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Morphological study of fruits, seeds and embryo in the tropical tribe Dipterygeae (Leguminosae-Papilionoideae)

Estudo morfológico de frutos, sementes e embriões na tribo tropical Dipterygeae (Leguminosae-Papilionoideae)

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Abstract

This work analyses and describes fruit, seed and embryo morphology of 12 Dipterygeae species. The fruit is quite distinct among genera, being a legume in *Taralea*, a drupoid legume in *Dipteryx* and a cryptosamara in *Pterodon*. It was observed that the three genera present distinct morphological characteristics in the epicarp, mesocarp and endocarp. These structures are strongly associated with the dispersal syndromes presented by the genera. Embryonic descriptions are provided for the first time in this manuscript for the three genera presented here and the main diagnostic characteristics are: (1) a gradual extent of development of the hypocotyl-radicle axis from *Taralea* (undeveloped) to *Dipteryx* (the most developed); (2) the plumules are entire in *Taralea* and pinnate in *Dipteryx* and *Pterodon*; (3) a cleft below the hypocotyl-radicle axis in *Taralea*, absent in the other genera, because of the strongly cordate base of the cotyledonar leaves; (4) differences in the degree of development of the hypocotyl-radicle axis between *D. alata*, *D. rosea* and *D. micrantha*. Dipterygeae presents a noticeable diversity of fruit, seed and embryo, *Taralea* being the most distinct of all. The results of this morphological analysis suggest an evolutive path for the diaspores in the clade, based on phylogenetic studies which show *Taralea* as sister to the clade constituted by *Dipteryx* and *Pterodon*.

Key words: diaspores, dispersion, taxonomy, Fabaceae.

Resumo

O presente trabalho analisa e descreve a morfologia de frutos, sementes e embriões de 12 espécies de Dipterygeae. O fruto é consideravelmente distinto entre os gêneros, sendo um legume em *Taralea*, um legume drupoide em *Dipteryx* e uma criptossâmara em *Pterodon*. Foi observado que os três gêneros apresentam características morfológicas distintas no epicarpo, mesocarpo e endocarpo. Essas estruturas são fortemente associadas com as síndromes de dispersão apresentadas pelos três diferentes gêneros. Descrições completas dos embriões são apresentadas pela primeira vez neste manuscrito para os três gêneros e as principais características diagnósticas encontradas são: (1) um gradual desenvolvimento do eixo hipocótilo-radícula de *Taralea* (não desenvolvido) a *Dipteryx* (bem desenvolvido); (2) as plúmulas são inteiras em *Taralea* e pinadas em *Dipteryx* e *Pterodon*; (3) uma fenda abaixo do eixo hipocótilo-radícula em *Taralea*, ausente nos outros dois gêneros, devido à base fortemente cordada das folhas cotiledonares; (4) diferenças no grau de desenvolvimento do eixo hipocótilo-radícula entre *D. alata*, *D. rosea* e *D. micrantha*. Dipterygeae apresenta uma notável diversidade de frutos, sementes e embriões, sendo os mais distintos encontrados em *Taralea*. Os resultados destas análises morfológicas sugerem um caminho evolutivo para os diásporos dentro do clado, com base nos estudos filogenéticos que apontam *Taralea* como irmã do clado constituído por *Dipteryx* e *Pterodon*.

Palavras-chave: diásporos, dispersão, taxonomia, Fabaceae.

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Introduction

Dipterygeae is a basal tribe of the subfamily Papilionoideae (Pennington *et al.* 2001; Wojciechowski *et al.* 2004) and is distributed from Central to South America. It is constituted by three genera: *Dipteryx* Schreb., *Pterodon* Vog. and *Taralea* Aubl. (Polhill 1981; Polhill 1994; Barham 2005). In the phylogeny of Cardoso *et al.* (2012) *Monopteryx* Spruce ex Benth. appeared as sister of the other Dipterygeae, although the branch is still weakly supported and the type species of the genus was not sampled in that study. So we still do not know if *Monopteryx* is monophyletic and if it is indeed sister of Dipterygeae clade. The tribe is a monophyletic group according to the phylogenetic analysis by Pennington *et al.* (2001), Wojciechowski *et al.* (2004) and Francisco (2010). The genera *Dipteryx* and *Taralea* occur mainly in the Amazonian moist forest, except for *Dipteryx alata* which occurs in dry areas of Central Brazil, Bolivia and Paraguay (Barham 2005). By the other hand, the genus *Pterodon* is common in the phytophysiognomies of the Brazilian "cerrado" (Almeida *et al.* 1998).

