Seed and embryo morphology of *Poecilanthe* (Fabaceae, Papilionoideae, Brongniartieae)

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This work analyses and describes seed and embryo morphology of eight *Poecilanthe* species. *Poecilanthe* species can be divided in four groups based on seed and embryo characters: (1) *P. amazonica*-type has overgrown seeds, bears cataphylls on the epicotyl and has an inflexed hypocotyls-root axis; (2) *P. effusa*-type has two types of trichomes on the epicotyl, which is longer than the hypocotyls-root axis; (3) *P. parvilora*-type has a visible lens and the raphe runs around three-quarters of the seed circumference; and *P. grandiflora*-type bears a one-lipped rim aril. *Poecilanthe* presents a remarkable diversity both in seed and embryo, which reinforces the belief that the genus is not monophyletic. Moreover, our results support the three major clades recognized by a preliminary phylogeny. © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, 158, 249–256.


INTRODUCTION

The genus *Poecilanthe* (Fabaceae, Papilionoideae, Brongniartieae), established by Bentham (1860), comprises ten South American species distributed from Colombia and French Guiana to East Argentina and Uruguay (Meireles & Tozzi, 2007). *Poecilanthe* species are shrubs or trees occurring in a wide range of habitats, such as flooded and non-flooded Amazonian forest, Atlantic rain forest, savannah (cerrado) and seasonally dry forests, including caatinga and restinga.

The genus has a remarkable morphological diversity. Geesink (1981) pointed out that *Poecilanthe* could be divided in two groups, one with unifoliolate leaves and racemose inflorescences and the other with imparipinnate leaves and paniculate inflorescences. The androecium can be monadelphous or diadelphous, with its anthers strongly dimorphic or just sub-equal and fruits can be internally septic or not (Meireles & Tozzi, 2007). According to Greinwald *et al.* (1995), one group of species accumulates α-pyridine alkaloids whereas the other group accumulates bicyclic quinolizidine alkaloids, with the α-pyridone type being absent.

Kirkbride, Gunn & Weitzman (2003) analysed four species of *Poecilanthe* and remarked that this genus presents two distinct seed morphologies. One group has a hard and glossy testa, straight embryonic axis and the seed length at right angles to the fruit length [e.g. *P. effusa* (Huber) Ducke, *P. itapuana* G.P.Lewis and *P. subcordata* Benth.]. The other group has a thin and dull testa, curved embryonic axis and the seed and fruit length parallel, as in *P. amazonica* (Ducke) Ducke.

Seed and embryo characters have been traditionally used in legume taxonomy. Many authors including Gunn (1981, 1984), Lima (1985), Lima (1989), Oliveira (1999) and Kirkbride *et al.* (2003), have shown the importance of such characters to legume taxonomy.

This work aims to improve the knowledge of *Poecilanthe* seed and embryo morphology and to check for useful characters to the taxonomy of this polymorphic genus.

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MATERIAL AND METHODS


In preparing the material for dissection, mature seeds were hydrated in boiling water for a variable time, depending on testa resistance. The embryonic axis and its details were photographed in a Nikon SMZ-U stereoscopic microscope with a Nikon D70s camera attached.

Descriptive terminology mainly follows Kirkbride et al. (2003). However, we decided to use the hypocotyl-root axis (Esau, 1977) rather than the radicle, as these structures were not easily distinguishable from each other.

Measurements were taken with a millimetric-scaled ruler or with the microscope micrometer when appropriate. Contrary to Kirkbride et al. (2003) seed measurements were taken with regard to the hilum position. Seed length was measured perpendicular to the hilum and width measured at the widest part at right angles to the other axis. Thickness was measured perpendicular to the plane of the other measurements.

RESULTS

*Poecilanthe* seeds are positioned in the fruit parallel to the fruit length, the hilum lack a faboid split (hilar groove) and the endosperm is absent in mature seeds. The embryo fills the seed cavity and the cotyledons are easily distinguishable from the embryonic axis; cotyledons are of the storage type, with a convex outer face, a basically smooth inner face and the base lobate.

However, the other characters are quite variable. The seeds may be overgrown (Fig. 1A, B) or of regular growth (Fig. 1C) and their faces parallel (Fig. 1C) or transversally (Fig. 1D) oriented to the fruit length. The hilum is parallel to the fruit suture (Fig. 1E) or curved downward to the endocarp (Fig. 1F, G). A rim-aril is present (Fig. 1H) or absent (Fig. 1I), the micropyple is visible (Fig. 1H, I) or not and the lens is distinguishable (Fig. 1I) or not. The raphe runs around one-half (Fig. 1J), three-quarters (Fig. 1L) of the seed circumference or it is not visible (Fig. 1M). A chalaza can be present (Fig. 1J–L) or absent (Fig. 1M); not branched (Fig. 1L) or presenting post-chalazal branches, which can reach the hilum (Fig. 1K) or not (Fig. 1J).

