

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

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- **Background and Aims** Seedlings of monocots are much more diverse than those of other angiosperms, often with very derived character states. This makes morphological interpretation difficult. The morphology of seedlings of most of the 16 families of the Poales alliance are only incompletely known. The present study aims first to develop an unambiguous terminology for the description of monocotyledonous seedlings. This makes possible clear morphological comparisons and the use of homologous terms for organs. Finally, plotting of well defined characters onto a molecular tree allows the polarization of character states.
- **Methods** Seedlings were grown in Petri dishes on moist filter paper under permanent light conditions and analysed using light and scanning electron microscopy. Only seeds collected at natural habitats or from plants with a well documented source were used. Seedling vouchers are deposited in the alcohol collection of Monocot seedlings in the Botanische Staatssammlung München (M).
- **Key Results** Based on an unambiguous terminology, seedlings of a great number of genera are described and presented as figures, representing all families of Poales except Ecdeiocoleaceae. Seedlings of Rapateaceae, Joinvilleaceae and Mayacaceae are described for the first time. Morphological comparisons reveal a plausible interpretation of even very modified organ structures, including those of the grass seedling.
- **Conclusions** This study demonstrates that detailed studies of seedling morphology can provide interesting morphological insights and also new facts for phylogenetic analyses. However, the morphological diversity of seedlings in the monocots is as yet incompletely known, and in some, e.g. Alismatales or Zingiberales, the seedling structure is particularly poorly understood in terms of comparative morphology.

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

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 *Streptochoeta* (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. Raunkiaer, 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 Ecdeiocoleaceae. 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. Centrolepidaceae and Flagellariaceae are represented in the literature by only two figures each: *Centrolepis* in Hieronymus (1873) and Tillich (1995); *Flagellaria* in Jacques-Felix (1988)

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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 alcohol collection at 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 1. Sources of species

| Taxon | Source of seeds | Seedling voucher in M* |
|--|---|------------------------|
| Arecaceae | | |
| <i>Lodoicea maldivica</i> Pers. ex H. Wendl. | Imported by a Munich Garden Market | |
| Bromeliaceae | | |
| <i>Guzmania nicaraguensis</i> Mez & C.F.Bak. | BG Munich 1996 | 2650 |
| <i>Pitcairnia corallina</i> Lind. & André | BG Munich 1996 | 2672 |
| <i>Portea leptantha</i> Harms | BG Munich 1996 | 2627 |
| Centrolepidaceae | | |
| <i>Centrolepis drummondii</i> Walp | BG TU Dresden 1995 | 2385 |
| <i>Centrolepis strigosa</i> Roem. & Schult. | BG TU Dresden 1994 | 2441 |
| Cyperaceae | | |
| <i>Elyna myosuroides</i> (Vill.) Fritsch | BG Oslo 1998 | 2854 |
| <i>Isolepis setacea</i> (L.) R. Br. | Germany, Thuringia, Tillich 08/1994 | 86 |
| <i>Mapania cuspidata</i> (Miq.) Uitt. | BG Munich 1999 | 2911 |
| Eriocaulaceae | | |
| <i>Eriocaulon</i> spec. | Peru, Amazonas, Weigend <i>et al.</i> 1997/416 | 2722 |
| <i>Paepalanthus</i> spec. 1 | Ecuador, Weigend 3891/1995 | |
| <i>Paepalanthus</i> spec. 2 | Ecuador, Weigend 3890/1995 | 2487 |
| Flagellariaceae | | |
| <i>Flagellaria indica</i> L. | Thailand, Prov. Patthalung, Tillich 10/2005 | 2031 |
| <i>Flagellaria indica</i> L. | Hengchun Tropical Botanical Garden Taiwan 2006 | 3322 |
| Joinvilleaceae | | |
| <i>Joinvillea ascendens</i> Gaudich ex Brongn. & Gris. | National Tropical Botanical Garden Hawaii 1998 | 2804 |
| Juncaceae | | |
| <i>Juncus maritimus</i> Lam. | Germany, Rügen, Tillich 09/1978 | 722 |
| <i>Luzula nivea</i> (L.) DC. | Germany, Bavaria, Tillich s.n. 08/1998 | 2358 |
| <i>Marsippospermum reichii</i> Buch. | Argentina, Neuquen, Weigend <i>et al.</i> 5851/2001 | 3109 |
| <i>Rostkovia magellanica</i> Hook. f. | Argentina, Rio Negro, Weigend <i>et al.</i> 6053/2001 | 3110 |
| Mayacaceae | | |
| <i>Mayaca fluviatilis</i> Aubl. | Cuba, Mina Iberica, Mangelsdorff s.n. 03/2002 | 3117 |
| Poaceae | | |
| <i>Achnatherum calamagrostis</i> (L.) P. Beauv. | Germany, Bavaria, Tillich 07/1995 | 2397 |
| <i>Gastridium ventricosum</i> (Gouan) Schinz & Thell. | BG Rennes 1995 | 2514 |
| Rapateaceae | | |
| <i>Guacamaya superba</i> Maguire | Venezuela, Edo Amazonas 10/1998 | 2907 |
| <i>Rapatea</i> spec. | Peru, Huanuco, Weigend 346/2001 | 3106 |
| <i>Schoenocephalum teretifolium</i> Maguire | Venezuela, Edo Amazonas 10/1998 | 2906 |

(Continued)

TABLE 1. *Continued*

| Taxon | Source of seeds | Seedling voucher in M* |
|--|---|------------------------|
| Restionaceae | | |
| <i>Chondropetalum tectorum</i> Raf. | BG Munich 1991 | 1977 |
| <i>Elegia racemosa</i> Pers. | BG Munich 1998 | |
| Thurniaceae | | |
| <i>Pronium palmita</i> E. Mey. | BG Palermo 1981 | 861 |
| Typhaceae | | |
| <i>Sparganium americanum</i> Nutt. | BG Michigan State University 1997 | 2737 |
| <i>Typha latifolia</i> L. | Germany, Thuringia, Tillich 10/1978 | 171 |
| Xyridaceae | | |
| <i>Orectanthe sceptrum</i> (Oliv.) Maguire | Venezuela, Auyan Tepui 06/2005 | 3297 |
| <i>Xyris natalensis</i> Alb. Nilsson | RSA, KwaZulu-Natal, Weigend & Driessle 1998/45 | 2793 |
| <i>Xyris</i> spec. | Peru, Chachapoyas, Weigend <i>et al.</i> 1998/499 | 2823 |

The table lists all species shown in Figs 3–9. Additionally, a large number of further species was analysed forming the background experience for this article (see Tillich, 1995, 2000).

