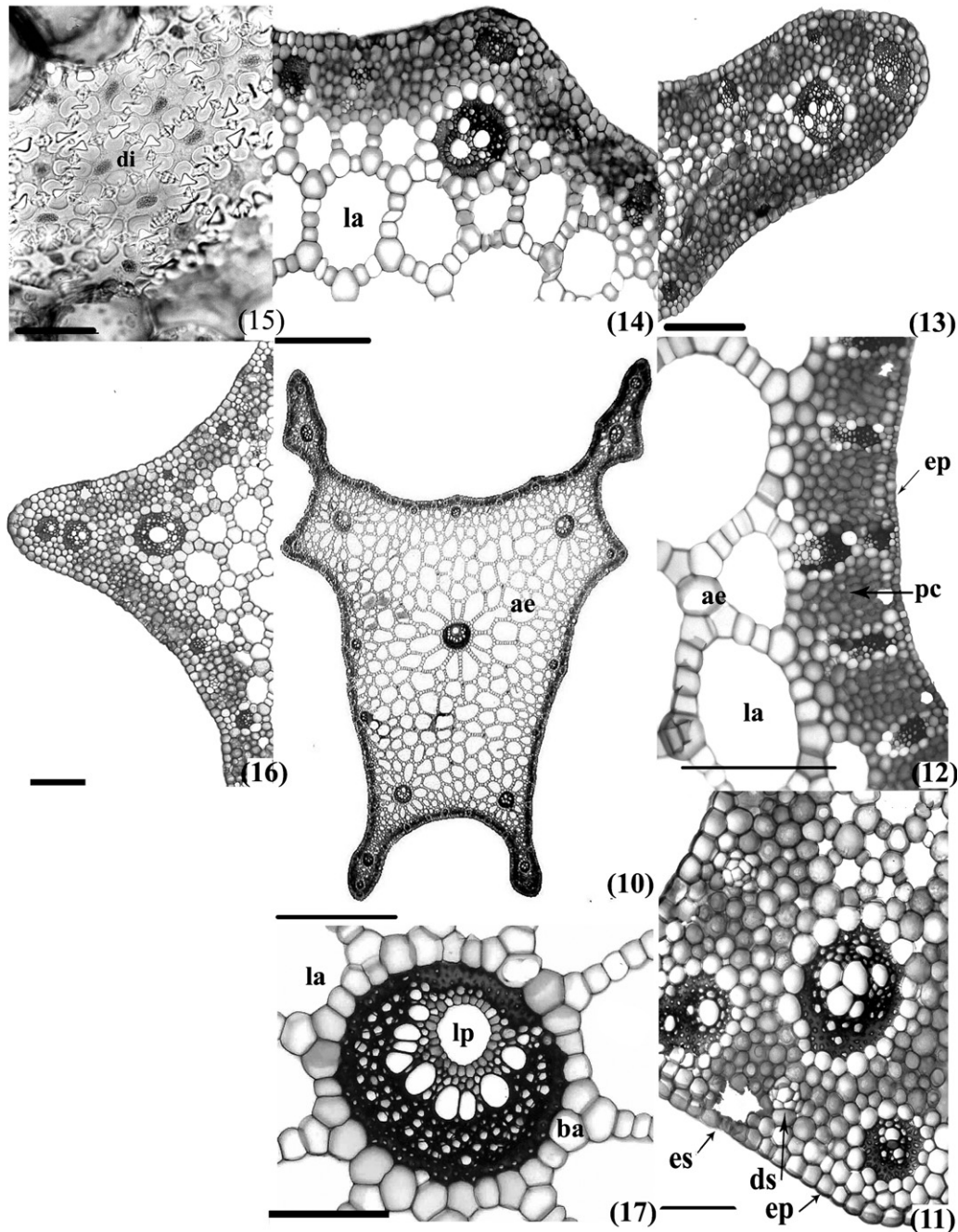
with some individuals showing a slightly undulated surface (Fig. 4), while others have eminently irregular surfaces (Figs. 5–6) or even winged extensions that can be canaliculate when very close together.

