Seedling Diversity and the Homologies of Seedling Organs in the Order Poales (Monocotyledons)

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INTRODUCTION

Among the most long-lasting and controversial discussions in the field of plant morphology is the question of the enigmatic organ homologies of the grass embryo/seedling. Since the beginning of the 19th century, more than 100 publications have addressed this issue. The literature is full of speculations and conflicting interpretations; no hypothesis has achieved general acceptance. It is noteworthy that most papers are based on the investigation of very few (mostly 1–3) species. Furthermore, the cultivated cereals are usually chosen to speculate about homologies. This neglects the diversity of approx. 700–800 genera (Clayton and Renvoize, 1986; Tzvelev, 1989) with more than 9000 species in this family. Despite the paucity of comprehensive studies of the seedling morphology of Poaceae, the basic traits obviously occur throughout the family, including giant bamboos and also early diverging genera such as Pharus and Streptochaeta (H.-J. Tillich, unpubl. res.). Evidently, the problem cannot be resolved by comparison of seedlings across the grass family. Therefore, the next step must be a comparative study of seedlings of the immediate relatives of Poaceae. The order Poales as recently circumscribed and subdivided by Linder and Rudall (2005) and Chase et al. (2006) may serve as a framework for such a comparison. Hydatellaceae is excluded from this study, since Saarela et al. (2007) have found this small family to be sister to Nymphaeales. Knowledge of seedlings of the Poales families varies widely. Besides the numerous papers on Poaceae, there is good information on the diversity of embryos and/or seedlings of Cyperaceae (Didrichsen, 1894, 1897; Schneider, 1932; van der Veken, 1965; Jacques-Felix, 1988) and Bromeliaceae (Irmisch, 1879; Müller, 1895; Smith and Downs, 1974; Gross, 1988; Pereira, 1989; Tillich, 1998). For Juncaceae, there are several descriptions of Juncus and Luzula (e.g. Raunkiær, 1895; Laurent, 1904; Tillich, 1985, 1994), but no information is available for the southern hemispheric genera. Knowledge of Restionaceae seedlings has recently been increased by Carlquist (1976), Kircher (1986), Meney et al. (1990), Tillich (1995), Pate and Meney (1999) and Linder and Caddick (2001). Pate and Meney (1999) also provide the first information about seedlings in the small Australian families Anarthriaceae and Eceiocoileaceae. Seedlings of Typhaceae (Typha and Sparganium) are described in detail by Tillich (1994). The first description of an Eriocaulaceae seedling dates back to Clarke (1859), but it left morphological details unresolved, a failure not overcome by more recent descriptions of the minute seedlings by Ramaswamy et al. (1981) and Scatena et al. (1993). For the following families, the information is increasingly scanty. Centrolopediaceae and Flagellariaceae are represented in the literature by only two figures each: Centrolopis in Hieronymus (1873) and Tillich (1995); Flagellaria in Jacques-Felix (1988).

Key words: Cotyledon, grass embryo, grass seedling, monocotyledons, organ homology, Poales, seedling glossary.

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and Tillich (1996). In the heterogeneous Xyridaceae there is knowledge only of Xyris (Tillich, 1994; Sajo and Rudall, 1999). In Thurniaceae only the Prionium seedling is known (Tillich, 1985), while seedlings of Joinvilleaceae, Mayacaceae and Rapateaceae have never been described or produced as figures. [Note: Hydatellaceae, until recently included in Poales, are properly to be referred to as Nymphaeales (Saarela et al., 2007). Details of their seedlings are unknown, except for a small sketch by Cooke (1983). Even an extended recent investigation of the morphology of this family (Rudall et al., 2007) gives no information about seedlings.]

In the present report, the seedling stage of a number of genera is described for the first time, and integrated with all available published information on other seedlings of Poales. The detailed descriptions aim for the establishment of homologous terms for the seedling organs, including the puzzling grass seedlings, and in polarization of character states.

If not otherwise mentioned, circumscriptions and names of orders are used sensu APG II (2003).

MATERIALS AND METHODS

The gathering of the seeds for this study has required the efforts of numerous collectors over a long period of time. Seeds from Botanical Gardens were used only in cases where the source of the plants from natural habitats is well documented (Table 1). For the larger families (Bromeliaceae, Cyperaceae and Poaceae), only a selection of the investigated species are mentioned; further information can be found in Tillich (1995). The seeds were sown in Petri dishes (20 × 5 cm) on moist filter paper at temperatures of 20–22 °C and permanent light. Under these conditions, the lengths of seedling organs are constitutive characters and as such are comparable. In Poales, no seeds require darkness to stimulate germination. Seedlings were analysed under a Wild MZ8 Stereo Microscope (Leica Microsystems, Bensheim, Germany) with photographic and drawing equipment. The small seedlings of Eriocaulaceae were additionally analysed in a scanning electron microscope LEO 438 VP (Leica Microsystems, Bensheim, Germany) using standard methods. Since seedling structure turned out to be generally uniform at the generic level, only a selection of studied seedlings is shown in Figs 3–9. Seedling vouchers are stored in the Herbarium of the Botanische Staatssammlung München (M).

RESULTS: MORPHOLOGICAL TERMINOLOGY

First the terms needed to describe monocot seedlings in general are standardized, a necessary pre-condition in order to discuss seedlings of Poales. Cross-references between terms are indicated in italics.