The members of Dipterygeae are generally trees with pinnate and stipulate leaves, the leaflets are opposite or alternate, without stipels. *Dipteryx* and *Taralea* present thick leaves with an alate rachis, while in *Pterodon*, the leaves are thin with a marginate rachis. The inflorescence is paniculed, the flower presents a calyx with the two adaxial lobes enlarged and the three inferior ones very reduced and a papilionaceous corolla (Polhill 1981). According to Francisco (2010) the flower has an extremely uniform structure among the three genera, and they can be distinguished only by the gynoecium morphology. *Taralea* has an hairy ovary which is as long as wide, while in *Pterodon* and *Dypteryx* the ovary is glabrous and longer than it is wide. Unlike the uniformity of the flower, the fruit is variable among the genera and is a potential source of characters for phylogenetic studies. The genus *Taralea*, for example, is characterized by the dehiscent fruits known as legumes, while *Pterodon* and *Dipteryx* have indehiscent fruits. In *Pterodon* the fruits are samaroids (cryptosamara according to Barroso *et al.* 1999) and *Dipteryx* is drupaceous (Barroso *et al.* 1999).

Seed and embryo characters have been traditionally used in legume taxonomy. Many authors, including Gunn (1981), Lima (1985), Lima (1989), Oliveira (1999), Kirkbride *et al.* (2003), and Meireles & Tozzi (2008) have shown the importance of such characters to legume taxonomy. Besides taxonomic information, the morphological analysis of fruits and seeds can provide ecological characteristics such as the type and capability of dispersion of the species (Van der Pijl 1956). In Dipterygeae we can find quite distinct dispersal patterns of the diaspores, where the typical genus *Dipteryx*, presents barochory, followed by a zoochorical sencondary dispersion (Almeida *et al.* 1990; Vieira-Jr. *et al.* 2007) or hydrochory (Ducke 1940). *Pterodon* is a typical genus of the open vegetation of the Brazilian "cerrado". Its fruits, classified as cryptosamara by Barroso *et al.* (1999), present the prerequisites for anemochory according to Janzen (1980) and finally, in *Taralea*, the fruits are elastically dehiscent, being it a characteristic of autochory, characterizing what Van der Pijl (1982) called ballistic dispersal. With this wide morphological variation, this paper aims to amplify the knowledge of the morphology of the fruits, seeds and embryo of the tribe Dipterygeae and allow relevant information for taxonomic and phylogenetic studies of the group.

Material & Methods

The vouchers of analyzed material are:

Dipteryx alata Vogel: BRASIL. MARANHÃO: Alto Parnaíba, 22.III.1978, fr., *C. A. Miranda 137* (RB); MATO GROSSO: Cáceres, Porto Limão, 03.III.2004, fr., *M.A. Carniello 101* (RB); MATO GROSSO: Cuiabá, Rondonópolis, 1.II.1986, fr., *A.M. Carvalho 2175* (RB); MATO GROSSO DO SUL: Campo Grande, Campus da UFMS, 28.III.2007, fr., *H.C. de Lima 6582* (RB); MATO GROSSO DO SUL: Nova Adralina, 28.III.1986, fr., *U. Pastore & R.M. Klein 82* (RB); MINAS GERAIS: Paracatu, 22.V.2010, fr., *A. Quinet et al. 2065* (RB); MINAS GERAIS: Pirapora, Rio das Pedras, 19.VII.1937, fr., *M. Burret 10091* (RB); MINAS GERAIS: Três Marias, 12.VII.2005, fr., *R.C. Forzza et al. 4002* (RB); PARÁ: São Felix do Xingú, 12.VI.1978, fr., *C.S. Rosário 52* (RB); TOCANTINS: Lagoa da Confusão, Ilha do Bananal, Parque Nacional do Araguaia, 26.III.1999, fr., *M. A. da Silva et al. 4156* (RB).

D. magnifica Ducke: BRASIL. AMAZONAS: Manaus, Reserva Florestal Adolpho Ducke, 9.XI.2008, fr., *L.P. de Queiroz et al. 13912* (INPA, RB); PARÁ: Rio Tapajós, 27.VIII.1916, fr., *A. Ducke 16400* (RB).

D. micrantha Harms: PERU. LORETO: Maynas Mishaina, 22.VII.1984, fr., *R. Vasquéz 5322* (RB).

D. odorata (Aubl.) Willd.: BRASIL. AMAZONAS: Boca do Rio Tocantins, 19.XI.1986, fl. and fr., *H.C. de Lima 2748* (INPA, RB); AMAZONAS: Santa Izabel do rio Negro, 9.VIII.1987, fr., *C.A. Cid Ferreira 9308* (RB); PERU, LORETO: University Arboretum on Rio Nanay, 7.VIII.1972, fl. and fr., *T.B. Croat 18863* (RB).