* Botanische Staatssammlung München.

buries the plumule in the case of hypogeal, remote germination of palms (see *germination modes*) (Fig. 3). In some genera, for example *Phoenix*, the cotyledonary 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 *cotyledonary hyperphyll*. Therefore, the apocole is here restricted to that part of the hyperphyll between the haustorium and cotyledonary sheath in hypogeal seedlings with remote germination (Fig. 2F, G and H). In the rare cases where the cotyledonary sheath elongates above the soil surface, the apocole 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), verlängertes Hals (Tschirch, 1890), Hals (Jönsson, 1902), cotyledonary axis (Tomlinson, 1990). Often this organ is interpreted as being the petiole (Blattstiel) of the cotyledon. This interpretation goes back to Bernhardt (1832) and is also used by, for example, Irmisch (1856a, b), Gatin (1909, 1912), Żurawska (1912), Arber (1925), Boyd (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 cotyledonary hyperphyll.

coleoptile (Mirbel, 1815). This is a tubular structure produced by meristematic activity of the marginal tissue of

the *cotyledonary sheath*. By means of this growth process the cotyledonary 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 cotyledonary 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. Gatin, 1906, 1909; Arber, 1925; Chouard, 1931; Uhl and Dransfield, 1987), ocrea (Żurawska, 1912), upper sheath (Sargent and Arber, 1915; Boyd, 1932), ligular sheath (Arber, 1925), verlängertes 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 cotyledonary 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.

Synonyms: Cotyledo, Kotyledo (Troll, 1943; von Guttenberg *et al.*, 1954; Pankow and von Guttenberg, 1957; Tillich, 1992), seed leaf (Arber, 1925; Duke, 1969), first leaf (Henderson, 2006).

cotyledonary hyperphyll. The cotyledonary 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 cotyledonary 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 cotyledonary 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 cotyledonary 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.

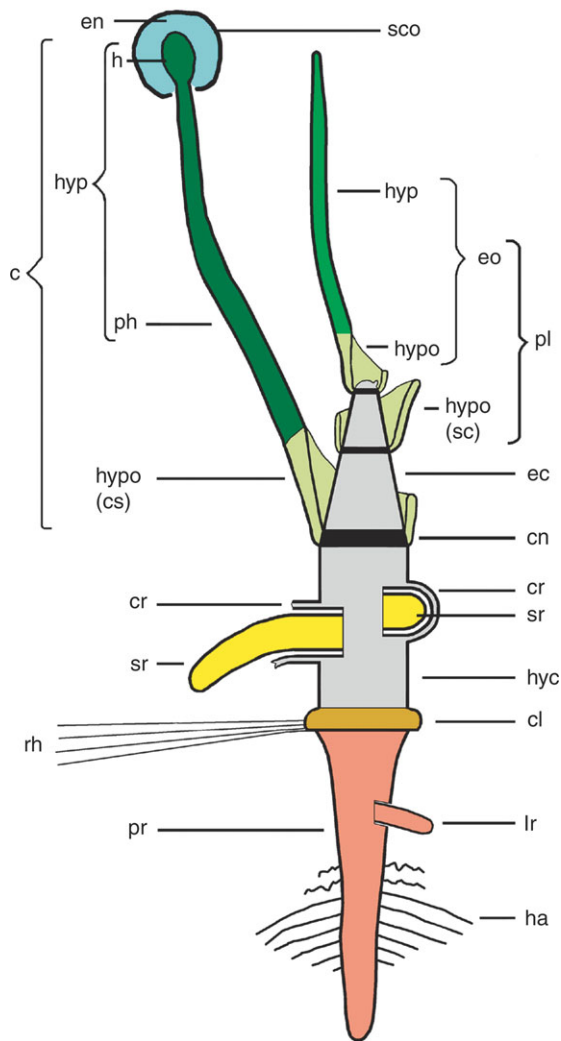


FIG. 1. Diagrammatic figure of a monocotyledonous seedling to visualize its organs, their spatial correlations and a set of important terms for the description of monocotyledonous seedlings. The coloration of organs and organ parts is identical to that in Figs 2, 10 and 11 to enable comparisons. The cotyledon type corresponds to Fig. 2B and Fig. 10D. Further explanation is given in the text. c, cotyledon; cl, collar; cn, cotyledonary node; cr, coleorhiza; cs, cotyledonary sheath; ec, epicotyl; en, endosperm; eo, eophyll; h, haustorium; ha, root hairs; hyc, hypocotyl; hyp, hyperphyll; hypo, hypophyll; lr, lateral root; ph, paneromer; pl, plumular leaf; pr, primary root; rh, collar rhizoids; sc, scale-like cataphyll; sco, seed coat; sr, shoot-born root.

cotyledonary hypophyll. 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), Spreite (Čelakovský, 1897) ‘sucker’, ‘corresponding to the leaf blade’ (Tomlinson, 1960), Sauger (Schlickum, 1896; Čelakovský, 1897), succer, succorial tip (Boyd, 1932), leaf blade (Henderson, 2006), scutellum (generally used for the haustorium of the Poaceae embryo).