The cotyledon base is notched (Fig. 1N), split (Fig. 1O) or groined (Fig. 1P, Q), concealing totally (Fig. 1O, Q), partially (Fig. 1P) or not the hypocotyl-root axis. The hypocotyl-root axis is inflexed (Fig. 2A) or straight (Fig. 2B, C). The plumule is poorly (Fig. 2D, E) or moderately (Fig. 2C, F) developed, presenting villose trichomes (Fig. 2C) or glabrous (Fig. 2D, F). The epicotyl may present some accessory structures such as thick reddish trichomes (Fig. 2C) or cataphylls (Fig. 2D).

The most important differences are summarized in Table 1.

**Poecilanthe amazonica** (Ducke) Ducke

Seeds 1 or 2 in number, overgrown, asymmetrical; if 1, the seed is transversally oblong, 11–18 × 22–27 × 4–5 mm; if 2, the seeds are D-shaped, 15–18 × 12–2 × 4–5 mm; compressed in cross section; margins irregular; face longitudinal to the fruit length. Testa thin (papyraceous), dull, smooth; hilum about 2–3 mm, parallel to the suture.

![Figure 1](https://example.com/figure1.png)

depressed in the seed, completely concealed by a funiculus remnant; aril absent; visible hypocotyl-root lobe; micropyle not visible; lens not visible; chalaza visible, opposite the hilum, darker and more wrinkled than the testa; post-chalazal branches present, under six in number, not reaching the hilum; raphe visible externally, slightly elevated. Cotyledons notched; hypocotyl-root axis not concealed, smooth outer face, plane inner face; embryonic axis 1.5–2.5 mm long, essentially aligned with the cotyledon length (just slightly oblique); hypocotyl-root axis inflexed, truncate; plumule bipartite, concave–triangular, glabrous, poorly developed, shorter than a quarter of the hypocotyl-root axis, both sides of it bearing a series of membranaceous cataphylls. (Figs 1A, B, E, J, N, 2D).

POECILANTHE EFFUSA (HUBER) DUCKE

Seeds (1–)2–4(–5) in number, not overgrown, symmetrical, widely elliptic, orbicular or slightly oblate, 9–13 × 7–12 × 3.5–6 mm; compressed or often plane-convex in cross section; margins regular; face transversal to the fruit length. Testa thin (papyraceous), dull, smooth; hilum 0.3–0.4 mm, curved downward, slightly projected, not concealed by a funiculus remnant; aril absent; hypocotyl-root lobe not visible; micropyle not visible; lens not visible; chalaza visible, opposite to the hilum, darker and more wrinkled than the testa; post-chalazal branches present, usually 8–12 in number; longitudinally orientated and reaching the hilum; raphe not distinguishable from the post-chalazal branches. Cotyledon base split, hypocotyl-root axis concealed; striate on outer face, concave on inner face; embryonic axis 2–3 mm, aligned with cotyledons length; hypocotyl-root axis straight, truncate to triangular; base of epicotyl surrounded by reddish, thick trichomes, crown-like; plumule bipartite, sagittate to oblong, margins and sometimes the ‘blades’ densely villose, moderately developed, longer than hypocotyl-root axis (usually twice its length); cataphylls absent. (Figs 1D, F, K, O, 2C).

POECILANTHE FALCATA (VELL.) HERINGER

Seeds 2–5 in number, not overgrown, symmetrical or asymmetrical, wide ovate-elliptic, sub-orbicular or orbicular, 18–22 × 16–20 × 3–5 mm; flattened in cross section, margins regular; face parallel with the fruit length. Testa thick (coriaceous), glossy, smooth; hilum 1.5–2 mm, curved downward to the endocarp, obliquely projected, not concealed; rim-aril present, one-lipped, tongued or not, lighter than the testa; hypocotyl-root lobe visible; micropyle visible, punctiform; lens not visible; chalaza not visible; raphe not visible. Cotyledon base groined, hypocotyl-root axis concealed; outer face smooth, inner face plane; embryonic axis 2.8–3.3 mm long; aligned with cotyledon length; hypocotyl-root axis straight, triangular; plumule bipartite, concave–triangular, glabrous, poorly developed, shorter than a quarter of the hypocotyl-root axis length; cataphylls absent. (Fig. 1H, M).