D. punctata (S.F.Blake) Amshoff: BRASIL. AMAZONAS: Manaus, Reserva Florestal Adolpho Ducke, 06.V.1988, fr., *D. Coêlho et al. d-24* (INPA, RB); PARÁ: Saracá-Taquera, 30.V.1978, fr., *N.T. Silva 4671* (RB), RIO DE JANEIRO: Rio de Janeiro, Jardim Botânico do Rio de Janeiro, 27.IV.1993, fr., *D.M. Tourinho 24* (RB).

D. rosea Spruce ex Benth.: BRASIL. AMAZONAS: São Gabriel da Cachoeira, Alto Rio Negro, 30.XI.1987, fr., *H.C. de Lima et al. 3357* (INPA, RB).

Pterodon abrubtus (Moric.) Benth.: BRASIL. BAHIA: Brotas de Macaúbas, no date, fl. and fr., *B.B. Klitgaard et al. 75* (AAU, K, RB); BAHIA: Poções, no date, fr., *S.B. da Silva 99* (RB); PIAUÍ: Caracol, Parque Nacional da Serra das Confusões, 8.IV.2009, fr., *G. Martinelli et al. 16245* (RB); PIAUÍ: Guariba, 17.VI.2007, fr., *G. Martinelli et al. 16152* (RB); TOCANTINS: Natividade, 24.VII.2007, fr., *M.M. Saavedra 494* (RB).

P. emarginatus Vogel: BRASIL. BAHIA: Correntina, 2.III.1991, fr., *L.G. Viollati 192* (RB); BAHIA: Formosa do Rio Preto, 21.IV.1998, fr., *R.C. Mendonça 3402* (RB); GOIÁS: Niquelândia, Macêdo, 27.VI.1996, fr., *M.L. Fonseca et al. 1012* (RB); MATO GROSSO: Xavantina, 1.V.1968, fr., *R.R. de Santos 1228* (RB); MINAS GERAIS: Santana do Pirapama, Serra do Cipó, 12.III.2009, fr., *D.C. Zappi et al. 2098* (RB); PIAUÍ: Baixa Grande do Ribeiro, Estação Ecológica Uruçuí-Uma, 11.IV.2009, fr., *G. Martinelli et al. 16386-a* (RB); SÃO PAULO: Bauru, Jardim Botânico Municipal de Bauru, 13.IX.2006, fl. and fr., *V.L. Weiser 712* (RB).

P. pubescens (Benth.) Benth.: BRASIL. MATO GROSSO: no date, fr., *J.G. Guimarães 308* (RB); MINAS GERAIS: Itapecerica, 30.V.1975, fr., *G.G. dos Reis 793* (RB); PIAUÍ: Serra Grande, no date, fr., *J.S. Assis 106* (RB); SÃO PAULO: Aramina, Povoado Canindé, 1.VI.1979, fr., *J.C.C. Ururahy 07* (RB); SÃO PAULO: Bebedouro, no date, fr., *J.G. Guimarães 1485* (RB); SÃO PAULO: Boa Esperança do Sul, Perdizes, 7.VII.1964, fr., *J.C. Gomes Jr. 2022* (RB).

Taralea cordata Ducke: BRASIL. AMAZONAS: Presidente Figueiredo, 29.I.1984, fr., *H.C. de Lima 2142* (INPA, RB).

T. crassifolia (Benth.) Ducke: BRASIL. RORAIMA: Amajari, Serra Tepequem, 29.XI.1964, fr., *B. Maguire 32617* (INPA, RB).

T. oppositifolia Aubl.: BRASIL. AMAZONAS: Manaus, 21.II.1937, fr., *A. Ducke 34957* (RB); PARÁ: Belém, 16.II.1923, fr., *A. Ducke 17120* (RB); PARÁ: Belém, Utinga, Barragem do Lago Água Preta, 21.XI.1994, fr., *S.M. Faria 853* (RB); PARÁ: Melgaço, 13.X.1991, fl. and fr., *A.S.L. da Silva 2374* (RB).

Before dissected, the seeds were hydrated by boiling in water until the point that its coat or testa could be removed. The fruits, seeds and embryo were photographed using a digital camera attached to the stereomicroscope Leica CLS 150X.

For the surface analyses (scanning electron microscope – SEM), the material was fixed in FAA 50 (Johansen 1940) for 24 h, dehydrated in an ethanolic series (Tucker 1993), dissected in a stereomicroscope, and critical point dried in a Leica EM CPD 030, mounted in aluminium stubs with carbon conductive adhesive tabs (Ted Pella, Redding, California, USA) and metalized. The samples were coated with gold-palladium in an Emitech K550X (West Sussex, United Kingdom). The micrographis were taken at 15, 20 or 30 kv with a Zeiss EVO 40 scanning electron microscope (Zeiss, Thornwood, USA) in the Laboratório de Biologia Estrutual of the Instituto de Pesquisas do Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Brazil.