Cotyledon

apocole (Cook, 1939; Tomlinson, 1961). This term was introduced to describe the elongating part of the cotyledon that

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Source of seeds</th>
<th>Seedling voucher in M*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Areceae</td>
<td>Lodoicea maldivica Pers. ex H. Wendl.</td>
<td>Imported by a Munich Garden Market</td>
</tr>
<tr>
<td>Bromeliaceae</td>
<td>Guzmania nicaraguensis Mez &amp; C.F.Bak.</td>
<td>BG Munich 1996</td>
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<td></td>
<td>Portea lepantana Harms</td>
<td>BG Munich 1996</td>
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<tr>
<td></td>
<td>Centrolepidaceae</td>
<td>BG Munich 1996</td>
</tr>
<tr>
<td></td>
<td>Centrolepis drammondii Walp</td>
<td>BG TU Dresden 1995</td>
</tr>
<tr>
<td></td>
<td>Centrolepis strigosa Roem. &amp; Schult.</td>
<td>BG TU Dresden 1994</td>
</tr>
<tr>
<td></td>
<td>Cyperaceae</td>
<td>BG Oslo 1998</td>
</tr>
<tr>
<td></td>
<td>Elyna myosuroides (Vill.) Fritsch</td>
<td>Germany, Thuringia, Tillich 08/1994</td>
</tr>
<tr>
<td></td>
<td>Isolepis setacea (L.) R. Br.</td>
<td>BG Munich 1999</td>
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</tbody>
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TABLE 1. Sources of species

(Continued)
buries the plumule in the case of hypogeal, remote germination of palms (see germination modes) (Fig. 3). In some genera, for example Phoenix, the cotyledonal sheath is also involved in this elongation growth. However, in the vast majority of comparable seedlings, the distance between seed and plumule is brought about by the exclusive elongation of the unifacial, proximal part of the cotyledonal hyperphyll. Therefore, the apocode is here restricted to that part of the hyperphyll between the haustorium and cotyledonal sheath in hypogeal seedlings with remote germination (Fig. 2F, G and H). In the rare cases where the cotyledonal sheath elongates above the soil surface, the apocode is sharply bent downwards and keeps the seed buried or close to the soil surface. In that case, it is usually a very thin, thread-like structure, with no major photosynthetic capacity (Fig. 2K).

Synonyms: Mittelstück, Zwischenstück (Klebs, 1885; Velenovský, 1907; Goebel, 1933), Leiter (Schlickum, 1896; Čelakovský, 1897), verlängerter Hals (Tschiehr, 1890), Hals (Jönsson, 1902), cotyledonal axis (Tomlinson, 1990). Often this organ is interpreted as being the petiole (Blattstiel) of the cotyledon. This interpretation goes back to Bernhardi (1832) and is also used by, for example, Irmisch (1856a, b), Gatlin (1909, 1912), Žurawksa (1912), Arber (1925, 1932), Tomlinson (1960), Bell (1991) and Henderson (2002). However, petiole or Blattstiel are inadequate terms, since in unifacial hyperphylls generally no sub-division occurs into petiole and blade. Thus neither a petiole nor a blade is a part of a cotyledonal hyperphyll.

coleoptile (Mirbel, 1815). This is a tubular structure produced by meristematic activity of the marginal tissue of the cotyledonal sheath. By means of this growth process the cotyledonal leaf margin is raised and forms the distal opening of the coleoptile, often as a narrow slit. The first plumular leaves emerge through this opening (Figs 2G–I and 11E).

Note that the coleoptile is often confused with a ligule. The development of a coleoptile has two pre-conditions: (a) the sheath is closed; and (b) the hyperphyll is unifacial. Only in this case does the cotyledonal leaf margin form a closed circle and can develop a tubular structure. Ligules are outgrowths across the adaxial surface of a bifacial leaf region. They occur in foliage leaves of adult plants in monocots and in other angiosperms. The coleoptile in its strict sense occurs only in cotyledons of monocots.

Synonyms: ligule (e.g. Gatlin, 1906, 1909; Arber, 1925; Choudar, 1931; Uhl and Dransfield, 1987), ocrea (Zurawska, 1912), upper sheath (Sargent and Arber, 1915; Boyd, 1932), ligular sheath (Arber, 1925), verlängerter Scheidenteil (Pankow and von Guttenberg, 1957), ochrea (Ginieis, 1952), tubular ligule (Tomlinson, 1960), prophyll (Jacques-Felix, 1988).

compact cotyledon. This is a cotyledon consisting of a haustorial hyperphyll and a short cotyledonal sheath, the latter neither tubularly elongated nor developing a coleoptile (Fig. 2E).

cotyledon, Keimblatt. Cotyledons are distinguished from all other leaves since they originate directly from tissues of a developing embryo. All other leaves come into existence as primordia protruding from an apical meristem. Nevertheless, it is sensible to consider the cotyledon as a leaf. Without exception, all monocots possess only one cotyledon.


cotyledonal hyperphyll. The cotyledonal hyperphyll is the part distal to the bifacial hypophyll of the cotyledon of monocots. Apart from a few questionable exceptions (e.g. in Amaryllidaceae and Liliaceae sensu stricto), the margins of the cotyledonal sheath join across the adaxial face of the hyperphyll base. Therefore, the hyperphyll including its haustorial tip can be interpreted as being unifacial.

Depending on functional differentiations or specializations, the cotyledonal hyperphyll appears in different forms.

(1) It is haustorial and is therefore completely hidden in the seed (Fig. 2C, E, I).
(2) It elongates considerably and creates some distance between the seed and cotyledonal sheath (apocole, Figs 2F–H, K and 3; phaneromer, Figs 1, and 2A, B).
(3) It has overtaken the main storage function in endospermless seeds, is globular to ovoid in shape and is the most voluminous part of the embryo, e.g. in Scheuchzeria, Cyanastrum and endospermless Araceae (Tillich, 2003b) (Fig. 2D).

Synonym: upper leaf part.
The cotyledonary hypophyll is the always bifacial basal part of the cotyledon. It appears in three principal forms:

1. It is a low cotyledonary sheath embracing the cotyledonary node without secondary outgrowths (Fig. 2A, B, D–F).
2. It is expanded, forming a blade-like assimilating structure (e.g. Costus, Caladium, Philodendron and Pitcairnia) (Fig. 2C).
3. It develops a coleoptile (Fig. 2G–I).