POECILANTHE GRANDIFLORA BENTH

Seeds 3–5 in number, not overgrown, somewhat symmetrical, wide ovate-elliptic or sub-orbicular, 18–23 × 15–18 × 2–4 mm; flattened in cross section, margins regular; face parallel with the fruit length. Testa thick (coriaceous), glossy, smooth; hilum 1–1.5 mm, curved downward to the endocarp, at most only very slightly projected, not concealed; rim-aril present, one-lipped, tongued or not, lighter than the testa; hypocotyl-root lobe not visible or difficult to distinguish; micropyle visible, punctiform; lens not visible; chalaza not visible; raphe not visible. Cotyledon base groined, hypocotyl-root axis concealed; outer face smooth, inner face plane; embryonic axis 2.8–3.3 mm long; aligned with cotyledon length; hypocotyl-root axis straight, triangular; plumule bipartite, concave–triangular, glabrous, poorly developed, shorter than a quarter of the hypocotyl-root axis length; cataphylls absent. (Fig. 1H, M).

Table 1. Summary of the most important diagnostic characters of Poecilanthe seeds and embryos

<table>
<thead>
<tr>
<th>Character/pattern</th>
<th>P. amazonica-type</th>
<th>P. effusa-type</th>
<th>P. parviflora-type</th>
<th>P. grandiflora-type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seed growth</td>
<td>Overgrown</td>
<td>Regular</td>
<td>Regular</td>
<td>Regular</td>
</tr>
<tr>
<td>Seed position within the fruit</td>
<td>Longitudinal</td>
<td>Transversal</td>
<td>Longitudinal</td>
<td>Longitudinal</td>
</tr>
<tr>
<td>Testa</td>
<td>Papery</td>
<td>Papery</td>
<td>Membranaceous</td>
<td>Coriaceous</td>
</tr>
<tr>
<td>Hilum</td>
<td>Straight</td>
<td>Downward</td>
<td>Straight</td>
<td>Downward</td>
</tr>
<tr>
<td>Aril</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>+</td>
</tr>
<tr>
<td>Micropyle</td>
<td>–</td>
<td>+</td>
<td>+</td>
<td>–</td>
</tr>
<tr>
<td>Lens</td>
<td>–</td>
<td>+</td>
<td>+</td>
<td>–</td>
</tr>
<tr>
<td>Raphe</td>
<td>1/2</td>
<td>0*</td>
<td>3/4</td>
<td>0</td>
</tr>
<tr>
<td>Chalaza</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>–</td>
</tr>
<tr>
<td>Post-chalazal branches</td>
<td>Not reaching the hilum</td>
<td>Reaching the hilum</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>HR axis inflection</td>
<td>Inflexed</td>
<td>Straight</td>
<td>Straight</td>
<td>Straight</td>
</tr>
<tr>
<td>HR axis concealment</td>
<td>Exposed</td>
<td>Concealed</td>
<td>Exposed tip/concealed</td>
<td>Concealed</td>
</tr>
<tr>
<td>Plumule development</td>
<td>Poor</td>
<td>Moderate</td>
<td>Moderate</td>
<td>Poor</td>
</tr>
<tr>
<td>Plumule/HR axis</td>
<td>&lt; 1/3</td>
<td>± 2</td>
<td>1/3–1</td>
<td>&lt; 1/3</td>
</tr>
<tr>
<td>Plumule trichomes</td>
<td>–</td>
<td>+</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Epicotyl base trichomes</td>
<td>–</td>
<td>+</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Cataphylls</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

HR, hypocotyl-root axis: +, present; –, absent; *probably present, but not distinguishable from the post-chalazal branches.
onic axis 3–3.5 mm long; aligned with cotyledon length; hypocotyl-root axis straight, triangular; plumule bipartite, concave–triangular, glabrous, poorly developed, shorter than a quarter of the hypocotyl-root axis length; cataphylls absent. (Fig. 1C, G).

**Poecilanthe hostmannii** (BENTH.) AMSHOOF

Seeds 3–7 in number; overgrown, symmetrical or asymmetrical, ovate, wide–elliptic or somewhat D-shaped, rarely transversally oblong, 15–22 × 12–21 × 4–8 mm; compressed or rectangular in cross section; margins irregular; face parallel with the fruit length. Testa thin (chartaceous), dull, wrinkled; hilum 0.8–1 mm, parallel to the suture, not projected, concealed by a funicus remnant; aril absent; hypocotyl-root lobe not visible; micropyle not visible; lens not visible; chalaza not visible externally, but internally visible, opposite to the hilum; post-chalazal branches present, under 8 in number, usually not reaching the hilum; raphe visible externally, slightly elevated. Cotyledons notched or groined; hypocotyl-root axis concealed at the base (tip exposed) or not, outer face smooth, inner face plane; embryonic axis 2.5–3 mm long, almost aligned with the cotyledon length (just slightly oblique); hypocotyl-root axis inflexed, truncate or triangular; plumule bipartite, concave–triangular, glabrous, poorly developed, shorter than a quarter of the hypocotyl-root axis length, both sides of it bearing a series of membranaceous cataphylls (Fig. 2A).