The epidermis of all species has tabular cells with thin walls, with stomata located at the same level as the other epidermal cells (Fig. 11). Under the epidermis are a number of layers of regular chlorenchyma cells that alternate with collateral vascular bundles (Fig. 12) and latex ducts (Fig. 11). Just below the chlorenchyma is an aerenchyma with large lacuna extending throughout the entire length of the petiole (Figs. 10, 12 and 14). These

lacunas are traversed by thin-walled brachiform diaphragm cells (Fig. 15).

The vascular bundles are of varying sizes in all species. The smallest bundles are situated among the chlorenchyma at the edges of the petiole (Figs. 11–14), while the largest bundles are more centrally located (Figs. 10 and 17). In those species with prominent ridges and winged expansions, the vascular bundles in these areas gradually diminish in size as they approach their outer edges (Figs. 13 and 16).

Vascular bundles within the aerenchyma demonstrate a uniform structure in all species analyzed (Fig. 17).



Figs. 10–17. Transverse section of petiole of *Echinodorus subalatus* subsp. *subalatus*. (10) General aspect, showing the aerenchyma as ground tissue, bar = 0.63 mm; (11) abaxial surface, bar = 270 μ m; (12) details of boundary, bar = 260 μ m; (13) adaxial surface with winged extensions, bar = 260 μ m; (14) vascular bundles of adaxial surface, bar = 260 μ m; (15) diaphragm cells, bar = 40 μ m; (16) details of lateral rib, bar = 180 μ m; (17) details of vascular bundle, bar = 260 μ m. (ae) Aerenchyma, (ba) sheath of vascular bundle, (di) diaphragm, (ds) secretory ducts, (ep) epidermis, (la) aerenchyma lacuna, (lp) protoxylem lacuna, (pc) chlorenchyma.

These bundles have a parenchyma sheath, which is the endoderm, and enclose pericyclic fibres associated with the phloem and xylem. The protoxylem lacunae are wide and delimited by parenchyma cells. An arc of metaxylem occupies a central position in the bundle, and situated adjacent to it is the phloem in “U” form (Fig. 17).

The bundles in the region of the chlorenchyma differ from the more internal bundles in having a smaller protophloem space, and a smaller number of metaxylem elements (Figs. 11 and 12).

All species have a prominent median arc of vascular bundles (Figs. 1–9), with the largest central vascular

Table 1. Comparative table of the anatomical characteristics of the petioles of species of *Echinodorus*

Characteristics	Species					
	<i>E. glandulosus</i>	<i>E. pubescens</i>	<i>E. palaeifolius</i>	<i>E. paniculatus</i>	<i>E. lanceolatus</i>	<i>E. subalatus</i>
Form in transversal section	Circular	Semicircular	Semicircular to polygonal	Triangular	Triangular	Triangular to hexagonal
Surface texture	Lightly ribbed	Lightly ribbed	Ribbed	Smooth	Smooth	Smooth to ribbed
Winged extentions	Absent	Absent	Present in polygonal forms	Present	Present	Present
Indumentum	Glabrous	Glabrescent to glabrous	Glabrescent to glabrous	Glabrous	Glabrous	Glabrous
Number of vascular bundles in series I (median arc)	13	11	9–13	9	9	7–11
Number of vascular bundles in series II	9	7	4–12	–	–	–
Number of vascular bundles in series III	11	11	2–6	–	–	–
Adaxial series	Present	Present	Present	Absent	Absent	Absent
Number of vascular bundles in adaxial series	8	6	6	–	–	–

bundle in central position, and a group of bundles that become reduced in size as they approach either extremity of the petiole.

In *E. glandulosus*, *E. pubescens* and *E. palaeifolius* there are two series of parallel arcs of abaxial vascular bundles below the central arc (arcs II and III, Figs. 2, 3, 7–9). On the adaxial side are a more internal series of semi-circular bundles. This series is formed by eight vascular bundles in *E. glandulosus* (Fig. 1a) and by six bundles in *E. pubescens* and *E. palaeifolius* (Fig. 2, 7–9). Further out, and bordering the entire periphery of the petiole, are smaller vascular bundles, especially in the areas near the ridges.