Only very rarely does the cotyledonary sheath itself elongate into a tubular structure above the soil surface, and the seed remains at the soil surface or buried since the apocole also elongates (Fig. 2K). This behaviour is known only in a few Iridaceae and Commelinaceae (Tillich, 2003a).

Synonym: basal leaf part.

cotyledonary sheath, Kotyledonarscheide. This is the basal, always bifacial part of a cotyledon embracing the cotyledonary node and protecting the plumule (Fig. 2E). In cases of development of a long coleoptile, the cotyledonary sheath may be completely suppressed in favour of the coleoptile. In such cases the cotyledonary hyperphyll originates very near the cotyledonary node (Figs 2H, I and 11E).

Synonyms: basal sheath (Arber, 1925), sheathing base (Boyd, 1932).

haustorium. The haustorium is the cotyledonary hyperphyll or the distal part of it that is inside the seed in contact with the nutritive tissue. When the haustorium is embedded in the endosperm, its shape is cylindrical, globular or flattened to some extent, depending on the shape of the seed. When it is laterally attached to the endosperm, its shape resembles a lens or shield. Often the haustorium increases in size during the germination process to keep contact with the dissolving endosperm. The spatial shape of the haustorium is predetermined by the available space inside the seed. Since the haustorium is part of a unifacial hyperphyll, it cannot bear a margin in a strict morphological sense, and any ribs, keels or other surface structures have no particular morphological significance. It thus cannot be considered a lamina, nor can it have a margin as has sometimes been suggested for the scutellum of Poaceae.

Synonyms: ‘Endtheil, der Lamina entsprechend’, ‘der Lamina entsprechende Spitze’ (Irmisch, 1856a, b), Sprête (Čelakovský, 1897) ‘sucker’, ‘corresponding to the leaf blade’ (Tomlinson, 1960), Sauger (Schlickum, 1896; Čelakovský, 1897), sucker, sectorial tip (Boyd, 1932), leaf blade (Henderson, 2006), scutellum (generally used for the haustorium of the Poaceae embryo).

phaneromer. This term is introduced here to name the proximal part of the cotyledonary hyperphyll that raises the seed well above the soil surface and is the first assimilating organ of the seedling (Figs 1 and 2B). In endospermless Alismatales with an enlarged storage hypocotyl (‘macropodous’ embryos/seedlings), the complete hyperphyll represents a phaneromer after shedding the empty seed coat (Fig. 2A). The phaneromer mostly grows straight upright and is usually terete. Rarely it is somewhat flattenend and widened, e.g. in Paris and Trillium. Curiously, this conspicuous part of the seedling has never been named, previously having been described, for example, as ‘green, upright, assimilating, threadlike part of the cotyledon’. In some cases its distal part at first or permanently bends sharply (e.g. in many Alliaceae and Hyacinthaceae, Fig. 2B), in extreme cases forming a ‘hairpin-like structure’ (Thongpukdee, 1989). In Poales such ‘hairpins’ are
reported for some Restionaceae (Pate and Meney, 1999; Linder and Caddick, 2001).

Synonyms: lamina or blade (Boyd, 1932; Smirnova, 1966), limb (Arber, 1925), limbe foliaire (Chouard, 1931).

scutellum

Haustorium

Sheath lobes, Scheidenlappen (Weberling, 1967, 1975). Sheath lobes are paired appendages of the sheath just below the junction with the hyperphyll, also found on foliage leaves. Since the cotyledonary hyperphyll is unifacial, the sheath lobes are often united across the base of the hyperphyll and form a single median sheath lobe (Figs 4D–F, and 9B).

Synonym: vaginal lobes (Weberling, 1975).

Seedling axis
collar, Wurzelhals (Troll, 1943, p. 2024 ff.). The collar is a morphologically distinguished basal zone of the hypocotyl, sometimes even a prominently bulging region, occurring in both monocotyledonous and dicotyledonous seedlings. It can be recognized by its ability to give rise to collar rhizoids, and often it is prominently swollen, thus increasing the rhizoid-bearing surface (Fig. 1). In extreme cases the collar is a disc-like extension around the hypocotyl base, or it bears an only one-sided outgrowth (periblast, epi-blast). In the literature the collar is often described as a transitional zone between the shoot and root. However, morphologically, the two are sharply delimited: the collar is covered by the shoot epidermis; the surface of the root, the rhizodermis, is exposed only after the calyptra is shed.

There is a gradual anatomical transition between root and shoot; this transition is only referred to as the collar, but occurs throughout the hypocotyl.

Synonyms: Wurzelknoten (Ascherson, 1883), collum (Warming, 1883), collet (de Vogel, 1979; Stevens, 2006).

collar rhizoids, Wurzelhalsrhizoide (Troll, 1943, p. 2027). These are unicellular trichomes developed from the collar epidermis (Fig. 1). They appear distinctly earlier than the first root hairs of the primary root, often before the root commences its elongation growth. Furthermore, they can usually be distinguished from root hairs by their greater length, density and/or longevity. They are responsible for the first close contact of the seedling with its substrate.