**Poecilanthe itapuana** G.P.LEWIS

Unfortunately the single available seed was insect damaged. We could observe, however, that the hilum is curved downward to the fruit wall and that it presents a one-lipped rim aril.

**Poecilanthe parviflora** BENTH

Seeds 1–2 in number, not overgrown, symmetrical or asymmetrical, wide–elliptic, sub-orbicular or oblate, 13–18 × 11–17 × 3–4 mm; flattened in cross section, margins regular; face parallel with the fruit length. Testa thin (chartaceous), dull, smooth; hilum 0.6–0.8 mm, parallel to the suture, not projected, partially (or rarely not) concealed by a funicus remnant, rim darker than the testa; aril absent; hypocotyl-root lobe not visible; micropyle visible, filled with a spongy tissue; lens visible, confluent with the hilum, mounded, linear; chalaza visible, more wrinkled and thicker than the testa; raphe visible, slightly elevated, running around three-quarters of the seed circumference. Cotyledon base groined, hypocotyl-root axis concealed or with the tip exposed; outer face smooth, inner face plane; embryonic axis 2.5–3 mm long; parallel with cotyledon length; hypocotyl-root axis straight, triangular; plumule bipartite, oblong (margin convex), glabrous; moderately developed, shorter than, or rarely the same length as the hypocotyl-root axis; cataphylls absent. (Figs 1I, L, P, 2F).

**Poecilanthe subcordata** BENTH

Seeds 1 (–2), not overgrown, symmetrical or asymmetrical, elliptic or D-shaped in outline, 11 × 8 × 2 mm; flattened in cross section, margins regular or nearly so; face parallel with the fruit length. Testa thick (coriaceous), glossy, smooth; hilum 0.6–0.8 mm, curved downward to the endocarp, slightly projected, not concealed; rim-aril present, one-lipped, tongued or not, colour similar to that of the testa; hypocotyl-root lobe slightly visible; micropyle visible, punctiform; lens not visible; chalaza not visible; raphe not visible. Cotyledon base groined, hypocotyl-root axis concealed; outer face smooth, inner face plane; embryonic axis 1.3–1.6 mm long; parallel with cotyledon length; hypocotyl-root axis straight, triangular; plumule bipartite, glabrous; poorly developed, shorter than a quarter of the hypocotyl-root axis length; cataphylls absent.

**Poecilanthe ulei** (HARMS) ARROYO & RUDD

Seeds 1–3 in number, not overgrown, asymmetrical, wide–elliptic, sub-obicular or oblate, 13–18 × 11–17 × 3–4 mm; flattened in cross section, margins regular; face parallel with the fruit length. Testa thick (coriaceous), glossy, smooth; hilum 1 mm, curved downward to the endocarp, slightly projected, not concealed; rim-aril present, one-lipped, tongued or not, lighter than the testa; hypocotyl-root lobe slightly visible; micropyle visible, punctiform; lens not visible; chalaza not visible; raphe not visible. Cotyledon base groined, hypocotyl-root axis concealed; outer face smooth, inner face plane; embryonic axis 2.5–2.7 mm long; parallel with the cotyledon length; hypocotyl-root axis straight, triangular; plumule bipartite, glabrous; poorly developed, shorter than a quarter of the hypocotyl-root axis length; cataphylls absent. (Figs 1Q, 2B, E).

**DISCUSSION**

**Comparative Seed and Embryo Morphology**

The morphology of seeds and embryos within *Poecilanthe* is shown to be highly variable. Based on these differences, we could distinguish four patterns of seed and embryo morphology within the genus: (1)
POECILANTHE SEED AND EMBRYO

P. amazonica-type; (2) P. effusa-type; (3) P. parviflora-type; (4) P. grandiflora-type. These types are characterized below and their most important morphological features are summarized in Table 1.

1. P. amazonica-type. This group is composed of the Amazonian species P. amazonica and P. hostmannii. Both have overgrown seeds, post-chalazal branches not reaching the hilum (Fig. 1J), an inflexed hypocotyl-root axis (Fig. 2A) and the presence of cataphylls on the epicotyl (Fig. 2D), as diagnostic characters.