E. lanceolatus and *E. paniculatus* do not have parallel arcs on the abaxial side, but rather an abaxial series perpendicular to the central bundle, in addition to the smaller peripheral bundles (Fig. 1). An adaxial series is not found in these species, only a large vascular bundle located more internally.

E. subalatus demonstrates variations in the placement of its vascular bundles, depending on the form of the petiole and the position of the section (Figs. 4–8). All of the specimens demonstrated mid-section arcs with between seven (Figs. 1–4) and 11 (Fig. 2–3, 5–9) vascular bundles. The other bundles are located near the extremities of the petiole, principally in the areas of the winged extensions and ribs. In these latter areas, there can be a sequence of between two and three bundles. Small bundles were observed along the entire perimeter of the petiole. An adaxial series was likewise

not seen in *E. subalatus*. *E. palaeifolius* demonstrates the same internal petiole vascular structure as *E. subalatus*.

Anatomical characteristics of the petioles of the species examined are presented in Table 1.

Discussion

The aerenchyma in petioles of species of *Echinodorus* has lactiferous ducts along the entire length of the petiole, as well as vascular bundles arranged in concentric series. The elevated number of vascular bundles seen in the most common species in the semi-arid region, such as *E. glandulosus*, *E. palaeifolius* and *E. pubescens*, may allow these amphibious aquatic plants to efficiently utilize available water resources in these ephemeral environments during the short wet season.

The lacunas seen in the aerenchyma of the species studied is characteristic of plants adapted to aquatic environments, and are thought to be responsible for providing oxygen to submersed or subterranean organs (Sculthorpe, 1967; Visser et al., 2003). These tissues also have a role in floatation (Sifton, 1945), buoying the petiole and allowing the leaves to remain above the surface of the water during periods of flooding. Fabbri et al. (2005) observed a significant increase in the size of the lacunas in the aerenchyma in populations of *Paspalum* exposed to flooding, presumably favouring their competitive position in these aquatic environments.

A second function of the petiole aerenchyma in these species is related to the physical structure of the plants. The reticulate form of the aerenchyma allows for maximization of petiole expansion with only a small increase in the total volume of tissue, providing adequate support for the leaves, as observed by Williams and Barber (1961) in Nymphaeaceae. The large number of lacunal intersections also gives this organ additional mechanical strength. It is also thought that this mechanical strength is aided by the vascular bundles, principally during the period when the water level is low and the petioles are fully exposed.

According to Sifton (1945), the flux of gases through the aerenchyma is slowed significantly by the diaphragm cells, although these cells have a mechanical function in petiole structure. The cells of the aerenchyma vary in form and occurrence in the many aquatic plant species (Sculthorpe, 1967). According to Scremin-Dias (2000), the diaphragm cells in the submersed or un-submersed leaves of *Echinodorus* have differing cell wall thicknesses and differing arrangements of their lateral projections. The cell walls were thick in the species examined here, similar to those described for amphibious populations of *E. paniculatus* by Scremin-Dias (2000) in the Brazilian Pantanal swamp.

The petioles of all the species studied have ducts for secreting latex. The presence of these structures is a form of specialization, and is considered by Dahlgren and Rasmussen (1983) to be an autapomorphic character of Alismataceae. Latex secreting structures are also present in other taxa of Alismatales, although Dahlgren et al. (1985) classified these structures into different anatomical categories. Additionally, the lack of ontogenetic studies does not allow us to establish homologous relationships between the latex secreting structures within the different families of Alismatales (Les and Haynes, 1995; Tomlinson, 1982).

The data presented in Table 1 allow the separation of a majority of the species examined. The form of the transverse petiole section, associated with the arrangement and number of vascular bundles, have the greatest diagnostic value among the species studied. An exception to this would be the species *E. lanceolatus* and *E. paniculatus*, whose petioles are anatomically similar.

The use of anatomical characteristics for taxonomic purposes allows the identification of fragmented material, and herbarium specimens, in addition to supplying useful information for establishing interrelations between taxa at the species and supra-species levels (Metcalf, 1968). This can be observed also in other groups of monocotyledons, such as *Heliconia* (Heliconiaceae), where characteristics such as the arrangement of fibre bundles in the abaxial region of the leaf, the size of the air canals in the mesophyll, and the form of the bracts provide important characteristics

in determining the variation that exists among the subgenera (Simão and Scatena, 2004).

