The aberrant inflorescence of *Luzula elegans* Lowe (Juncaceae) compared to other *Luzula* species

C.P. KÖBELE und H.-J. TILLICH

Abstract:

The aberrant inflorescence of *Luzula elegans* Lowe, the only annual species of the genus, is described. It differs strongly from all other inflorescence types found in *Luzula* L. However, each of the traditionally recognized subgenera (Pterodes Griseb., Anthelaea Griseb., Luzula (= Gymnodes Griseb.)) has an inflorescence type of its own. The results support the separation of *Luzula elegans* as an additional subgenus Marlenia as firstly proposed by EBINGER (1963). Subgenus Pterodes has the most ancestral inflorescence type, while in the subgenera Anthelaea, Luzula and Marlenia different derived stages are found.

Zusammenfassung:

Introduction

*Luzula elegans* Lowe has a quite isolated position within the genus *Luzula*. CHRTEK & KRISA (1974) even described it as a separate genus Ebingeria. The name Ebingeria refers to a detailed study published by EBINGER (1963). He pronounced the differences between *L. elegans* and the remaining species of the subgenus Anthelaea, in which *L. elegans* was traditionally integrated since BUCHENAU (1865, 1906). Due to a number of morphological, anatomical and cytological differences, EBINGER proposed a subgenus Marlenia, consisting of *L. elegans* only. The isolated position of *L. elegans* is also pronounced by the fact that it is the only annual species in the genus.

Among the unique features of *L. elegans* is the inflorescence structure. Supplementary to the recently published analysis of the inflorescences of the Juncaceae (KÖBELE & TILLICH 2001), the present study adds an analysis of the aberrant inflorescence of *Luzula elegans* and aims to give an extended overview of the inflorescence types in *Luzula*.

The earliest investigation of the inflorescences of the Juncaceae was published by BUCHENAU (1865). He considers *L. elegans* (named *L. purpurea* L. de Buch) being a member of
subgenus *Anthelaea*, but emphasizes the unique character of its inflorescence. A more
detailed study of the inflorescence structure was given by Ebinger (1963). Unfortunately, his
terminology is somewhat unclear, and this makes it difficult to find unequivocal homologies
to the inflorescences of the remaining *Luzula* species.

**Results and discussion**

The inflorescence of *L. elegans* superficially resembles those of subgenus *Pterodes* rather than
subgenus *Anthelaea*, i.e. a single flower embraced by two bracts is found at the end of long
internodes, thus the compound inflorescence has a loose habitus (figs. 1a, 2). As was recently
shown for Juncaceae, the single flower with two bracts at its base represents a one-flowered
spikelet. The flower originates from the axil of the lower bract and takes a pseudoterminal
position. The upper bract is sterile (Köbele & Tillich 2001).

It is characteristic for most species of *Juncus* and *Luzula*, that the paraclades overtop the
axis from which they originate. This behaviour gives rise to the typical anthelodium. How-
ever, the relative main axis usually remains in a straight position when overtopped by lateral
branches (fig. 1b). On the other hand, in *L. elegans* the main shoot is bent sideways in a more
or less right angle by the lowermost paraclade, which itself continues the upright direction of
the axis below and thus forms a sympodial continuation of the branching system. This
behaviour is repeated by the paraclades of the next orders. Thus the complete inflorescence
has an apparently straight and homogeneous main axis, which indeed is a monochasium (figs.
1a, 2, 4b). Ebinger (1963) calls this monochasial axis a pseudorachis.

At the (bended) main axis also the second paraclade of first order can repeat the behaviour
of the first one, so that a double-bended main axis results (fig. 1a).

This unique inflorescence of *L. elegans* differs strongly from that of the three traditionally
recognized subgenera of *Luzula*. Following Ebinger (1963), a fourth subgenus *Marlenia*,
consisting of *L. elegans* only, should be added:

Subgen. *Pterodes*,
Subgen. *Anthelaea*,
Subgen. *Luzula* sensu Ebinger 1963 (=Subgen. *Gymnodes* of Buchenau 1906),
Subgen. *Marlenia*.

Each subgenus is characterized by its own typical inflorescence type (fig. 4). This may
serve as an additional important argument for the natural circumscription of the subgenera. As
can be seen from table 1, subgenus *Marlenia* is the most outstanding taxon in *Luzula*. The
remaining subgenera are characterized essentially by inflorescence and seed characters.

All inflorescence types recognised so far in *Luzula* can be arranged in a morphological
sequence. The probably ancestral inflorescence is found in subgenus *Pterodes*. Here the one-
flowered spikelets (florescences) are separated by long internodes, the inflorescence has a
very loose appearance (figs. 1b, 3a, 4a). The very same inflorescence structure is developed in
1999), as was recently described by Köbele & Tillich (2001). It is noteworthy that *Juncus*
sect. *Steirochloa* is closest to *Luzula* also with respect to anatomical characters (Cutler
1969).