Synonyms: Haarkrans (Warming, 1880), Wurzelknotenbehaarung (Ascherson, 1883), poils absorbants (Laurent,
cotyledonary node. The cotyledonary node is the first (lowest) node of the seedling axis where the cotyledon is inserted, its base usually encircling the node (Fig. 1).

epiplast (Richard, 1811). The epiplast is a one-sided outgrowth of the collar. In typical form it is found in a great number of grass seedlings. When the collar of a grass seedling (= the first coleorhiza) bears rhizoids, the epiplast may increase the rhizoid-bearing surface considerably.

epicotyl. This is the first internode above the cotyledonary node (Fig. 1). In monocots, this internode is mostly very short, so that the first plumular leaf is basally embraced by the cotyledonary sheath or coleoptile.

hypocotyl. The hypocotyl is the shoot axis segment below the cotyledonary node (Fig. 1). Usually, it is inconspicuous except for the collar region. There is often an abrupt change in diameter between the hypocotyl base and the slender primary root, then the collar covers the flat base of the hypocotyl. Seedlings occasionally have a well elongated hypocotyl, even while growing in permanent light, e.g. Tacca and some Juncaceae (Fig. 7H and L). In many aquatic Alismatales the hypocotyl is the storage organ of the embryo and therefore it is much enlarged, the ‘macropodous’ seedlings of Arber (1925).
mesocotyl (Čelakovský, 1897). In monocotyledonous seedlings, the more or less elongated axis segment between the haustorium and coleoptile is the mesocotyl. In fact, it is an epicotyl that is congenitally fused with basal coleoptile tissue (Fig. 11F, G) (Pankow and von Guttenberg, 1957; von Guttenberg and Semlow, 1957).

periblast (Tillich, 1992). This is an extended, disc- or umbrella-shaped collar, usually conspicuously covered by collar rhizoids. It occurs in monocots and in also dicotyledonous seedlings. Typical examples are known in, for example, Commelinaceae and Myrtaceae (Troll, 1943, p. 2026; Baranov, 1957; Beltrati, 1978).

Synonyms: Ringwulst, collar ‘kragenförmig erweitert’ (Troll, 1943), coleorhiza (Baranov, 1957).

plumule. The plumule is the apical bud of the seedling, giving rise to the plumular leaves (cataphyll, eophyll).

**Plumular leaves**

cataphyll, Niederblatt. Along any shoot, the cataphyll is a leaf below the foliage leaves. It is more or less reduced to its sheathing base (hypophyll) and thus appears scale-like, often poor in chlorophyll or lacking it (e.g. bud scales). When cataphylls occur in seedlings, they are the first leaves after the cotyledon (Fig. 1).

Synonym: scale leaf.

eophyll (Tomlinson, 1960), Primärblatt. In seedlings, eophylls are the first plumular leaves with noteworthy photosynthetic activity, but are distinctly simpler in shape and smaller in size than the foliage leaves of the adult shoot (metaphylls) (Fig. 1). When the adult plant bears
only scale leaves as, for example, in *Ruscus*, *Semele*, *Danae* and *Restionaceae*, the eophylls are the only foliage leaves of the plant.

**Synonym:** primary foliage leaf; seedling leaf (Pate and Meney, 1999; Linder and Caddick, 2001).

**Roots**

coleorhiza (Mirbel, 1815), Wurzelscheide. When shoot-born roots are initiated in a young seedling axis, the growing root tip often stimulates cell elongation growth in the peripheral tissue of its mother organ, thus enabling this

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**Fig. 7.** Seedlings of the Cyperid clade. (A–E) Cyperaceae. (F) Thurniaceae. (G–K) Juncaceae. (A–C) *Isolepis setacea*, three stages of seedling development. (D) *Elyna myosuroides*. (E) *Mapania cuspidata*. (F) *Prionium palmita*. (G) *Luzula nivea*. (H, I) *Marsippospermum reichii*, with I showing a detail of H. (J) *Juncus maritimus*. (K) *Rostkovia magellanica*. a, appendix at top of coleoptile; bh, blade-like cotyledonary hypophyll; cl, collar; cp, coleoptile; cr, coleorhiza; cs, cotyledonary sheath; eo, eophyll; f, fruit; hy, hypocotyl; mc, mesocotyl; ph, phaneromer; pr, primary root; ra, radicle; rh, collar rhizoids; s, seed; sc, scale-like cataphyll; sr, shoot-born root. Scale bars in A and B = 0.5 mm; C, D, F, I and J = 1 mm; G, H and K = 3 mm; (E) = 5 mm.

**Fig. 8.** Seedlings of the Restiid clade. (A, B) Centrolepidaceae. (C–F) Restionaceae. (G) Anarthriaceae. (A) *Centrolepis strigosa*. (B) *Centrolepis drummondii*. (C) *Chondropetalum tectorum*. (D) *Elegia racemosa*. (E) *Cannomois grandis*. (F) *Willdenowia incurvata*. (G) *Anarthria prolifera*. [E and F are from Linder and Caddick (2001), and G is modified from Pate and Meney (1999)]. cl, collar; cp, coleoptile; cs, cotyledonary sheath; eo, eophyll; f, fruit; hy, hypocotyl; ph, phaneromer; pr, primary root; rh, collar rhizoids; s, seed; sr, shoot-born root. Scale bars in A–D = 1 mm.
tissue to grow out forming a structure like the finger of a glove, the coleorhiza around the young root (Fig. 1). After the root has broken through, the coleorhiza remnants form a cuff around the root base. Roots originating from adult shoots as well as lateral roots never form a coleorhiza.

collar roots, Grenzewurzeln (Weber, 1936). Collar roots are those originating at the collar level. They either occur in small numbers, representing the number of xylem poles in the root bundle (e.g. Commelinaceae), or are produced in great numbers from conspicuously swollen collars (e.g. Marantaceae).

lateral root, Seitenwurzel. A lateral root is one that originates endogenously from any other root.

primary root, Primärwurzel. The primary root is that developing from the radicle of the embryo. It is the only root of the seedling of exogenous origin (Yamashita, 1991).

radicle. A radicle is an exogenously initiated root meristem of the embryo. Apart from a very few exceptions in Alismatales (see Yamashita, 1970, 1972, 1976), it originates at the root pole of the embryo, i.e. at the attachment point of the suspensor. During germination, it develops into the primary root.

root hairs. Root hairs are unicellular trichomes developed from trichoblasts of the rhizodermis.

root pole. The root pole is the region of an embryo opposite the plumule, where the suspensor is attached.
shoot-born root, sprossbürtige Wurzel (Troll, 1937). This is a root endogenously initiated in a shoot axis (Fig. 1, and 11B, G).