The more internal vascular bundles in the petioles of *E. glandulosus* and *E. pubescens*, and the semicircular forms seen in *E. palaefolius*, are arranged in five series or arcs, and are similar to those seen in *E. macrophyllus* (Kunth) Micheli and in *Sagittaria montevidensis* Chamisso and Schlechtendal by Meyer (1932, 1935). There are a larger numbers of vascular bundles in the arcs and in the abaxial series of *E. glandulosus* and *E. palaefolius* than are seen in *E. pubescens*, *E. macrophyllus* and *S. montevidensis*. The vascular bundles in the petioles of *Echinodorus* are characteristically arranged in arcs, similar to their placement in Hydrocharitaceae (Ancibor, 1979), but differ from that seen in other aquatic plants such as Nymphaeaceae (Conard, 1905) and Hydrostachyaceae (Jäger-Zürn, 1998) where they are disposed in a circular pattern.

On the other hand, *E. paniculatus* and *E. lanceolatus* demonstrate a different arrangement of the vascular system, with a median arc and a series of abaxial vascular bundles oriented perpendicular to the central bundle, in addition to smaller bundles within the chlorenchyma. This pattern is similar to that seen in species with a triangular petiole cross-section, such as *E. subalatus* (L.Q. Matias 400, Fig. 10), *Echinodorus tenellus* (Scremin-Dias, 2000) and *Sagittaria sagittifolia* L. (Tomlinson, 1982). However, other species of aquatic plants that have a triangular petiole (such as some species within the genus *Nuphar*) have vascular bundles distributed in circles (Sculthorpe, 1967). The pattern of petiole vascular bundles seen in Alismataceae is more similar to that encountered in representatives of the family Hydrocharitaceae—with *Halophila* having a median arc with three bundles, and *Hydrocharis* and *Limnobium* having from five to seven bundles (Ancibor, 1979).

E. subalatus subsp. *subalatus* demonstrated a significant variation in the form of the petiole cross-section, as well as in the number and placement of the vascular bundles. This variation demonstrates the plasticity of this species—which has a wide distribution from Mexico to the north of Argentina (Haynes and Holm-Nielsen, 1994). Haynes and Holm-Nielsen (1986) have, in fact, proposed that the intermediate forms be considered subspecies. This anatomical variation may also indicate a species complex, as suggested by Fasset (1955) who linked the characteristic of angular petioles to an *E. subalatus*–*E. paniculatus* complex.

The arrangement of vascular bundles in series or in arcs is a distinguishing characteristic of inter-specific anatomical patterns for most of the species examined, except only of *E. paniculatus* and *E. lanceolatus*. These latter two species also have scapes with very similar anatomical patterns; and their seeds have micro-morphological reticulate-foveolate surface patterns.

Additionally, they share many macro-morphological characteristics as they have basically the same habit (Matias et al., unpublished data). Only the presence of glands on the fruit of *E. lanceolatus* distinguishes it from *E. paniculatus*. However, Guimarães (1999) described a collection of *E. paniculatus* (Guimarães 96 SPF) with small glands on the fruits, and Micheli (1831) noted the presence of glands on young fruits of this species. As such, the limits between these two species are certainly not well defined (and it must be decided if, in fact, species status is appropriate, or if other infra-specific categories may be applicable).

Meyer (1932, 1935) was the first to use the arrangement of the vascular bundles in series in taxonomic studies of representatives of the family Alismataceae. Later, this same characteristic was used to classify the fossil species *Heleophyton helobiaeoides* Erwin and Stockey (1989). A comparison of the vascular systems of the species analyzed in the present work with that seen in *H. helobiaeoides* reveals a similarity between the latter and the arcs of vascular bundles of *E. palaeifolius* and *E. glandulosus*. All three species have five series of vascular bundles and an elevated number of vascular bundles in each arc. These observation needs to be examined in more detail in later studies in order to better clarify the evolutionary relationships in Alismataceae.

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