Aquatic Botany 129 (2016) 19–30

Contents lists available at ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

Morphological and anatomical patterns in Pontederiaceae (Commelinales) and their evolutionary implications

Danilo José Lima de Sousa[a,*], Vera Lucia Scatena[b], Ana Maria Giulietti[a], Aline Oriani[b]

[a] *Programa de Pós-Graduação em Botânica, Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana, Feira de Santana, Bahia, Brazil*
[b] *Departamento de Botânica, Instituto de Biociências, Universidade Estadual Paulista, Rio Claro, SP, Brazil*

ARTICLE INFO

Article history:
Received 28 February 2015
Received in revised form
19 November 2015
Accepted 24 November 2015
Available online 27 November 2015

Keywords:
Aquatic plants
Brazilian semi-arid
Evolution of vegetative characters
Water availability

ABSTRACT

Pontederiaceae include six genera and approximately 35 species of aquatic plants. The family exhibits great variation in morphology that makes the characterization of species and the understanding of infrafamilial relationships difficult. Twenty species were studied from collections made at the reproductive stage, aiming to establish morphological and anatomical patterns to better understand the taxonomy and evolution of the family. In order to include all species of the family, herbarium specimens were analyzed together with information available in the literature. Four morphological patterns were established for the family: Pattern I—stems with short internodes and alternate, petiolate leaves; Pattern II—stems with long internodes and alternate, petiolate leaves; Pattern III—stems with long internodes and alternate, sessile leaves; Pattern IV—stems with long internodes and verticillate, sessile leaves. The stems have atactosteles and in the species of Pattern I they are rhizomatous. The leaf petiole, the reproductive axis, the inflorescence bract petiole and the peduncle have monosteles and are distinguished from one another by the number of rings of collateral vascular bundles, and by the presence or absence of a fistula. The morphological patterns may represent synapomorphies of infrageneric groups and are related to the life form of the species. Based on current phylogenies, Pattern I is a plesiomorphic condition, including emergent species, and Patterns III and IV are the most derived and include submersed species. This is consistent with variation in water availability in the environment having influenced the diversification of Pontederiaceae during the course of their evolution.

1. Introduction

The family Pontederiaceae consists of six genera and approximately 35 species of aquatic plants (Cook, 1998; Barrett, 2004). The genera *Eichhornia* Kunth (∼8 spp.), *Heteranthera* Ruiz et Pav. (∼13 spp.) and *Pontederia* L. (∼6 spp.) have pantropical distributions; *Monochoria* Presl. (∼7 spp.) occurs in Africa, Asia and Australia; *Scholleropsis* H. Pers. (1 sp.) occurs in Africa and Madagascar, and *Hydrothrix* Hook. (1 sp.) is endemic to Brazil, occurring mainly in the northeast region (Hooker, 1887; Cook, 1996). The centre of diversity of the family is in the Neotropical region, where four genera and about 25 species are found (Seubert, 1847; Schultz, 1942; Castellanos, 1958; Crow, 2003). Brazil has the largest number of species of the family (23 spp.), with the majority of them occurring in dry areas, in temporary pools, on the margins of rivers, and in streams (Amaral et al., 2014; Sousa and Giulietti, 2014).

The aquatic habit and the tubular and zygomorphic flowers are the main characteristics that distinguish Pontederiaceae (Cook, 1998). The species are perennial or annual herbs with varied life forms, including free-floating, floating-leaved, emergent and submersed plants (Sculthorpe, 1967; Barrett and Graham, 1997). Because they can occur in different types of environments, the species exhibit broad diversity in morphology and have different vegetative and reproductive strategies (Sculthorpe, 1967; Barrett and Graham, 1997; Cook, 1998). Such great morphological diversity makes the characterization of the species and the standardization of their descriptive terminology difficult.

