ORIGINAL ARTICLE

Inflorescence morphology and flower development in *Pinguicula alpina* and *P. vulgaris* (Lentibulariaceae: Lamiales): monosymmetric flowers are always lateral and occurrence of early sympetaly

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Abstract Earlier interpretations of shoot morphology and flower position in *Pinguicula* are controversial, and data on flower development in Lentibulariaceae are scarce. We present scanning electron microscopy about the vegetative shoot, inflorescence and flower development in *Pinguicula alpina* and *P. vulgaris*. Analysis of original data and the available literature leads to the conclusion that the general pattern of shoot branching and inflorescence structure is uniform in all the *Pinguicula* species studied so far. The inflorescence is a sessile terminal umbel that is sometimes reduced to a solitary pseudoterminal flower. Flower-subtending bracts are either cryptic or present as tiny scales. A next order lateral shoot develops in the axil of the uppermost leaf, below the umbel. It is usually though not always homodromous, i.e., the direction of the phyllotaxy spiral is the same as in the main shoot. Among *Pinguicula* species that overwinter as a hibernaculum, the initiation of floral organs takes place in the same year as flowering in *P. vulgaris*, and 1 year earlier in *P. alpina*. Early congenital petal fusion ('early' sympetaly) is documented in *Pinguicula*, though most other members of Lamiales exhibit 'late' sympetaly. Sporadic occurrence of rudiments of two posterior stamens in *Pinguicula* is confirmed. A speculation is made that, in angiosperms, monosymmetric flowers cannot be terminal on shoots bearing more than two (or three) phyllomes.

Introduction

In the vast majority of angiosperms, shoot branching is axillary (gemmaxillary plants, Gatsuk 1974). As a consequence, in angiosperm inflorescences, flowers are either terminal or they develop axillary on axes of different order. Flower-subtending bracts represent key architectural markers in inflorescences (Prenner et al. 2009). When subtending bracts of lateral flowers are missing (ebracteate inflorescences: Troll 1964; Weberling 1989), it is normally assumed that they were ancestrally present but then lost in the course of evolution (e.g., Endress 2010). Sometimes, rudiments of flower-subtending bracts can be found in early developmental stages. In ebracteate inflorescences of the model plant *Arabidopsis*, the presence of cryptic flower-subtending bracts is postulated on the basis of comparative morphology, investigations of gene expression patterns and the re-appearance of bracts in some mutants (Long and Barton 2000; Baum and Day 2004; Choob and Penin 2004; Penin 2008). In some taxa, the absence of visible flower-subtending bracts could be due to their incorporation into lateral flowers as a perianth member or by means of formation of 'hybrid' structures combining features of a flower-subtending bract and a perianth member (reviewed in Buzgo and Endress 2000; Buzgo et al. 2006; Remizowa et al., in press).

There are, however, some flowering plants for which less orthodox patterns of flower arrangement have been reported.

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Among them, considerable attention has been paid to water lilies, a group belonging to the basal grade of angiosperms. Many authors interpret flowers of *Nymphaea* as being extra-axillary and replacing some leaf sites along the genetic spiral on the rhizome (Raciborski 1894; Cutter 1961; Weidlich 1976; Schneider et al. 2003; Grob et al. 2006), while others suggest that the apparent position of flowers in the same spiral as the leaves is due to a reduction of the subtending leaf component of a primordium that would potentially give rise to both a sub-tending leaf and an axillary bud (Chassat 1962; Endress and Doyle 2009). Similar problems exist with the interpretation of flower arrangement and shoot branching patterns in several other members of the order Nymphaeales (Sokoloff et al. 2009).

Another angiosperm lineage with unusual branching patterns is the euasterid family Lentibulariaceae (the bladder-wort family) that belongs to the order Lamiales (APG, III The Angiosperm Phylogeny Group 2009). The members of the family are carnivorous, often aquatic plants. The structure of vegetative organs is highly modified in the largest genus of the family, *Utricularia*, and the precise recognition of principal organ categories (roots, stems and leaves) is problematic (Rutishauser and Sattler 1989; Sattler and Rutishauser 1990; Rutishauser and Isler 2001; Jeune et al. 2006). Nevertheless, inflorescence organization and devel-opment appear to be normal in *Utricularia*, and flowers of most species are arranged into bracteate racemes (Eichler 1875; Kamienski 1891; Taylor 1989; Kirchoff et al. 2008).