The following characteristics were observed in this study: fruit shape; epicarp, mesocarp and endocarp consistencies; seed shape; testa structure; hilum, micropile, raphe, aril and lens features; embryo shape; hypocotyl-radicle axis and plumule type.

The terminology adopted for classifying the fruits is based on the work by Barroso *et al.* (1999) and the descriptions of seeds and embryos are from the paper by Kirkbride *et al.* (2003).

Results

Dipteryx Schreb., Gen. Pl. 2: 485. 1791, nom. cons
Figs. 1a-d; 2a-d

Monospermic drupoid legume, indehiscent, globose, slightly compressed dorso-ventrally, circular, eliptic or ovate; calix deciduous; epicarp woody, glabrous when mature, scrub, surface not vesiculose, rugose, brown; mesocarp thick with venated surface, fribose, woody, porous, light brown, sometimes divided into two layers;

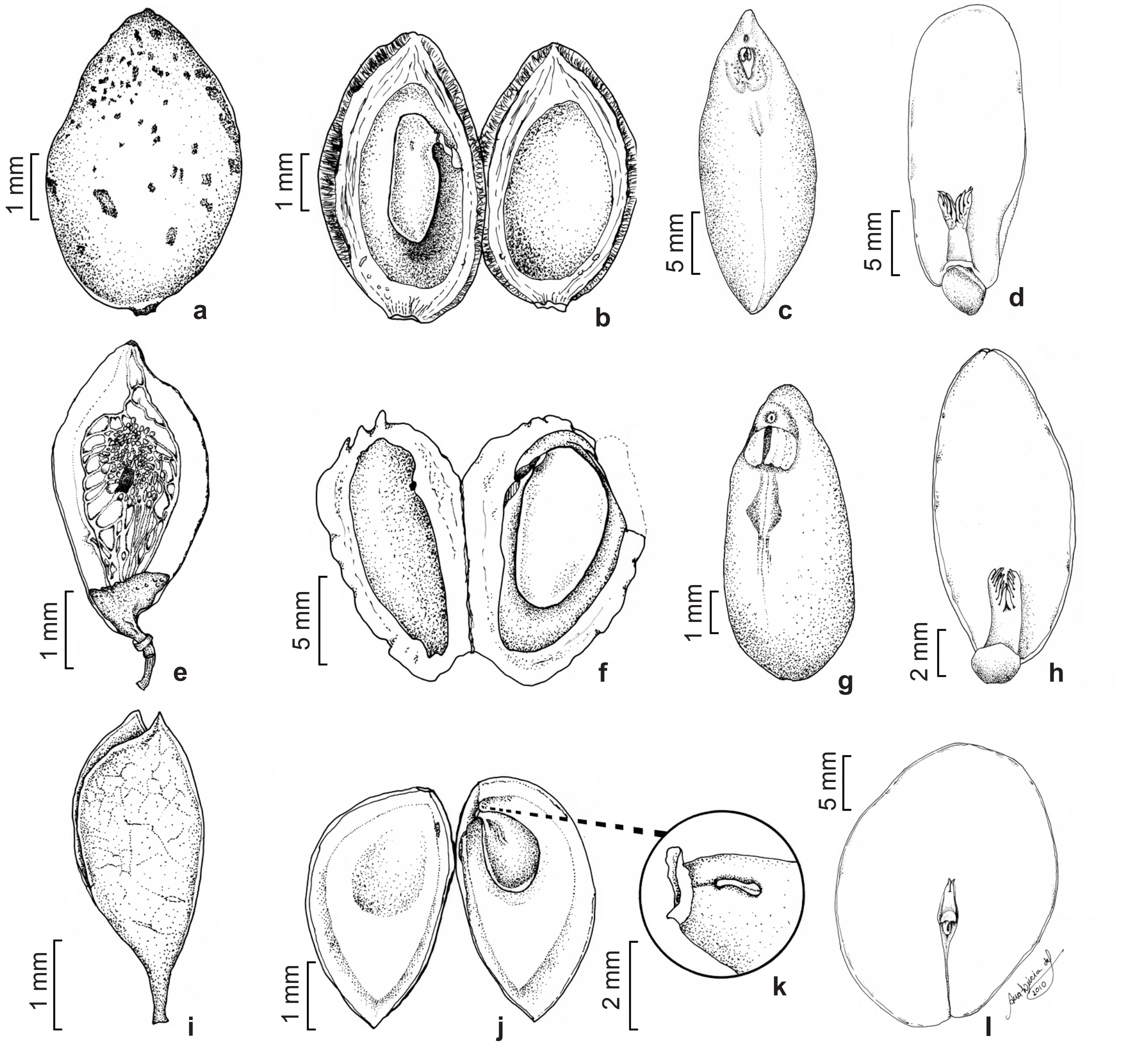

Figure 1 – a-l. camera lucida drawing of fruits, seeds and embryo of Dipterygeae – a. fruit of *Dipteryx rosea*; b. inner portion of the fruit and seed insertion in *D.* rosea; c. seed of *D. alata*; d. embryo of *D. alata*; e. fruit of *Pterodon emarginatus*; f. inner portion of the fruit and seed insertion in *P. emarginatus*; g. seed of *P. emarginatus*; h. embryo of *P. emarginatus*; i. fruit of *Taralea crassifolia*; j. inner portion of the fruit and seed insertion in *T.* crassifolia; k. hilum detail of *T. crassifolia*; l. embryo of *T. crassifolia* (a,b *H.C.de Lima 3357*; c,d *M.A.Carniero 101*; e-h *R.C.Mendonça 3402*; i-l *B.Maguire 32617*).

endocarp thin, coriaceous-fibrose, scrub, reddish brown, fused to the mesocarp, not covered by spongy tissue, dehiscent after decomposition of the mesocarp. Seed elliptic to oblong or linear, slightly compressed dorsoventrally, aril absent; testa rugose, coriaceous, black; raphes not visible; hilum elliptic, sub basal or lateral; lens inconspicuous; endosperm absent; embryo straight; cotyledon elliptic, crass, with the external surfaces slightly convex, wrinkled; hypocotyl-radicle axis straight, central on the cotyledons, with ca. 1/5 of the size of the cotyledons; plumule well developed.

Pterodon Vogel, Linnaea 11: 384. 1837.

Figs. 1e-h; 3a-b

Cryptosamara, monospermic, indehiscent, compressed dorso-ventrally, ovate or rarely oblong, centrally inflated; calyx deciduous; epicarp woody, glabrous, surface vesicular, black, splitting irregularly with the external mesocarp; mesocarp thick, venation strongly apparent at the center with balsamic vesicles around the seed chamber, becoming inconspicuous toward the wings; endocarp fibrous or spongeous, coriaceous, winged;