A recent taxonomic study of the family, including about 50% of the species, highlighted the need for detailed morphological study of the vegetative and reproductive organs (Sousa and Giulietti,

* Corresponding author.
E-mail addresses: danilojls@yahoo.com.br (D.J.L.d. Sousa), vscatena@rc.unesp.br (V.L. Scatena), anagiulietti@hotmail.com (A.M. Giulietti), alineoriani@yahoo.com.br (A. Oriani).

http://dx.doi.org/10.1016/j.aquabot.2015.11.003
0304-3770/

2014) and showed for example, that the inflorescences, frequently described as racemose (Kunth, 1815; Lowden, 1973; Horn, 1985; Cook, 1998; Strange et al., 2004), are in fact cymose (Sousa and Giulietti, 2014). This lack of information makes it difficult to establish homologies in attempting to understand infrafamilial phylogenetic relationships.

Previous studies with Pontederiaceae have examined seed anatomy (Coker, 1907), seedling morphology (Tillich, 1994), reproductive biology (Barrett and Anderson, 1985; Barrett, 1988; Cunha and Fischer, 2009; Cunha et al., 2014), floral morphology (Endress, 1995), and floral anatomy (Strange et al., 2004; Simpson and Burton, 2006). Anatomical data for the vegetative organs can be found only in the work of Olive (1894), who studied the leaves and stems of five species of the family; of Schwartz (1926), who applied the study of vegetative anatomy to the systematics of Pontederiaceae, and of Cheadle (1970), who studied the characters of vessel elements in twelve species of the family.

Data on morphological evolution in the family have been presented by Kohn et al. (1996), using reproductive characters. Hypotheses concerning the origin of the aquatic habit in Pontederiaceae were proposed by Barrett and Graham (1997) that considered the aquatic habit as a plesiomorphic condition in the family thus constituting a homology linking Pontederiaceae and Philydraceae within the Commelinales. These authors discussed the evolution of life forms, duration of life cycle, developmental patterns of leaves and floral morphology and they also considered the emergent life form as plesiomorphic and the precursor of the others (floating and submersed).

Phylogenetic studies have been undertaken in Pontederiaceae based either on morphology (Eckenwalder and Barrett, 1986) or on molecular markers, both plastid genes (Graham et al., 2002) and nuclear genes (Ness et al., 2011). In these analyses, only the genus *Monochoria* appears to be monophyletic while the others form paraphyletic or polyphyletic groups, which shows there is a need to accumulate new morphological and anatomical data in order to better define homologies and re-define taxa. Identifying morphological patterns will probably help to recognize ecological groups in Pontederiaceae, and combined with a future phylogenetic reconstruction, should help to clarify the evolution of vegetative characters and the phylogenetic relationships.

In this context, the objective of the present study was to survey morphological and anatomical patterns and life forms in Pontederiaceae, addressing the following questions: is it possible to establish morphological patterns in Pontederiaceae considering its morphological diversity? Are the morphological patterns related to the different life forms found in the family? Do the morphological patterns reflect taxonomic groups or phylogenetic relationships? What are the probable selective pressures that have driven the evolution of the morphological patterns?

2. Material and methods

For the morphological study, individuals of 20 species in reproductive phase were collected in Brazil, in the states of Bahia, Ceará, Goiás, Mato Grosso and São Paulo, in rivers and temporary ponds during the rainy season (Table 1). Part of the material was made into herbarium specimens and deposited at the HUEFS herbarium and part was fixed in FAA_{50} (Johansen, 1940) and stored in 70% alcohol for anatomical study.

Table 1
Specimens collected for the morphological study.