paneromer. 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 paneromer after shedding the empty seed coat (Fig. 2A). The paneromer mostly grows straight upright and is usually terete. Rarely it is somewhat flattened 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

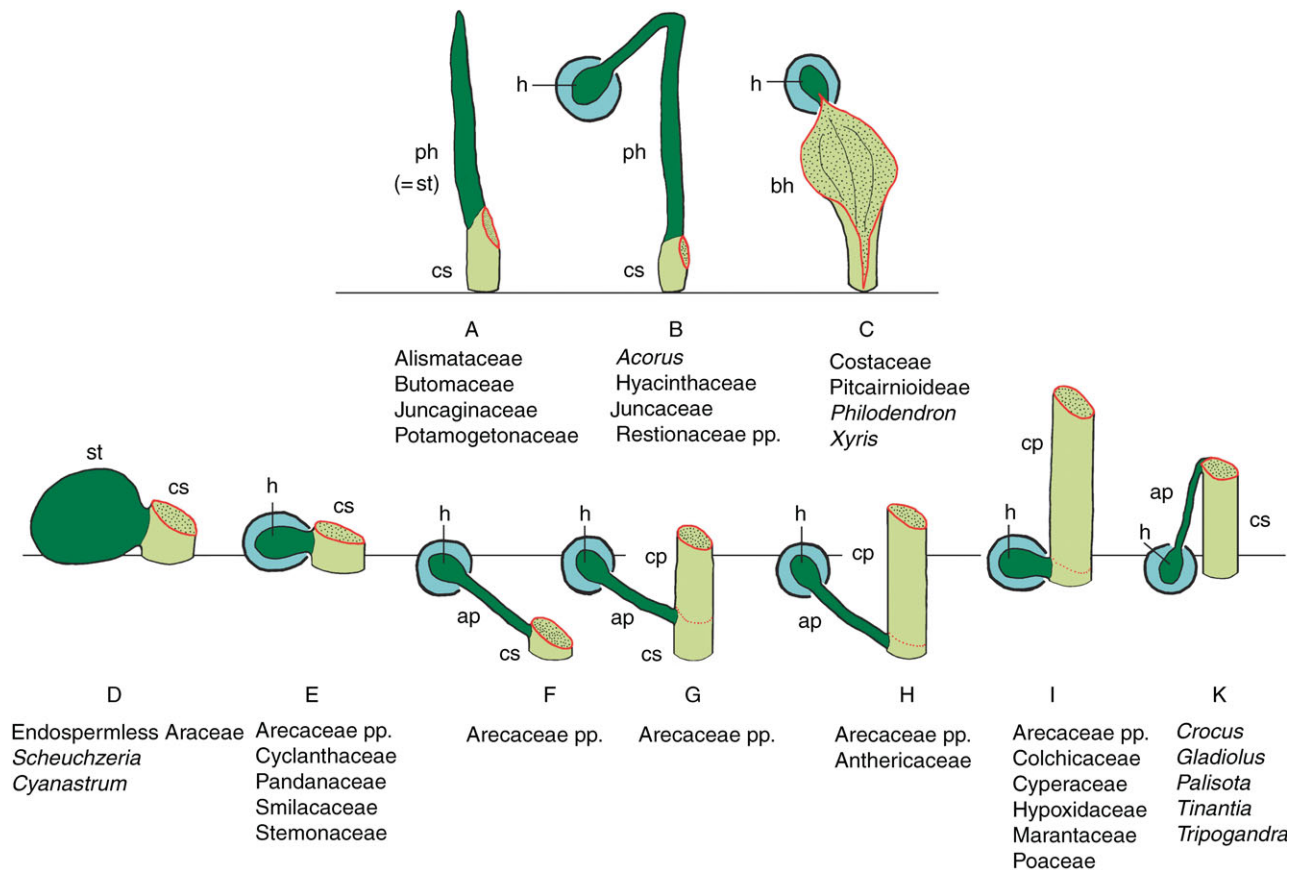


FIG. 2. Diversity in the structure of the cotyledon of monocots. The unifacial hyperphyll region is shown in dark green and the bifacial hypophyll in light green. The morphological leaf margin is indicated in red; the visible part of the upper (adaxial) leaf surface is stippled. (A–C) Epigeal germination; (D–K) hypogeal germination. In (G–I), the original position of the leaf margin before the coleoptile growth has commenced is stippled in red. The horizontal lines indicate ground level. Below each type some examples are given. Further explanation is given in the text. ap, apocole; bh, blade-like hypophyll; cp, coleoptile; cs, cotyledonary sheath; h, haustorium; ph, phaneromer; st, storage hyperphyll.

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, epiblast*). 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 not restricted to 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), Wurzelknoten-behaarung (Ascherson, 1883), poils absorbants (Laurent,

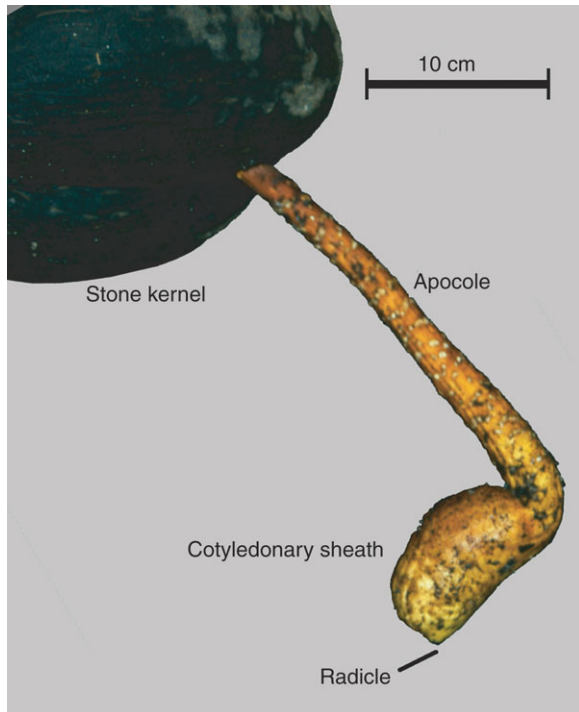


FIG. 3. Young seedling of *Lodoicea maldivica* with remarkable remote germination. The apocolle has grown vertically downwards, pushing the cotyledonary sheath and radicle far away from the fruit deep into the soil.