Germination mode

hypogeal vs. epigeal. This couplet of terms relates to the position of the seed relative to the soil surface during germination. In hypogeal germination, the seed remains below ground or at least at ground level. In epigeal germination, the seed is raised well above the soil surface.

In all seed plants except monocots, hypogeal germination equals the hypogeal position of cotyledons, while in the case of epigeal germination the cotyledons are raised above the ground either remaining included in the seed or expanded and assimilating. Therefore, in all seed plants except monocots, the definition of both terms may relate to the position either of the seed or of the cotyledons (e.g. Bell, 1991).

In monocots, the situation is very different. The cotyledon is partly inside and partly outside the seed, and/or partly above and partly below ground. For instance, the seed, including the haustorial part of the cotyledon, may be buried, but a coleoptile is above ground and has photosynthetic function. Thus, the terms epigeal and hypogeal should generally be used only with respect to the position of the seed relative to the soil surface. In the case of epigeal germination, in dicotyledonous seedlings the seed is raised by an elongating hypocotyl, and in monocots by the cotyledon (Figs 2A–C, and 11C, D). The seedling axis in monocots remains generally very short. In seed plants other than monocots, the epicotyl may be long or short in both epigeal and hypogeal germination (see de Vogel, 1979). This implies that except for the hypocotyl, no lengths of other axis segments should be part of a definition of the epigeal or hypogeal germination mode (see Bell, 1991; Stevens, 2006).

cryptocotylar vs. phanerocotylar (Duke, 1965, 1969). These terms characterize germination types with the cotyledons remaining in the testa or escaping from it during germination. Since in monocots the cotyledon is usually partly inside and partly outside the seed, these terms are hardly applicable to their seedlings. Only seedlings from endospermless seeds could be regarded as phanerocotylar after shedding the empty seed coat (Fig. 2A, D).

remote vs. adnate (Martius, 1823). These terms were introduced to describe palm seedlings. In the case of remote germination, a non-haustorial part of the cotyledonary hyperphyll creates some distance between the seed or fruit and the sheath (apocole) (Figs 2F–H and 3). In the case of adnate germination, the hyperphyll is completely haustorial and does not undergo elongation, the cotyledonary sheath developing adjacent to the seed or fruit (Fig. 2E and I). In these cases the short connecting part between the sheath and haustorium that passes the seed coat or fruit wall does not require a term of its own, and it should not be termed an apocole as was unfortunately done by Linder and Caddick (2001).

Synonyms: sometimes adjacent is used instead of adnate (e.g. Gatin, 1906; Tomlinson 1990).

DESCRIPTION OF SEEDLINGS

The sequence of the following descriptions is based on the phylogenetic tree of Linder and Rudall (2005), modified after Chase et al. (2006) with better resolution of early branching families and with Sparganiaceae including Sparganiaceae (Fig. 12). Hydatellaceae are excluded.

Early branching families (Fig. 4)

Bromeliaceae (Fig. 4A–C). The cotyledonary hyperphyll is haustorial and the first plumular leaves are eophylls. However, seedling structure supports the traditional subdivision of this family into three sub-families. Unfortunately, seedlings of Ayensua and Brocchinia, which have recently been identified as a sister group to the rest of the family (Terry et al., 1997; Horres et al., 2000) are unknown. Seedlings in Bromelioidae possess a compact cotyledon, the haustorium forms a right angle with the seedling axis, and the primary root grows moderately in length (Fig. 4B). In Pitcairnioideae, all known seedlings are uniform in structure (Dyckia, Fosterella, Hechtia, Lindmania, Pitcairnia and Puya), despite the recently recognized paraphyletic nature of the group (Horres et al., 2000). The cotyledonary hypophyll is blade-like, the hypocotyl is distinctly elongated and bears the first shoot-born root(s), and the primary root grows well (Fig. 4A). In Tillandsioideae the cotyledonary sheath and hyperphyll are straight and there is a strong tendency for the primary root to be reduced (Fig. 4C); in several Tillandsia species it is only a vestigial stump without function and is soon replaced by shoot-born roots.

Typhaceae (including Sparganiaceae; Fig. 4G, H). Except for its distal haustorium, the cotyledonary hyperphyll develops into a green phaneromer. In Typha it is a long, slender organ with the minute seed at its top. In Sparganium it is shorter and thicker due to the heavier drupe. Furthermore, both genera are characterized by a short hypocotyl, a narrow collar with dense, long rhizoids, and a slender primary root, soon accompanied by stronger shoot-born roots. The first plumular leaves are linear eophylls. In Sparganium the cotyledonary sheath bears a small median sheath lobe.

Rapateaceae (Fig. 4D–F). The compact cotyledon with an open sheath develops a median sheath lobe of moderate length. The first plumular leaves are green eophylls. The hypocotyl has no collar region and bears no rhizoids. In Guacamaya and Schoenocephalium, the primary root grows only a few millimetres and bears some short, relatively thick root hairs (Fig. 4D and F). In Rapatea and Cephalostemon the primary root fails to develop, and the root pole is covered by the firmly fixed operculum. The first roots break through from the hypocotyl region (Fig. 4E).
Xyrid clade (Fig. 5)

Mayacaceae (Fig. 5A–C). The cotyledon of the small Mayaca seedling is reduced to its haustorial part completely hidden inside the seed. It is attached to the cotyledonary node without any sign of a cotyledonary sheath. At the root pole there is no radicle, and therefore no primary root can develop. The first plumular leaf is a pale scale-like cataphyll, followed by simple-shaped green eophylls. The first shoot-born root breaks through only several weeks after germination has commenced.