The second-largest genus of the family Lentibulariaceae is *Pinguicula*, comprising about 100 species (Degtjareva et al. 2006; Casper and Stimper 2009) distributed in arctic, temperate and tropical areas of Eurasia, Africa and America (Casper 1966). Like other members of the family, species of *Pinguicula* are carnivorous plants that usually grow in nutrient-poor habitats. Unlike *Utricularia*, *Pinguicula* is char-acterized by well-recognizable roots, stem and leaves, though the roots are unusual in having no root cap (Rutishauser and Isler 2001; Kirchoff et al. 2008). The leaves of *Pinguicula* are entire and form a basal rosette.

Flower arrangement of *Pinguicula* is, however, a subject of controversy. Among foliage leaves of the rosette, one can see a number of flowers on long stalks. Most commonly, one to three flowers are formed. Although flowers of *Pinguicula* are sometimes reported to be axillary (e.g., Heslop-Harrison 2004), most authors admit that no individ-ual leaf can be recognized as a flower-subtending phyllome. Several hypotheses have been proposed to explain the posi-tion of flowers on the shoot of *Pinguicula*: (1) like those of *Nymphaea*, flowers of *Pinguicula* are lateral and extra-axillary, substituting some leaf sites along the same genetic spiral (Raju 1969: reported for *P. vulgaris*); (2) the flowers in *Pinguicula* form a terminal inflorescence represented by a sessile umbel, which is often reduced to a single flower (Wydler 1857; Dickson 1869; Eichler 1875; Troll 1964;

Brunaud and Turlier 1971; see also Fischer et al. 2004: reported for *P. lusitanica*, *P. villosa*, and *P. vulgaris*); (3) each flower in *Pinguicula* occupies a morphologically ter-minal position; it is displaced in a lateral position by a new leaf rosette developing in the axil of the uppermost foliage leaf (Grob et al., 2007: reported for *P. moranensis*).

Apart from considerable discrepancies among views on the morphological nature of flower arrangement in *Pingui-cula*, the previously examined species do not cover all major groups of the genus. Cieslak et al. (2005) recognized five major clades of *Pinguicula* based on analyses of plastid markers, and their results are generally congruent with anal-yses of a nuclear marker (Degtjareva et al. 2006). The species studied earlier in relation to flower position on the shoot belong to Clade I of Mexican/Central American/ Caribbean species (*P. moranensis*), Clade III of mainly East Asian species (*P. villosa*), Clade IV of Holarctic species (*P. vulgaris*) and Clade V, which is characterized by a tropical growth type (*P. lusitanica*). In this article, we report developmental data on *P. alpina*, which belongs to the monospecific Clade II. Although *P. alpina* is an arctic-alpine Eurasian species (Casper 1966), molecular phyloge-netic data show its sister-group relationships to Clade I of tropical American species (Cieslak et al. 2005, but see Degtjareva et al. 2006). The molecular phylogenetic place-ment of *P. alpina* contradicts earlier views (e.g., Casper 1966) and has no obvious morphological support (Cieslak et al. 2005). Apart from *P. alpina*, we have made observations of shoot structure and flower arrangement in *P. vulgaris*, because two different morphological interpretations are available in the literature for this species.

Erbar (1991) and Erbar and Leins (2011) highlighted the phylogenetic significance of characters related to early flow-er development (especially the mode of the formation of the corolla tube) in asterids. Despite extensive recent investiga-tions of flower development and evolution in the members of the order Lamiales (sensu APG, III The Angiosperm Phylogeny Group 2009) (e.g., Endress 1994, 1998, 1999, 2001; Donoghue et al. 1998; Reeves and Olmstead 1998; Bello et al. 2004; Sehr 2005; Mayr and Weber 2006; Borg et al. 2008; Borg and Schönenberger 2011; Erbar and Güldena 2011), detailed developmental data for several families, including Lentibulariaceae, are still absent (Erbar and Leins 2011). Pub-lished data on flower development in *Pinguicula* and other Lentibulariaceae are fragmentary. So far, the most comprehen-sive developmental study is the extensively illustrated work of Dickson (1869) on flowers of *P. vulgaris*, which was based on observations made using light microscopy. Grob et al. (2007) documented some stages of flower development in *P. mora-nensis* using scanning electron microscopy (SEM). Since the descriptions for these two species differ, developmental data might be a source of phylogenetic and taxonomic information in *Pinguicula*. We present new SEM data on flower

development in *P. alpina* and *P. vulgaris*, and compare them with earlier observations on *P. vulgaris* and *P. moranensis*.