1904; Jacques-Felix, 1988), hypocotylar hairs (Baranov, 1957).

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).

epiblast (Richard, 1811). The epiblast 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 epiblast 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).

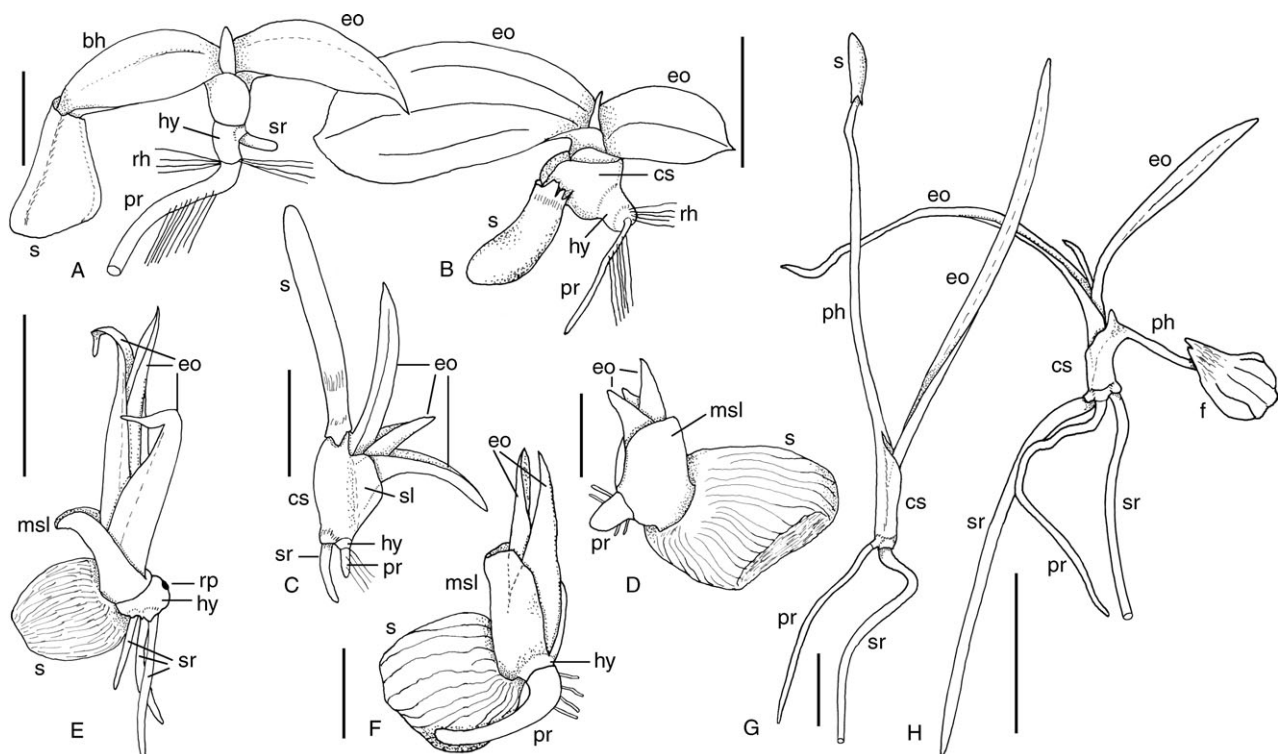


FIG. 4. Seedlings of early branching Poales. (A–C) Bromeliaceae. (D–F) Rapateaceae. (G and H) Typhaceae. (A) *Pitcairnia corallina*. (B) *Portea leptantha*. (C) *Guzmania nicaraguensis*, with the hairy exotesta removed. (D) *Guacamaya superba*. (E) *Rapatea* sp. (F) *Schoenocephalium teretifolium*. (G) *Typha latifolia*. (H) *Sparganium americanum*. bh, blade-like cotyledonary hypophyll; cs, cotyledonary sheath; eo, eophyll; f, stone kernel of the drupe; hy, hypocotyl; msl, median sheath lobe; ph, phaneromer; pr, primary root; rh, collar rhizoids; rp, root pole; s, seed; sl, sheath lobe; sr, shoot-born root. Scale bars in A, C, D, F, G = 1 mm; B = 3 mm; E, H = 5 mm.