Xyridaceae (Fig. 5J, K, L). There is a great difference between seedlings of Xyris and Orectanthe. The open cotyledonary hypophyll of the Xyris seedling is broadened to a narrow ovate blade (Fig. 5J, K). At the junction to the small hyperphyllary haustorium, the cotyledon is sharply recurved, the seed therefore is hidden below the end of the hypophyllary blade. The series of plumular leaves begins at once with ensiform (isobilateral) eophylls. The distinct collar of the short hypocotyl bears dense rhizoids. The weak primary root is soon replaced by a vigorous shoot-born root.

A picture greatly differing from Xyris is presented by the hypogeal Orectanthe seedling (Fig. 5L). Its cotyledon is of the compact type; the plumule soon bears a large number of bifacial eophylls. The collar is devoid of rhizoids; the primary root grows only 2–3 mm in length and has a few short and relatively thick root hairs. Most of the seedling is hidden in the loose outer tests (detached in Fig. 5L); only the distal eophylls are projecting from that cover. Perhaps the failure of rhizoids can be explained by this behaviour.

Eriocaulaceae (Figs 5D–H and 6). The seedlings of this family show extreme organ reductions similar to Mayacaceae. Here again, the cotyledon is reduced to its haustorial part inside the seed. There is no indication of a cotyledonary sheath that could embrace the first eophyll. The root pole does not develop a radicle or a primary root. In several species, details of seedling structure are obscured by dense hairs around the base of the first leaf (Fig. 6). The rhizoids of the collar region may be short and thick or long and slender (Figs 5E and 6). The first endogenous root breaks through the collar opposite the plumule. This is close to the behaviour of the Poaceae embryo.

Cyperid clade (Fig. 7)

Thurniaceae (Fig. 7F). The South African genus Prionium, formerly included in Juncaceae, was identified as a separate family Prioniaceae by Munro and Linder (1998) and has recently been combined with the Amazonian genus Thurnia to form an extended family Thurniaceae (Chase et al., 2006). While seedlings of Thurnia are unknown, the seedling of Prionium palmita was described by Tillich (1985). It resembles Juncus with epigeal germination; the cotyledon has a long phaneromer. The first plumular leaves are linear, bifacial eophylls. The hypocotyl always possesses a unique trait of the family. Mapania has a shorter and wider coleoptile than seedlings of Cyperoideae (Fig. 7E).

In a number of Cyperoideae, the coleoptile is the first effective assimilating organ, since there is a massive chlorenchym along its adseminal side, while abseminally there are often only two cell layers with chlorophyllous cells. The massive chlorenchymous part is often extended by an appendix on top of the distal opening (Fig. 7C). The first plumular leaves are bifacial eophylls. The hypocotyl including its collar region is inconspicuous, but dense collar rhizoids are generally found. The basal part of the coleoptile is often congenitally fused with the elongating epicotyl, thus forming a mesocotyl (Fig. 7D).

Juncaceae (Fig. 7G–L). The cotyledon always possesses a long, upright phaneromer. The eophylls are flattened or terete. The widespread genera Juncus and Luzula have a short hypocotyl (Fig. 7G and K), but in Marsippospermum and Rostkovia from the southern hemisphere it is of considerable length (Fig. 7H, I and K). The collar generally bears long, dense rhizoids.

Restioid clade (Fig. 8)

Centrolepidaceae (Fig. 8A, B). The very small seedlings possess a straight phaneromer; the haustorial tip is hidden in the minute seed. The basal end of the hypocotyl is indicated as a collar only by the development of a dense ring of rhizoids, and joins the primary root without any change in diameter. Eophylls are produced immediately.

Restionaceae (Fig. 8C–F). The common germination pattern in Restionaceae is exemplified by the African genera Chondropetalum and Elegia (Fig. 8C, D); see also Linder and Caddick (2001). The phaneromer bears a small haustorial tip inside the seed. In Chondropetalum the hypocotyl is differentiated into a short cylindrical axis segment and a somewhat swollen collar, while in Elegia the hypocotyl is represented only by a collar plate. In Chondropetalum, the primary root is somewhat narrower than the hypocotyl, but in Elegia it is weak, and the collar rhizoids grow from the lower face of the collar plate. The primary root has very limited growth and is soon replaced by shoot-born roots breaking through from the collar region, but there is no coleorhiza (Fig. 8D). A similar pattern was described by Kircher (1986) for the Australian Leptocarpus similis. Hypogeal germination is known for the Willdenowia clade of the African Restionaceae (Linder and Caddick 2001). A well developed coleoptile is documented for Willdenowia, Mastersiella and Cannomosis (Linder and
Caddick, 2001, see Fig. 8E, F). For other hypogaeal genera, details of the cotyledon structure are unknown.

Anarthriaceae (Fig. 8G). The figure of the Anarthria prolifera seedling is taken from Pate and Meney (1999). The cotyledon develops a long, straight phaneromer, and the first plumular leaves are eophylls.

Graminid clade (Fig. 9)

Flagellariaceae (Fig. 9A, B). The cotyledon of Flagellaria is of the compact type. Its open sheath has two low sheath lobes partly united with a short median sheath lobe. The hypocotyl is represented only by a bulging collar covered with short rhizoids. The primary root is well developed. The first plumular leaf is a cataphyll, followed by a few leaves transitional to eophylls. The internode above the first cataphyll is much elongated, as is typical for many climbing species in monocots.

Joinvilleaceae (Fig. 9C–E). The cotyledon of Joinvillea possesses a short coleoptile; the hyperphyll is haustorial and completely hidden in the seed. The hypocotyl has a very short cylindrical part and a somewhat bulging collar which is covered with rhizoids all over its surface; in some seedlings the collar is more elaborated on the side away from the seed, resembling an epiblast (Fig. 9C). The primary root grows out without branching. Eophylls are produced from the beginning. The first shoot-born roots originate from the hypocotyl region, at first covered by a distinctive coleorhiza (Fig. 9D).