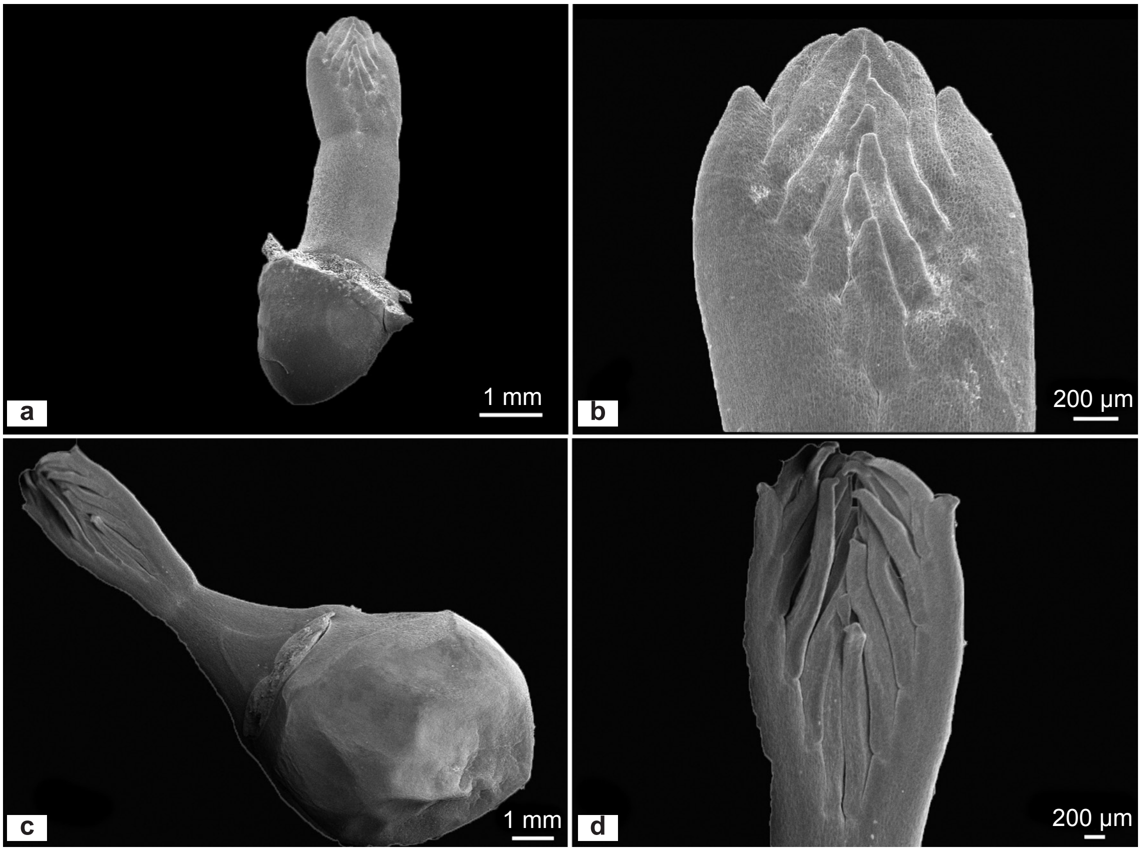

Figure 2 – a-d. SEM of embryos of *Dipteryx* – a. embryo of *Dipteryx alata*; b. detail of the plumule *D. alata*; c. embryo of *D. micrantha*; d. detail of the plumule of *D. micrantha*.

funicle thick, ca. 2 mm long. Seed elliptic to oblong, slightly compressed dorsoventrally, with a reduced aril around the hilum; testa smooth, coriaceous, light brown; raphes long, going from the hilum to the base of the seed, darker than the testa; hilum partially or completely hidden by the aril, circular, located on the side of the seed; lens apparent, adjacent to the hilum, oblong to elliptic, darker than the testa; endosperm absent; embryo straight; cotyledons smooth, crass, with the external surfaces convex; hypocotyl-radicle axis straight, central to the cotyledons, with ca. ¼ of the size of the cotyledons; plumules well developed.

Taralea Aublet, Hist. Pl. Guiane 745. 1775.

Figs. 1i-l; 3c-d

Monospermic or dispermic legume, with elastic dehiscence, dorsiventrally compressed, asymmetric elliptical; calyx deciduous; epicarp woody, irregular surface, glabrous, black, not brittle; mesocarp thin, woody; endocarp light brown, coriaceous, strongly fused to the mesocarp. Seed circular to ovate, dorsoventrally compressed, aril absent; testa slightly rugose, coriaceous, dark brown to black; raphes inconspicuous; hilum hidden by funicle vestige, circular, basal; lens inconspicuous; endosperm absent; embryo straight; cotyledons ovate or circular, smooth or wrinkled, crass, with the external surfaces slightly convex; hypocotyl-radicle axis straight, central to the cotyledon, with ca. 1/8 of the size of the cotyledons, having a fissure below the radicle until the half of the cotyledons; plumules poorly developed.

The main diagnostic characteristic of the fruits, seeds, and embryo of Dipterygeae are summarized in Table 1.