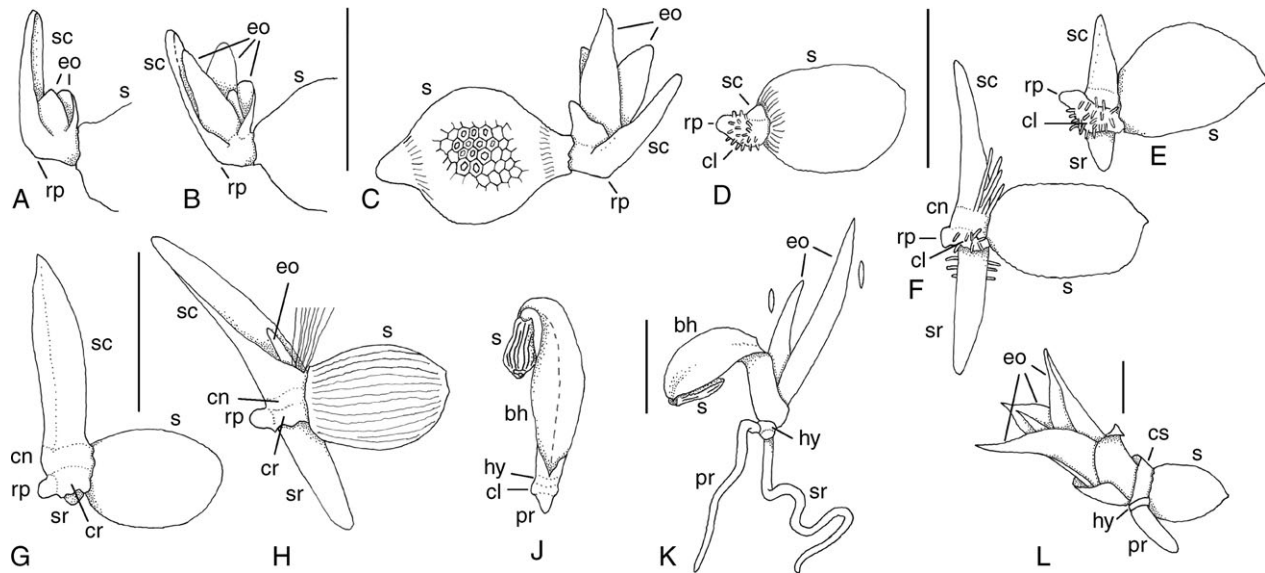


FIG. 5. Seedlings of the Xyrid clade. (A–C) Mayacaceae. (D–H) Eriocaulaceae. (J–L) Xyridaceae. (A–C) *Mayaca fluviatilis*, three stages of seedling development. (D–F) *Paepalanthus* spec. 1, three stages of seedling development. (G, H) *Paepalanthus* spec. 2, two stages of seedling development; collar rhizoids and hairs at the leaf base are omitted. (J) *Xyris natalensis*, young seedling. (K) *Xyris* sp., a more advanced stage. (L) *Orectanthe sceptrum*, the loose outer testa is removed. Further explanation is given in the text. bh, blade-like cotyledonary hypophyll; cl, collar; cn, cotyledonary node; cr, coleorhiza; cs, cotyledonary sheath; eo, eophyll; hy, hypocotyl; op, operculum; pr, primary root; rh, collar rhizoids; rp, root pole; s, seed; sc, scale-like cataphyll; sr, shoot-born root. Scale bars in A–L = 1 mm; M = 0.5 mm.

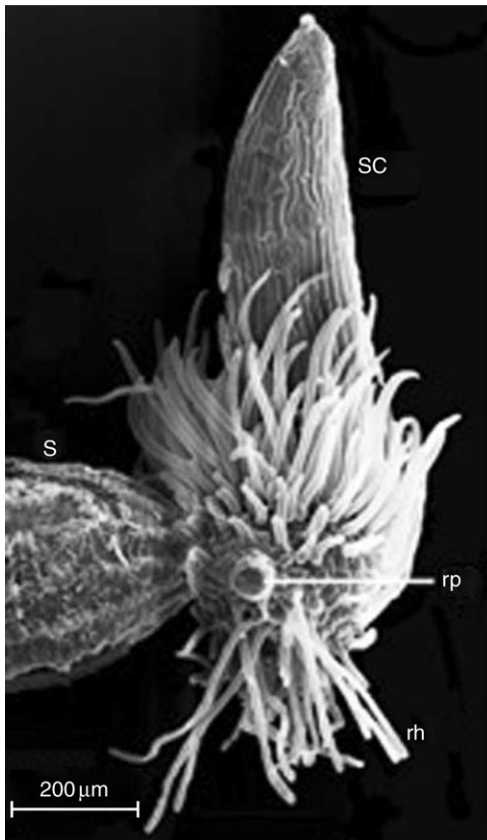


FIG. 6. *Eriocaulon* spec. SEM photograph of a seedling. Note the difference between the thin rhizoids and dense tuft of upright trichomes camouflaging the plumular region. rh, collar rhizoids; rp, root pole; s, seed; sc, first scale leaf.