Material and methods

Material of *Pinguicula alpina* L. and *P. vulgaris* L. was collected in NW Russia twice a month during the vegetation season of 2006 (20 individuals of each species each time). The following specimens were used: *Pinguicula alpina* L., Murmansk province, W of Apatity, near the experimental section of the Polar-Alpine Botanical Garden Institute (PABGI), 25.v.2006, leg. V.N. Andreeva; *P. alpina*, Murmansk province, Khibiny mountains, near Kirovsk, Mt. Vud'yavrchorr, Botanical cirque, leg. V.A. Kostina; *P. vulgaris* L., Murmansk province, Khibiny mountains, near Kirovsk, at the foot of the S slope of Mt. Kukisvumchorr, leg. V.A. Kostina. Additional material of *P. vulgaris* was collected in June 2011 from the same population in Kirovsk. Flowering rosettes of *P. vulgaris* were also observed by the first author in 2007-2011 at White Sea Biological Station of Moscow State University (North Karelia). Voucher specimens of field-collected species were deposited at the Herbarium of the Moscow State University, Moscow, Russia (MW; *P. alpina*, V.A. Kostina no. 1; *P. vulgaris*, V.A. Kostina no. 2).

The plant material was fixed and stored in 70% ethanol. Shoot morphology was studied with an Olympus SZX7 stereomicroscope. For detailed morphological and developmental studies of *P. alpina*, a scanning electron microscope (SEM) was used. For SEM, dissected shoot apices of *P. alpina* with young flowers were dehydrated using 96% ethanol and 100% acetone. Dehydrated material was critical-point dried using a Hitachi HCP-2 critical point dryer, mounted onto the stubs using double-sided sticky tape, coated with Pt/Pd using a Eiko (Tokyo, Japan) IB-3 ion coater and observed using a JSM-6380LA SEM (JEOL, Tokyo, Japan) under 20 kV at Moscow University. The material of *P. vulgaris* was dehydrated using absolute ethanol and critical-point dried using an Autosamdri-815B critical-point drier (Tousimis Research, Rockville, MD, USA), coated with platinum using an Emitech (Kent, UK) K550 sputter coater and examined using a Hitachi (Wokingham, UK) cold-field emission SEM S-4700-II at 1 kV at Royal Botanic Gardens, Kew.

Results

Shoot morphology and development in *Pinguicula alpina*

Pinguicula alpina is characterized by a temperate growth form with overwintering in a winter bud. The winter bud (hibernaculum) has four or five fleshy bud scales followed by the four to six young foliage leaves of the next season's rosette. By late August or early September, a terminal inflorescence containing one or two (rarely three) lateral flowers forms in the center of the bud. Occasionally, quite reduced scaly flower-subtending bracts can be observed. By autumn, all the floral parts are initiated, at least in the lowermost flower. The inflorescence axis remains shortened, and the inflorescence is sessile throughout the development. Pedicels of individual flowers are short, but visible before anthesis. At flowering, the pedicels grow into long stalks, and the inflorescence can be characterized as an umbel. In all but one of the dissected plants (see below for the unusual case), apart from the terminal inflorescence, a hibernaculum contains a young next order shoot with seven to nine young leaves. These leaves (at least basal ones) will expand during the next season, and this shoot will ultimately form a terminal hibernaculum. To summarize, the shoot apical meristem forms numerous leaves before it is terminated by an umbel; these leaves can be divided in the following types: (1) the two prophylls and several subsequent leaves are foliage leaves that form a rosette later in the same season when flowering of the umbel of previous order shoot took place; (2) bud scales of the hibernaculum; (3) foliage leaves that form a rosette before the flowering of the next season.