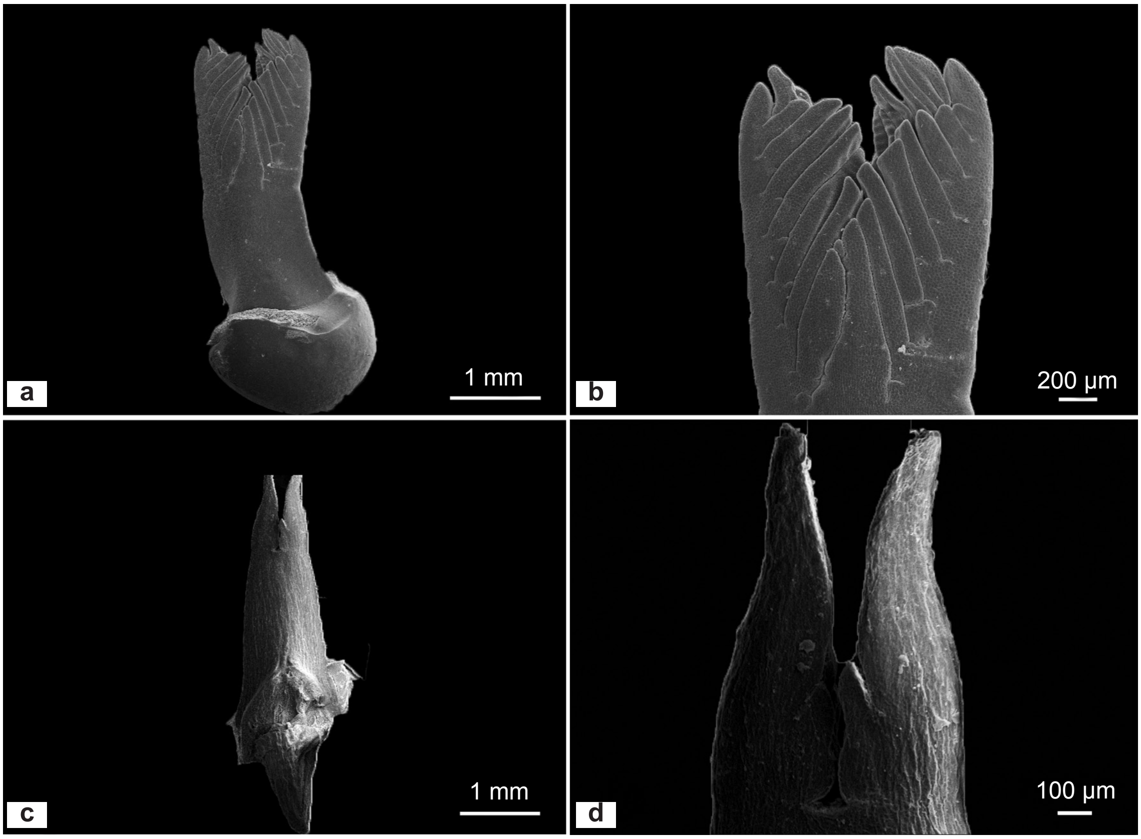

Figure 3 – a-c. SEM of the embryos of *Pterodon* and *Taralea* – a. embryo of *Pterodon emarginatus*; b. detail of the plumule of *P. emarginatus*; c. embryo of *Taralea crassifolia*; d. detail of the plumule of *T. crassifolia*.

Discussion

Diaspores morphology, dispersal considerations and systematic implications

Leguminosae is a highly heterogeneous family in several aspects. Although the name of the family refers to a type of fruit, its diversity is equally or even higher than other features. Thus, a detailed observation of the external or structural morphology of fruits and seeds is, in some cases, of great importance in the improvement of taxonomic knowledge. In Dipterygeae, the three genera can be promptly distinguished observing the fruit types and seeds morphology, making the study of diaspore morphology very useful taxonomically within the tribe.

Considering the phylogenetic analyses presented by Francisco (2010) and Cardoso *et al.* (2012) and the results obtained in this paper, it is possible to suggest an evolutionary path of the fruits in this clade. Because they are dehiscent in *Taralea*, which is sister to the clade composed by *Pterodon* and *Dipteryx,* and both have indehiscent fruit, we can infer that the fruit changed from dehiscent to indehiscent within this clade.. The cryptosamaras is a synapormorphy for the species of *Pterodon,* and the globose and drupoid legume a synapomorphy for the species of *Dipteryx*.

Fruits in the basal genus *Taralea* are elastically dehiscent, with a thin pericarp, exposing the seeds during the dispersion (Fig. 1i,j). We emphasize the observation of a persistent portion of the funicle coating the hilum (Fig. 1j,k), which is probably involved in a secondary dispersal by ants (Beattie & Culver 1982).