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

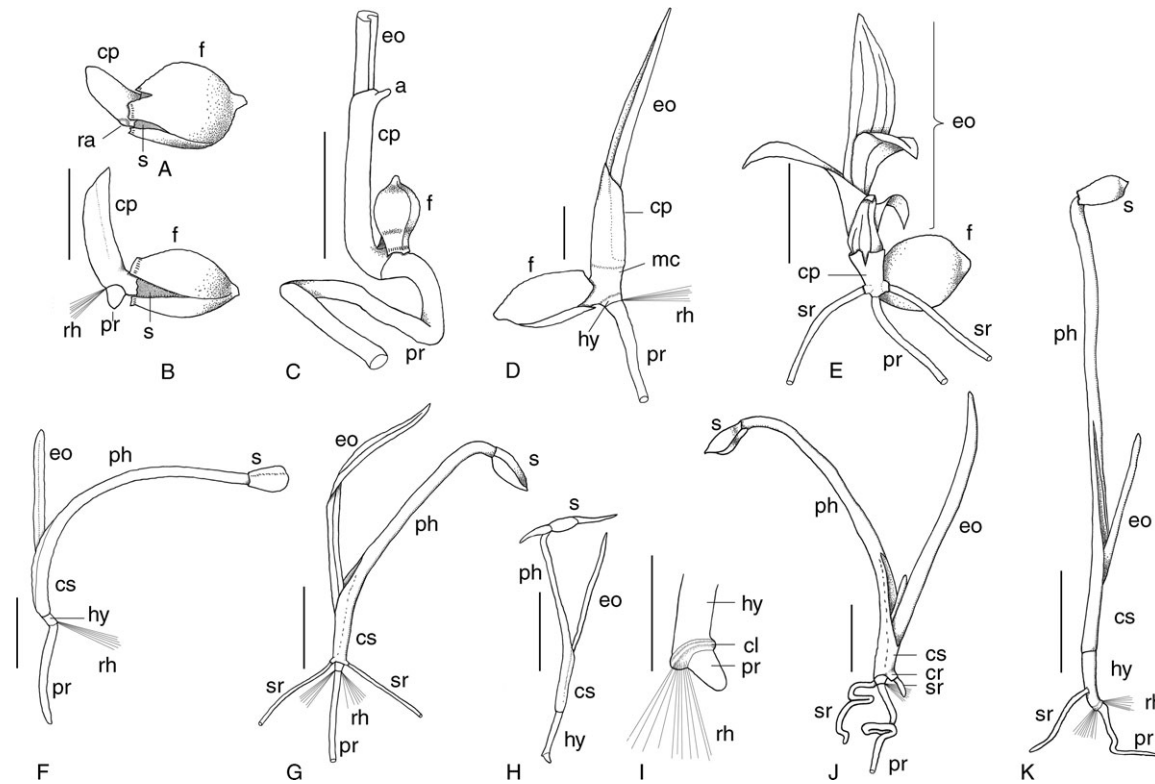


FIG. 7. Seedlings of the Cyperid clade. (A–E) Cyperaceae. (F) Thurniaceae. (G–K) Juncaceae. (A–C) *Isolepis setacea*, three stages of seedling development. (D) *Elyna myosuroides*. (E) *Mapania cuspidata*. (F) *Prionium palmita*. (G) *Luzula nivea*. (H, I) *Marsippospermum reichii*, with I showing a 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.

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 Menev, 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

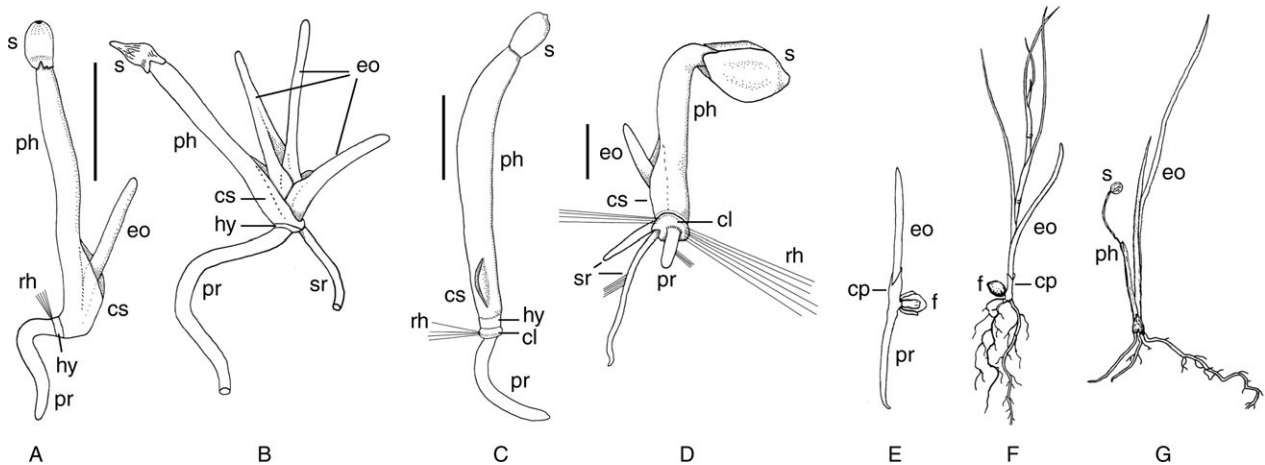


FIG. 8. Seedlings of the Restiid clade. (A, B) Centrolepidaceae. (C–F) Restionaceae. (G) Anarthriaceae. (A) *Centrolepis strigosa*. (B) *Centrolepis drummondii*. (C) *Chondropetalum tectorum*. (D) *Elegia racemosa*. (E) *Cannomois grandis*. (F) *Willdenowia incurvata*. (G) *Anarthria prolifera*. [E and F are from Linder and Caddick (2001), and G is modified from Pate and Menev (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.