Species	Voucher
Eichhornia azurea (Sw.) Kunth	D.J.L. Sousa et al. 239
E. crassipes (Mart.) Solms	D.J.L. Sousa et al. 307
E. diversifolia (Vahl) Urb.	D.J.L. Sousa 99
E. heterosperma Alexander	L.Q. Matias et al. 619
E. paniculata (Spreng.) Solms	D. J. L. Sousa et al. 203
E. paradoxa (Mart. ex Schult. & Schult. f.) Solms	D.J.L. Sousa et al. 319
Heteranthera multiflora (Griseb.) C.N.Horn	D.J.L. Sousa et al. 325
H. oblongifolia Mart. ex Schult. & Schult. f.	D.J.L. Sousa et al. 270
H. peduncularis Benth.	D.J.L. Sousa et al. 327
H. reniformis Ruiz & Pav.	D.J.L. Sousa et al. 210
H. rotundifolia (Kunth) Griseb.	D.J.L. Sousa et al. 209
H. seubertiana Solms.	D.J.L. Sousa et al. 308
H. zosterifolia Mart.	D.J.L. Sousa 400
Hydrothrix gardneri Hook. f.	D.J.L. Sousa et al. 211
Pontederia cordata L.	D.J.L. Sousa 401
P. parviflora Alexander	D.J.L. Sousa 503
P. rotundifolia L. f.	D.J.L. Sousa et al. 339
P. sagittata C.Presl	D.J.L. Sousa 403
P. subovata (Seub.) Lowden	D.J.L. Sousa et al. 329
P. triflora Seub.	D.J.L. Sousa et al. 445

Herbarium specimens were also studied from the following collections: ALCB, EAC, ESA, GH, HRCB, HRB, HST, HUEFS, HUFSCAR, HURB, HVASF, IPA, MAC, MBM, MOSS, NY, PEUFR, RB, SP, SPF, UEC, UFP and UFPB. Taxa included in this study based on herbarium specimens were as follows: *Eichhornia meyeri* A.G.Schulz, *Eichhornia natans* (P. Beauv.) Solms, *Heteranthera callifolia* Rchb. ex Kunth, *Heteranthera dubia* (Jacq.) MacMill., *Heteranthera limosa* (Sw.) Willd, *Heteranthera mexicana* S. Watson, *Heteranthera spicata* C. Presl, *Monochoria cyanea* (F.Muell.) F. Muell., *Monochoria hastata* (L.) Solms, *Monochoria korsakowii* Regel & Maack, and *Monochoria vaginalis* (Burm.f.) C. Presl. Data from *Monochoria africana* (Solms) N.E.Br., *Monochoria australasia* Ridl., *Monochoria brevipetiolata* Verdc., and *Scholleropsis lutea* H.Pierrier were obtained from a survey of the literature (Solms-Laubach, 1883; La Bathie, 1936; Castellanos, 1958; Lowden, 1973; Horn, 1985; Cook, 1989, 1998) (Table 2). The morphological patterns were proposed based on the following criteria: length of stem internodes, phyllotaxy, and presence or absence of petiole in the leaves. These criteria were established by the authors based on the morphological variation found in the family.

For the anatomical study, the species chosen were those most representative of each recognized morphological pattern: *Eichhornia paniculata* (Pattern I), *Heteranthera reniformis* (Pattern II), *Heteranthera zosterifolia* (Pattern III) and *Hydrothrix gardneri* (Pattern IV). Cross sections were made in the mid-region of the stem internodes, the leaf petiole, the reproductive axis, the petiole of the inflorescence bract and the peduncle. The fixed material was dehydrated in an *n*-butyl series and embedded in historesin (Gerrits and Smid, 1983). The sections were made with a rotary microtome (Leica RM 2245) at a thickness of 8 μm, stained in periodic acid, Schiff's reagent (PAS) and toluidine blue (O'Brien et al., 1964; Feder and O'Brien, 1968) and mounted on permanent slides with Entellan (Merck). For the rhizome we also used material embedded in PEG (Richter, 1985), sectioned at a thickness of 12 μm and stained with basic fuchsin and astra blue (Roeser, 1972). The results were documented with images obtained with a capturing device (Leica DFC 450) attached to a microscope (Leica DM4000B), using LAS software for image digitization (Leica Application Suite V 4.0.0).

The definition of life forms followed the classification of Sculthorpe (1967) which includes: emergent—plants rooted into the substrate, with emersed leaves and inflorescences; free-floating—plants with roots below the water surface, not rooted in the substrate, with emersed leaves and inflorescences; floating-leaved—plants rooted into the substrate with leaves floating on the water surface and the inflorescences emersed; and submersed—plants rooted into the substrate with submersed leaves and emersed inflorescences. The emergent species were classified as erect or procumbent, following Barrett and Graham (1997).