The genus *Pterodon* presents samaras, with a first degradation of the epicarp and mesocarp during the maturity (Fig. 1e). The wing-shaped tissue is the endocarp (Paiva *et al.* 2008) and it covers a single seed during the dispersion. Then, a second degradation of tissue probably helps the in the seed establishment. For this reason, the

Table 1 – Morphological characteristics of fruits, seeds and embryo of Dipterygeae genera. + = presence; - = absence.

Characters/Genera	***Dipteryx***	***Pterodon***	***Taralea***
Fruit type	Drupoid legume	Criptosamara	Legume
Dehiscence	-	-	+
Epicarp	Non vesicular	Vesicular	Non vesicular
Mesocarp	Thick, surface not venated	Thick, venated surface, showing balsamic vesicles	Thin
Endocarp	Coriaceous-fibrous, scrub, not covered by spongeous tissue, dehiscent after decomposition of the mesocarp	Fibrous or spongy,coriaceous, winged, fused to the mesocarp	Coriaceous, strongly fused to the mesocarp
Seed shape	Elliptic to oblong or linear, slightly compressed dorsiventrally	Elliptic to oblong, slightly compressed dorsiventrally	Circular to ovate, compressed dorsiventrally
Testa	Rugose	Smooth	Rugose
Aril	-	+	-
Raphe	-	+	-
Lens	-	+	-
Position of the hilum	Sub basal or lateral	Lateral	Basal
Embryo texture	Wrinkled	Smooth	Smooth or wrinkled
Hypocotyl-radicle axis	1/5 of the size of the cotyledons	1/4 of the size of the cotyledons	1/8 of the size of the cotyledons
Plumule	Well developed	Well developed	Poorly developed

fruits of *Pterodon* are referred by Barroso *et al.* (1999) as a cryptosamara, The samaroid fruits are characterized for being dry and light fruits with shapes that enable the wind to carry the diaspores, which is also called as anemochory (see Vand der Pjil 1982). Anemochory is a syndrome associated with open habitats with absence of physical barriers and wind availability (Janzen 1980) and environments subjected to high wind incidence (Bullok & Clark 2000; Tackenberg *et al.* 2003). It can explain the concentrated occurrence of the genus in the Cerrado, a very distinct environment of the Amazonian Forests, the center of diversity of Dipterygeae.