In subgenus *Anthelaea* only the proximal internodes of paraclades of lower orders are
elongated, but then several paraclades of higher orders develop rather short internodes and
gather to a more or less dense group at the distal part of lower order paraclades (figs. 3c, 4c).
Finally, in subgenus *Luzula* the paraclades are differentiated into two clearly different types,
the so-called short paraclades and long paraclades (Troll 1965, S. 99). The short paraclades
bear only a basal prophyll, a very short epipodial internode and the one-flowered co-
florescence. Several of these short praclades are grouped together at the distal end of the
main axis to form a „spike“ of higher order, a complex pseudo-florescence. Below this distal
agglomeration the synflorescence bears the long paraclades, which repeat the behaviour of
the main axis (fig. 3d, 4d). Correlated to the differentiation into these two types of para-
clades is a strong tendency of a truncation of the synflorescence, i.e. the loss of the distal
spikelet (main florescence). Also the distal spikelet (coflorescence) of long paraclades often
fails to develop (fig. 4d). This phenomenon is found in several families with polytelic syn-
florescences (WEBERLING & TROLL 1998), and it must be recognized as an far advanced
character state. The aberrant inflorescence of subgenus Marlenia represents a much derived
state of its own.

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Table 1: Selected character states of the subgenera of *Luzula*, from data of Buchenau (1906), Malheiros et al. (1947), Nordenskold (1949), Ebinger (1963), and own observations.

<table>
<thead>
<tr>
<th>character</th>
<th>subgenus <em>Pterodes</em></th>
<th>subgenus <em>Marelena</em></th>
<th>subgenus <em>Anthelaea</em></th>
<th>subgenus <em>Luzula</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>inflorescence</td>
<td>much branched anthelodium; all florescences long pedicelled</td>
<td>monochasial main axis, composed of successive first paraclades of increasing order</td>
<td>much branched anthelodium; florescences of higher order shortly pedicelled and crowded</td>
<td>often truncate synflorescence; with distal, crowded short paraclades and proximal long paraclades</td>
</tr>
<tr>
<td>seed</td>
<td>conspicuous chalazal (distal) caruncula</td>
<td>no caruncula, but very thick mucilaginous cover</td>
<td>caruncula missing or micropylar (basal), but very small</td>
<td>caruncula micropylar (basal), conspicuous</td>
</tr>
<tr>
<td>life span</td>
<td>perennial</td>
<td>annual</td>
<td>perennial</td>
<td>perennial</td>
</tr>
<tr>
<td>chromosomes</td>
<td>n = 6; &lt; 2 μm</td>
<td>n = 3; 4 – 6 μm</td>
<td>n = 6; &lt; 2 μm</td>
<td>n = 6; &lt; 2 μm</td>
</tr>
<tr>
<td>leaf epidermis cells</td>
<td>ca. 40 × 110 μm anticlinal walls wavy</td>
<td>ca. 70 × 280 μm anticlinal walls smooth</td>
<td>ca. 40 × 110 μm anticlinal walls wavy</td>
<td>ca. 40 × 110 μm anticlinal walls wavy</td>
</tr>
<tr>
<td>stomata</td>
<td>ca. 40 μm long</td>
<td>ca. 100 μm long</td>
<td>ca. 40 μm long</td>
<td>ca. 40 μm long</td>
</tr>
<tr>
<td>mechanical tissue</td>
<td>present</td>
<td>absent</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>at leaf margin</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>root endodermis cells</td>
<td>U-shaped</td>
<td>O-shaped</td>
<td>U-shaped</td>
<td>U-shaped</td>
</tr>
</tbody>
</table>
Fig. 1: *Luzula*. Schematic elevations of inflorescences. a: *L. elegans*; b: *L. pilosa*. Cf1, Cf2, Cf3: coflorescences of praclades of 1\textsuperscript{st} order (originating from the main axis); Ma: main axis; Mf: main florescence; Pc1, Pc2, Pc3: consecutive paraclades of 1\textsuperscript{st} order; Pc1.1, Pc1.1.1, Pc1.1.1.1: paraclades of increasing higher order;
Fig. 2: *Luzula elegans*. Distal part of the inflorescence shown in fig. 1a. Abbreviations as in fig. 1.
Fig. 3: Partial inflorescences of *Luzula*. a: *L. elegans* (subgen. Marlenia); b: *L. luzuloides* (subgen. Anthelaea); c: *L. pilosa* (subgen. Pterodes); d: *L. campestris* (subgen. Luzula).
Fig. 4: Diagrammatic comparison of the inflorescences of the subgenera of *Luzula*. a: subgen. *Pterodes*; b: subgen. *Marlenia*; c: subgen. *Anthelaea*; d: subgen. *Luzula*. The squares represent one-flowered florescences. The prophylls are omitted to increase the clearness. Note the tendency of truncation at the main axis and the long-paraclades in subgen. *Luzula*. 

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