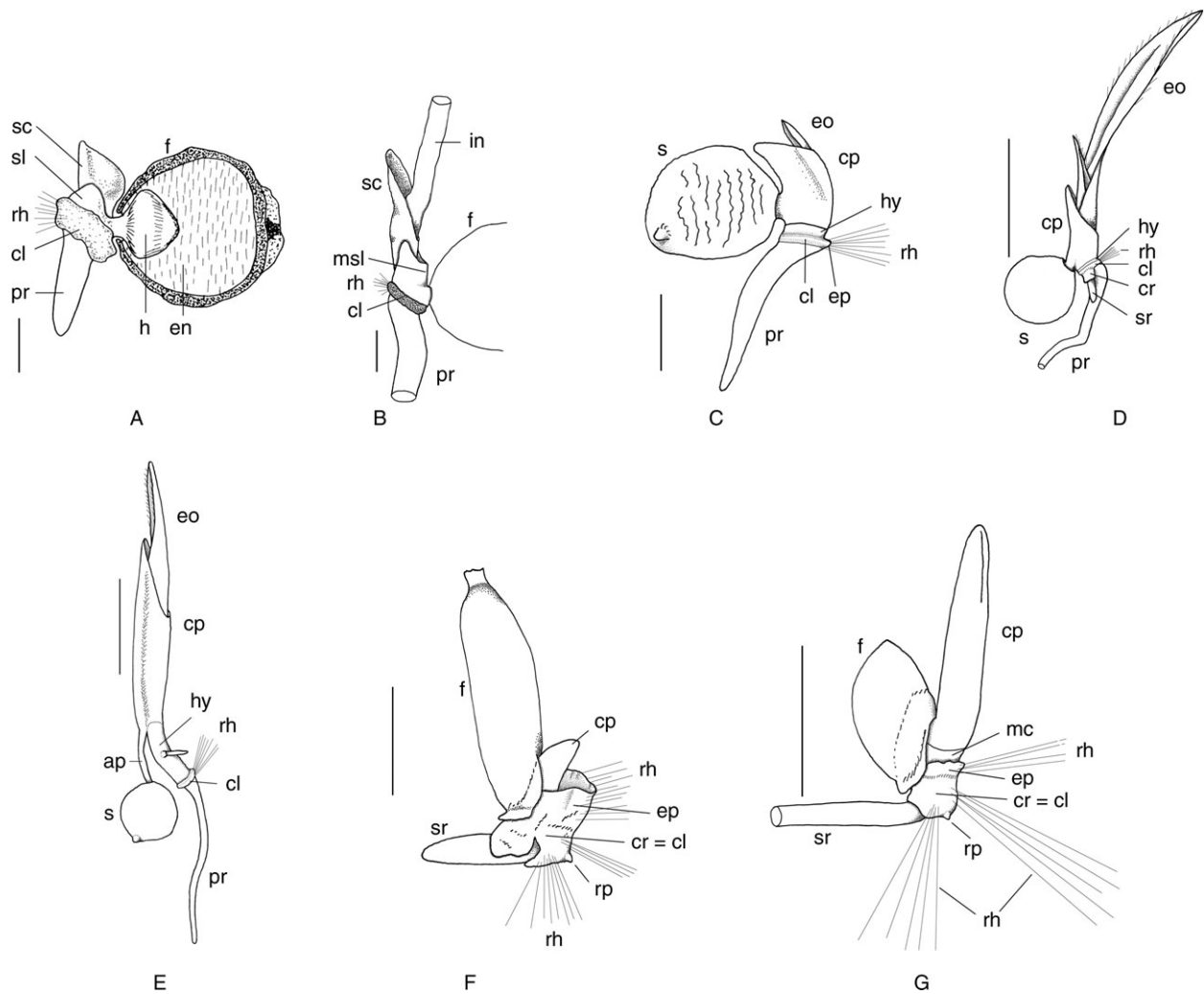


FIG. 9. Seedlings of the Gramineid clade. (A, B) Flagellariaceae: *Flagellaria indica*. (A) Young seedling, stone kernel and endosperm in long section [modified from Tillich (1996)]. (B) Detail of an older seedling. (C–E) Joinvilleaceae: *Joinvillea ascendens*. (C) Young seedling with the collar somewhat extended similar to an epiblast. (D) An older seedling. (E) A seedling sown deeply buried. (F, G) Poaceae. (F) *Achnatherum calamagrostis*. (G) *Gastridium ventricosum*. Further explanation is given in the text. ap, apocole; cl, collar; cp, coleoptile; cr, coleorhiza; en, endosperm; eo, eophyll; ep, epiblast; f, fruit; h, haustorium; hy, hypocotyl; in, internode; mc, mesocotyl; msl, median sheath lobe; pr, primary root; rh, collar rhizoids; rp, root pole; s, seed; sc, scale-like cataphyll; sl, sheath lobe; sr, shoot-born root. Scale bars in A–C, F, G = 1 mm; D, E = 3 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, Grenzwurzeln (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.

Synonym: secondary root (Henderson, 2006).

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).

Synonym: seed root (Linder and Caddick, 2001), seminal root (Pate and Meney, 1999).

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).

Synonyms: adventitious root [an unfortunate term, see Bell (1991)], Beiwurzel (Reinke, 1871; von Guttenberg, 1968), shoot-borne root (Tillich, 1995; Henderson, 2006).

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. admote (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 admote 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 admote (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 Typhaceae 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 Bromelioideae 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 *Schoenocephalum*, 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 testa (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 *Juncaceae* with epigeal germination; the cotyledon has a long phaneromer. The first plumular leaves are linear, bifacial eophylls. The hypocotyl has an inconspicuous collar which bears dense rhizoids; the primary root is weak and soon replaced by shoot-born roots.

Cyperaceae (Fig. 7A–E). The seedlings are characterized by a cotyledon with a well developed coleoptile; the hyperphyll is haustorial and hidden in the seed. The coleoptile either breaks through the fruit wall prior to the primary root (Fig. 7A), or the coleoptile and the primary root may emerge in parallel and elongate synchronously, until the coleoptile turns upright and the root downwards into the soil. The early development of the coleoptile combined with an often delayed development of the primary root is 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 achlorophyllous 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.

Restiid 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 *Cannomois* (Linder and

Caddick, 2001, see Fig. 8E, F). For other hypogeal genera, details of the cotyledon structure are unknown.

Anarthriaceae (Fig. 8G). The figure of the *Anarthria prolifera* seedling is taken from Pate and Menev (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).

Ecdeiocoleaceae. The seedling of an *Ecdeiocolea* is described by Pate and Menev (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 cotyledonary 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