We identified the seeds of P. amazonica and P. hostmannii as overgrown. Corner (1951) coined this term to refer to some seeds for which growth is limited by the fruit cavity. These overgrown seeds may be recognized by their relatively large size, filling the seed cavity and often becoming distorted in shape (Fig. 1A, B), and by the poorly differentiated testa. However, Kirkbride et al. (2003) pointed out that it is difficult to determine unlimited seed growth in the absence of anatomical studies. Consequently, we identified those seeds as overgrown because they appear to be, but this observation needs to be confirmed by further studies.

The notched cotyledon base (Fig. 1N) exposing the hypocotyl-root axis is the most common pattern in this group, but the groined cotyledon base may also be present.

We consider the structures adjacent to the plumule as cataphylls for the following reasons: they are hyaline and fragile and apparently the leaves are not primordial, so not part of the plumule. Many seedlings present cataphylls between the eophylls and cotyledons (Lima, 1989), corresponding to the part where the structures are attached in the embryo of this Poecilanthe group. Oliveira (1999) has shown that embryos of Platypodium elegans Vog. present primordial cataphylls on the epicotyl and Lima (1989) described cataphylls on seedlings of this species.

Lima (1989) suggested that the presence of cataphylls on seedling epicotyls is associated with environmental stress, especially in periodically flooded forests. In this case, P. amazonica is a typical tree from Amazonian flooded forests and, P. hostmannii, despite not growing in flooded forests, occurs in riverside vegetation.

2. P. effusa-type. This group is represented by the Amazonian species P. effusa. This species occurs mainly in drier vegetation, never in flooded forests or riparian vegetation. A transverse orientation of the seed face with the fruit length (Fig. 1D), the post-chalazal branches reaching the hilum (Fig. 1K), a concave inner cotyledon face, a split cotyledon base (Fig. 1O), reddish trichomes surrounding the base of the epicotyl (Fig. 2C) and the villose plumule (Fig. 2C), 2 times longer than the hypocotyl-root axis, are unique characters.

There are two different trichome types on the embryo of this species. The plumule trichomes are thin, long and greyish and the basal ones on the epicotyl are thick and reddish. The nature and function of these two different trichome types deserves more detailed anatomical studies and histochemical tests.

3. P. parviflora-type. This group comprises only P. parviflora. This species is distributed from Argentina and Paraguay to southern Brazil, mainly within riparian forests. The diagnostic characters for this group are the presence of a visible lens (Fig. 1I), a raphe running around up to three-quarters of the seed circumference (Fig. 1L) and a moderately developed, glabrous plumule (Fig. 2F).

4. P. grandiflora-type. The last group contains the extra-Amazonian species P. falcata, P. grandiflora, P. subcordata and P. ulei, all occurring mainly in dry vegetation types. The group is easily recognized by its thick (coriaceous) testa, a hilum curved downwards to the endocarp (Fig. 1G) and a one-lipped rim-aril (Fig. 1H). Poecilanthe itapuana presents all characters cited above and, even without complete material, we suggest it belongs to this group.

RELEVANCE TO POECILANTHE TAXONOMY

The morphological and chemical heterogeneity of Poecilanthe has been long recognized (Geesink, 1981; Greinwald et al., 1995; Klitgaard, 1995; Kirkbride et al., 2003). Some authors have already suggested that Poecilanthe comprises two distinct groups (Geesink, 1981; Ross & Crisp, 2005). Our findings increase the total evidence of how heterogeneous Poecilanthe is and reinforce the belief that Poecilanthe is not a natural group.

Actually, a preliminary cladistic analysis (Meireles, Lavin & Tozzi, unpubl. data) reveals Poecilanthe as non-monophyletic and recognizes three major clades: (1) P. amazonica + P. hostmannii; (2) P. effusa + P. ovalifolia; (3) the extra-Amazonian clade (including all the extra-Amazonian species). The seed and embryo morphology largely supports these three clades, as three of the four seed and embryo types can be exclusively assigned to a lineage: (1) P. amazonica + P. hostmannii clade (P. amazonica-type); (2) P. effusa + P. ovalifolia clade (P. effusa-type); and (3) extra-Amazonian clade (P. grandiflora-type). However, the phylogeny reveals P. parviflora within the extra-Amazonian clade and no separate lineage (except the species itself) is assigned to the P. parviflora-type. The differences from the P. parviflora-type to the P. grandiflora-type, may be related to the riparian habitat where P. parviflora grows, as in

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with some *Pterocarpus* and *Machaerium* species (Lima, 1989).

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