Ecdieicoleaceae. The seedling of an Ecdieicolea is described by Pate and Meney (1999), but the description is questionable, providing more questions than answers. The published figure shows a plant grown from an obviously deeply buried seed. This has caused an unusual elongation of the epicotyl to transfer the plumule to the soil surface; the first plumular leaves are eophylls. There is no information about the cotyledon structure. It is hard to understand how a plumule with young eophylls can move a long distance through soil substrate without any protection by scales or a coleoptile. More detailed information is urgently needed.

Poaceae (Fig. 9F, G). The one-seeded fruit (caryopsis) contains the haustorial cotyledonal hyperphyll (scutellum) laterally attached to the copious endosperm. The cotyledonary sheath is very short but the coleoptile is well developed. The hypocotyl is represented only by its collar region, which is transformed by an early developing shoot-born root into a coleorhiza. In several cases, this coleorhiza is shared by more than one endogenous root. For instance, in Triticum, there are usually three, while in Coix up to five are found (see Yamashita and Ueno, 1992). The root pole is located at the distal tip of this coleorhiza, but there is no trace of an exogenously initiated primary root. In about half of all grass genera, the collar has a scale-like extension (epiblast). This scale may be a small, inconspicuous structure, or it is remarkably developed, embracing the seedling base for three-quarters of its circumference, interrupted only by the scutellum, e.g. in species of Stipa, Festuca and Achnatherum (Fig. 9F). In other cases it is much elongated, nearly equalling the coleoptile in length (e.g. in Leersia). The collar including the epiblast is usually covered with long rhizoids. Early meristematic initiation of an epicotyl includes the coleoptile base; the fusion product is known as a mesocotyl. It can elongate considerably by an intercalary meristem, depending on light conditions or depth of sowing. However, in some Panicoideae it elongates greatly even in permanent light.

**DISCUSSION**

Seedlings of monocotyledons have a complex structure (Figs 1 and 2). Unfortunately, the literature contains a lot of only superficial seedling descriptions, together with an inexact and often incorrect or misleading terminology. This problem is also obvious in recent comprehensive glossaries (e.g. Stevens, 2006). The terms for the seedling structures defined and used here help us to think of the evolution of the highly derived monocot seedlings.

The most diverse seedling organ in monocots is the cotyledon (see Fig. 2). In Fig. 10 the morphological relationships between the main cotyledon types of Poales are shown. It is important to note that the three presumably derived types (Fig. 10B–D) can be reached directly from the compact cotyledon by only one step each. On the other hand, a direct switch between any of the derived types is impossible. A transformation of, for example, a...
phaneromeric cotyledon into a coleoptile bearing one requires a reversal to the compact cotyledon stage; in other words, it takes two steps.

In Fig. 12 the cotyledon types are plotted on a phylogenetic tree. The tree is based on Linder and Rudall (2005), but some changes have been made. The basal branching grade is modified following Chase et al. (2006). Hydatellaceae have been excluded (see Introduction).

The Xyrid clade is dominated by the compact cotyledon type, with a strong tendency to miniaturization and organ reductions in Mayacaceae and Eriocaulaceae. Xyris is clearly separated from Orectanthe by its blade-like cotyledonary hypophyll (Fig. 5J, K). The isolated position of Xyris was emphasized by Rudall and Sajo (1999) and Michelangeli et al. (2003).

In the Cyperid and Restioid clades, the phaneromeric cotyledon is predominant. However, in both clades one group each has coleoptiles: the Cyperaceae and at least some members of the Willdenowia sub-clade of Restionaceae, respectively. As is documented in Fig. 10, a direct switching from a phaneromeric cotyledon to a coleoptile bearing one is impossible for morphological reasons. Thus, we have to assume a shared ancestor of Juncaceae and Cyperaceae with a compact cotyledon. A similar problem occurs in Restionaceae. Here only phaneromeric cotyledons on the one hand and those with coleoptiles on the other hand are known in detail (Fig. 8C–F). Coleoptiles have been described in a few nut-fruited, hypogeally germinating genera of the Willdenowia clade (Linder and Caddick, 2001). However, seedling figures available show only older stages of seedling development so that it is not possible to identify details of the cotyledon structure.

Since the phaneromeric cotyledon obviously is an apomorphy for the Restiid clade, it is plausible to assume that a number of the hypogeally germinating genera in the Willdenowia clade possess a compact cotyledon representing a reversal and an intermediate stage on the way to coleoptiles. This assumption is supported by the fact that the Australian Alexgeorgia ganopoda has a compact cotyledon as described by Pate and Meney (1999). Alexgeorgia is one of the very rare examples of a genus comprising two different seedling types. While A. subterranea and A. nitens have the epigean structure typical for all other Australian Restionaceae, A. ganopoda is hypogeal, its compact cotyledon thus presumably representing a reversal (Meney et al., 1990; Pate and Meney, 1999). Furthermore, A. ganopoda is exceptional in producing scale-like cataphylls immediately, while in all other epigeal or hypogeal genera of the family the first plumular leaves are eophylls.

In the Graminid clade, Flagellariaceae is sister to Joinvilleaceae, Ecdieiocoleaceae and Poaceae, and has a compact cotyledon, albeit that there is a tendency for a low median sheath lobe (Fig. 9B). Joinvilleaceae and Poaceae possess a well-developed coleoptile.

In Fig. 9E an example is shown of the alteration of organ characters if the seed germinates while buried at some depth in soil. Such conditions lead to elongation of organs otherwise telescoped or inconspicuous. In the Joinvilllea seeding, the hypocotyl is very elongated and the hyperphyll is stretched to the same degree, so that an apocole is formed which never develops under light conditions. Also the coleoptile is much longer. The bulging collar with numerous rhizoids is a stable character.