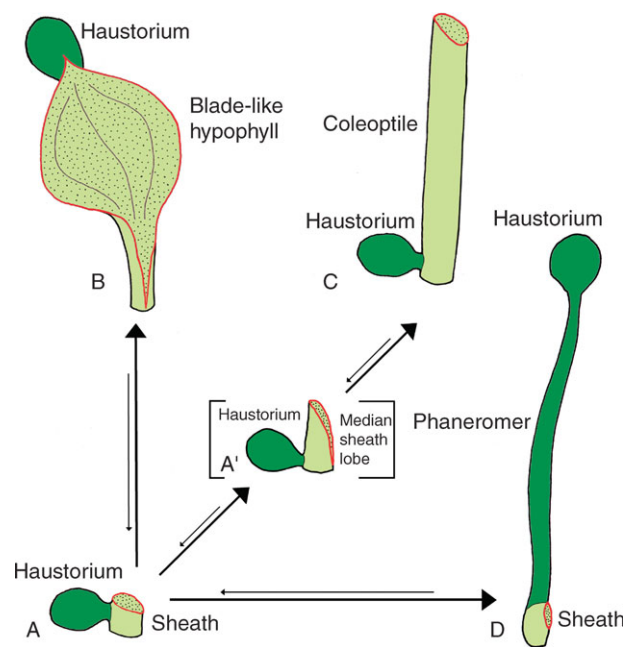


FIG. 10. Cotyledon types in Poales. The arrows indicate the presumed phylogenetic relationships. If the compact cotyledon (A) is taken as the ancestral type, each of the derived types (B, C and D) can be achieved by only one step each. A' symbolizes an eventual intermediate stage to a coleoptile. This is the most parsimonious explanation of the relationships between these cotyledon types. A switch between any of the derived types would require two steps, passing the compact cotyledon stage.

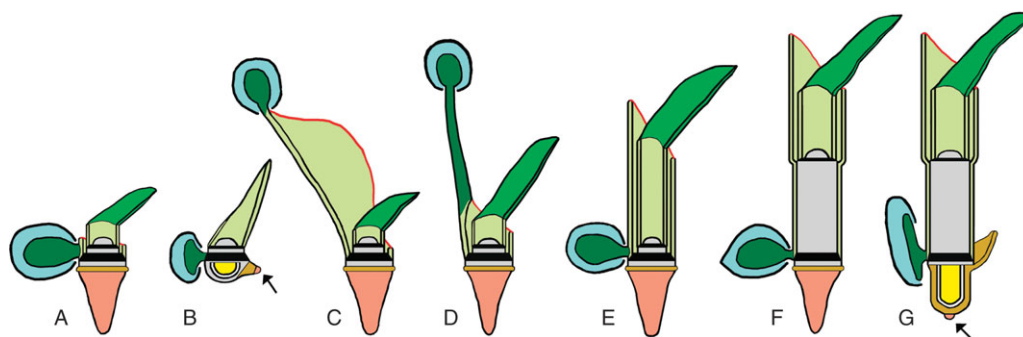


FIG. 11. Schematic figures of seedling types in Poales. (A) Seedling with compact cotyledon (Bromeliaceae pp., *Flagellaria*). (B) Cotyledon without a sheath; primary root undeveloped (Eriocaulaceae, Mayacaceae). (C) Cotyledon with a blade-like expanded cotyledonary hypophyll (Bromeliaceae–Pitcairnioideae, *Xyris*). (D) Cotyledon with a phaneromer (Typhaceae, Juncaceae, Thurniaceae, Restionaceae pp., Centrolepidaceae, Anarthriaceae). (E) Cotyledon with a coleoptile (Joinvilleaceae, Restionaceae pp.). (F) Cotyledon with a coleoptile and mesocotyl (Cyperaceae). (G) Cotyledon with a coleoptile and mesocotyl; primary root undeveloped (Poaceae). The arrows point to the root pole with an undeveloped primary root. Further explanation is given in the text.

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).

As can be seen from the tree in Fig. 12, the early branching groups principally have all the cotyledon types found in core Poales. The compact cotyledon is predominant in Bromeliaceae, but in the Pitcairnioideae the cotyledonary hypophyll is expanded to a blade-like structure. Typhaceae including Sparganiaceae have a phaneromeric cotyledon. In Rapateaceae the cotyledon is again more or less the compact type, but with the pronounced development of a median sheath lobe. This can perhaps be understood as a preliminary stage of a coleoptile (Fig. 10).

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 Restiid 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 epigeal 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, Ecteiocoleaceae 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 *Joinvillea* seedling, 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 Ecteiocoleaceae 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/Ecteiocoleaceae/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

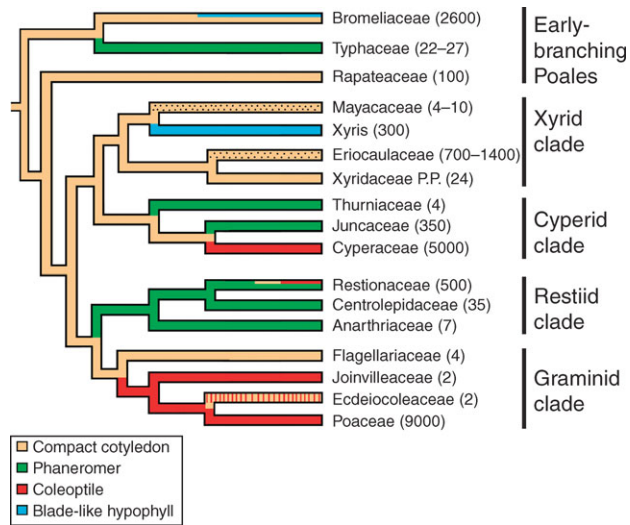


FIG. 12. Distribution of the cotyledon types of Poales. The tree is based on Linder and Rudall (2005), but Hydatellaceae is omitted from the Xyrid clade; the grade of early branching Poales is modified following Chase *et al.* (2006). Stippling in the Eriocaulaceae and Mayacaceae branch indicates complete reduction of the cotyledonary sheath.

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 Pitcairnioideae, 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–Pitcairnioideae 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.

- (1) An embryo laterally attached to the endosperm with a lens-shaped haustorium: Centrolepidaceae.
- (2) A coleoptile: Joinvilleaceae, Cyperaceae.
- (3) Mesocotyl formation: Cyperaceae.
- (4) An elaborated collar, with an extension at the abterminal side similar to an epiblast: Joinvilleaceae.
- (5) Complete reduction of the primary root: Eriocaulaceae, Mayacaceae.
- (6) The first shoot-born root growing in a direction opposite to the plumule, with a coleorhiza formed from collar tissue: Eriocaulaceae.

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. Eriocaulaceae) 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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