In *Dipteryx* the fruits are drupaceous, with a very hard and fibrous epicarp and mesocarp (Fig. 1a,b). Among species, the surface of the epicarp seems to have a taxonomic importance in the case of *D. alata* and *D. micrantha,* which are grooved externally while the majority of species have a smooth epicarp (Fig. 1a). In this genus, the dispersal of the seeds is primarily barochoric, which needs a long period of tissues degradation to expose the seed; or can be made secondarily by rodents, which also can bury the seeds and improve the range of distances (Forget & Milleron 1991; Saravy *et al.* 2003). The seeds of *Dipteryx* can attract rodents maybe due to the presence of unsaturated oil, protein, calcium and phosphorus, and in the case of *D. alata* and *D. lacunifera* they taste like peanut, being appreciated even by humans (Togashi 1993; Vieira-Jr. *et al.* 2007). During the study of the diaspores we observed a capability to flotation of *D. odorata* and *D. rosea*, and in accordance to what was mentioned by Ducke (1940), we suggest the hidrochory as an alternative dispersal syndrome in the Amazonian Forest, once some species are near flooded areas.

A tendency of the fruit tissues to concentrate balsamic resins in the pericarpic vesicles was observed in *Pterodon* and *Dipteryx*. As they are lacking in *Taralea*, but present in the other two genera (Lewis *et al.* 2005) this can be inferred as a synapomorphy of the clade Pterodon + Dipteryx. Kirkbride *et al.* (2003) related the presence of balsamic oil ducts in the mesocarp of *Pterodon*. The essential oil of *Pterodon emarginatus* is used in some traditional medicine (Brandão *et al.* 2002). In *Dipteryx*, the mesocarp is porose (Fig. 1b) with sparse oil vesicles, which in *D. rosea* are markedly aromatic and in *D. lacunifera* the vesicles are well developed.

The seed morphology

Groth & Liberal (1988) and Barroso *et al.* (1999) suggest that because the external and internal characteristics of the seeds are less modified by the environment, they constitute secure criteria for families, genera and even species identification and delimitation.

In Dipterygeae the seed characters are source of important diagnostic characters. In *Taralea* for example, seeds are compressed and the hilum is basal (Fig. 1j,k) while in the other genera the seeds are more dilated and the hilum is lateral (Table 1). The seeds of *Taralea* present variation concerning the testa color being black in *T. reticulata* and pale-brown in *T. crassifolia*. Seeds of *Pterodon* are in general uniform, but there are color variations among species. However, structures such as lens and raphe are apparent, the last one occurring from the lateral hilum to the seed base. A relevant and unique character of the genus is the presence of the aril coating the hilum (Fig. 1g). This reduced aril can be associated with secondary dispersal (Westoby *et al.* 1982). The presence of these characters can be used to identify the genus within the tribe. For *Dipteryx* seeds, a relevant taxonomic characteristic for species identification was observed on the surface of the testa, which is foveolate in *D. alata* with a gradual reduction of this characteristic in *D. micrantha*, *D. odorata* and *D. rosea*.

Embryo morphology and taxonomic considerations

The embryo of the tribe presents typical characteristic of Leguminosae such as the endosperm lacking, crass cotyledons and a well-developed plumule. However, their morphology show a clear distinction among genera, where a gradual extent of development of the hypocotyl-radicle axis was verified, being undeveloped in *Taralea*, becoming more evident in *Pterodon* than in *Taralea* and strongly evident in *Dipteryx* where it is more distinct than in the two other genera (Figs. 2a-d, 3a-d). It was observed a gradual fusion of the plumules, where in *Taralea* they are entire, without the pinnate pattern of the primary leaves as was observed in the two other genera. This characteristic can be interpreted as a plesiomorphy within the group (Figs. 2a-d, 3a-d), once this genus appears as basal within the tribe in the phylogenies of Pennington *et al.* (2001), Francisco (2010) and Cardoso *et al*. (2012)

In *Taralea*, the most distinctive characteristic found is the cleft below the hypocotyl-radicle axis (Fig. 1l). Such cleft is because of the strongly cordate base of the cotyledonar leaves, and because of it the lateral basal portions of the blades are longer than the hypocotyl-radicle axis in initial stage. This characteristic is exclusive to the group.

Despite the embryos of the different species of *Dipteryx* present a superficial resemblance, we found differences in the degree of development of the hypocotyl-radicle axis between *D. alata* and *D. micrantha* (Fig. 2a,c). It was also observed that *D. rosea* presents a degree of development in the hypocotyl-radicle axis between *D. alata* and *D. micrantha* (not shown).

So, we conclude that the study of fruit, seed and embryo morphology can provide good diagnostic characters to distinguish among the different genera of the tribe and also to differentiate species within each genus.

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