The information about Ecdieiocoleaceae is scarce and inconsistent. The only seedling figure in Pate and Meney (1999) relates to a plant grown from a deeply buried seed. Details of the cotyledon are unknown. If it bears a coleoptile, the complete clade of Joinvilleaceae/Ecdieiocoleaceae/Poaceae would appear in red in Fig. 12. However, if the cotyledon is of the compact type, this had to be interpreted as a reversal. The much elongated internode is only the
result of germination occurring at a great depth, and it may be absent or present in the same population depending on how deeply the seed is buried (Linder and Caddick, 2001). Therefore, this structure does not require a term of its own such as ‘epicotyledonary rhizome’. The term rhizome should be restricted to horizontally growing axes with some storage function, growing mono- or sympodially at one end and decaying at the opposite end.

Figure 11 is designed to help see homologies of seedling organs or organ parts across all Poales; the colouring of organs is identical to that in Figs 1 and 2. The cotyledonary node, indicated as a thick black bar, is at the same level in all figures. In general, the hypocotyl is telescoped, and in Fig. 11A–E the epicotylary axis also remains short. Given identical growth conditions, i.e. seeds not deeply buried, this is the predominant behaviour in Poales, and also in monocots in general. Figure 11A relates to Bromeliaceae, except Pitcairniioideae, to Orectanthe and to Flagellaria. In the latter genus, the compact cotyledon is somewhat modified by a low median sheath lobe (Fig. 9B). Figure 11B represents the extremely reduced seedlings of Mayacaceae and Eriocaulaceae. The completely reduced primary root is replaced by an endogenously originating shoot-born root. The blade-like expanded cotyledonary hypophyll (Fig. 11C) is restricted to Bromeliaceae–Pitcairniioideae and to Xyris. More widespread is the phaneromer (Fig. 11D), which is typical for Typhaceae and predominant in the Cyperid and Restiid clades. The cotyledon with a coleoptile (Fig. 11E) is found in Joinvilleaceae, Cyperaceae spp. and the Willdenowia group of Restionaceae (Linder and Caddick 2001). The majority of Cyperaceae possess the seedling type shown in Fig. 11F. Here the epicotyl is modified to a mesocotyl. The elongated epicotyl in this case is congenitally fused to the coleoptile base. The ontogenetic process leading to this often misinterpreted structure was described in detail by von Guttenberg and Semlow (1957) and Pankow and von Guttenberg (1957). Finally, Fig. 11G gives a complete interpretation of the Poaceae seedling. The special characters of the grass seedling can be observed scattered over the Poales families.

Thus, the grass seedling can be interpreted as a summary of characters occurring in a scattered fashion in the Poales. Some authors found the first root of the grass embryo to be a shoot-born root, but proposed diverging interpretations for the coleorhiza. Mostly it was interpreted as a reduced primary root (Paschkow, 1951; Guignard, 1961; Guignard and Mestre, 1971; Tzvelev, 1975; Philip and Haccius, 1976; Cocucci and Astegiano, 1978), but Yamashita (1973) and Skvortzov (1977) interpreted it as being homologous to the hypocotyl or the lower part of it, stating that the primary root is completely reduced. This interpretation corresponds to Fig. 11G. The first coleorhiza and the epiblast have identical tissue structures; when rhizoids are developed, they are found on the coleorhiza and the epiblast. The Poaceae embryo is covered by an epidermis, continuous over the coleoptile, epiblast and coleorhiza, i.e. a shoot epidermis. The first coleorhiza never exposes the secondary, inner surface (rhizodermis). The collar rhizoids growing from the coleorhiza and the epiblast are shoot axis trichomes and not root hairs. A collar that bears rhizoids is found in many monocotyledonous and dicotyledonous seedlings (see above).

However, there is one character unique to Poaceae, i.e. the very great development of the embryo in the seed with a well differentiated shoot-born root and young leaves visible inside the coleoptile. The embryo in a ripe caryopsis resembles a resting seedling rather than an embryo. The constant characters of seedlings of Poaceae found throughout the family are: (a) the scutellum-shaped haustorium; (b) the coleoptile; (c) the missing primary root; and (d) the collar transformed into the coleorhiza of the first shoot-born root. The development of collar rhizoids and of an epiblast is presumably an ancestral character in the family; cases where they are missing represent a derived state.

Some general conclusions can be drawn from these investigations. Descriptions of seedlings satisfying the comparative morphologist and the systematist as well require some important pre-conditions. First, after overcoming the eventual quiescence of seeds by appropriate methods,
identical growth conditions for all seedlings under comparison are necessary. Comparison of a seedling grown from a deeply buried position with a different seedling started at ground level will no doubt reveal morphological differences, but they would be absolutely misleading. Secondly, the descriptions should be as detailed as possible using an unambiguous system of terms. Thirdly, only comparisons of fully developed seedlings can reveal meaningful results. Unfortunately, these simple rules are widely overlooked. Often inaccurate or overly simple terminologies are taken from the older literature and used to fill data matrices, sometimes without looking at what is being described (Michelangeli et al., 2003). This problem was extensively discussed by Weber (2003). With respect to seedlings, the oversimplified distinction of epigeal vs. hypogeal germination is in general usage. However, both ‘types’ are very heterogeneous, and an (epigeal) phaneromeric and a (hypogeal) compact cotyledon are closer to each other than the phaneromeric one is to the epigeal cotyledon with a blade-like widened hypophyll (see Figs 2 and 10). It is also misleading to compare resting embryos to determine organ homologies. In Poales the developmental stage of the resting embryos ranges from undifferentiated, nearly proembryonic embryos (e.g. Erica caucaliaeae) to the well-developed embryo in Poaceae. The comparison of such embryos may lead to the assumption that the scutellum of Poaceae is a unique organ without any homology to other Poales (e.g. Rudall et al., 2005).

Given an unambiguous terminology and detailed morphological analyses, the extraordinarily diverse seedlings of Poales (and of monocots in general) can be analysed in a way that makes possible accurate descriptions and allows convincing use of homologous terms. Among the most important results of the present study is a consistent explanation for the homologies of the puzzling grass seedling.

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Tillich — Seedlings of Poales