The phyllotaxy is spiral, either clockwise or anticlockwise, and follows the Fibonacci pattern (Fig. 1). The flower-
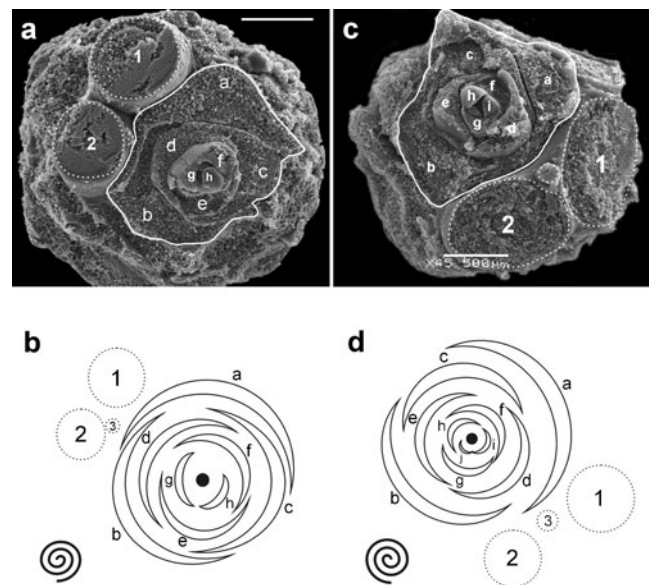

Fig. 1 Shoots of *Pinguicula alpina* with different chiralities. Frontal view of shoot apices (**a**, **c**) and their diagrams (**b**, **d**). In **a** and **b** (collected 1 September 2006), eight leaves (a-h) form an anticlockwise spiral. In **c** and **d** (collected 1 September 2006), ten leaves (a-j) form a clockwise spiral. 1, 2, 3 are flowers that are formed on a shoot of preceding order. Scale bars=500 μm. In figs. 1, 2, 3, 4, leaves and flowers of the main axis are numbered starting from the first well-visible leaf or flower. So, in fig. 1, a number of foliage leaves preceded flowers on the main axis

subtending bracts are inserted in positions that follow precisely the genetic spiral of the phyllotaxy of the preceding foliage leaves, which supports the conclusion about the terminal position of the umbel. When flower-subtending bracts are not visible, their supposed sites can be deduced from the position of flowers and their symmetry planes, as flowers of *Pinguicula* are monosymmetric. These supposed sites of (cryptic) bract insertion also follow the phyllotaxy of the main shoot. A next order lateral shoot develops in the axil of the uppermost foliage leaf, just below the umbel (e.g., Fig. 2d-f, where the umbel is one-flowered). Its prophylls (labeled 1 and 2 in Fig. 2d, e) are foliage leaves morphologically similar to the subtending leaf. The phyllotaxy of the lateral shoot usually has the same chirality as the main shoot (i.e., homodromous), so that the entire individual apparently maintains either clockwise or anticlockwise shoot chirality established in the seedling throughout its life. The two

prophylls of the lateral shoot initiate sequentially. The first prophyll is initiated on the anodic side of the axil of the subtending leaf. The anodic end of a leaf is oriented in the direction up the genetic spiral of the phyllotaxy toward the younger end, while the cathodic end is oriented toward the beginning of the genetic spiral (Korn 2006). The second prophyll is initiated on the cathodic side of the axil of the subtending leaf, and the next phyllome is inserted on a radius between the subtending leaf and the first prophyll. This stable mode of arrangement of the first phyllomes on a lateral shoot is responsible for the false impression that the genetic spiral of the next year shoot continues the spiral of the previous year (if the inflorescence is ignored).

In one dissected plant (Fig. 2a-c), a hibernaculum had a performed terminal umbel and, in addition, shoots of the two next orders (rather than one order in other dissected plants). It is most likely that, in this plant, inflorescences of two subsequent orders would flower during the next season. One umbel terminates the first order shoot, while another umbel terminates the second order shoot. In the examined plant, the second order shoot developed only two foliage leaves (prophylls) before terminating in its umbel. The third order shoot develops in the axil of the second prophyll of the second order shoot. It bears several young leaves. Importantly, in this plant, the first and the second order shoots have a clockwise spiral of phyllotaxy, while the third order shoot has an anticlockwise spiral.

In our material of *P. alpina*, shoot branching was observed only in the axil of the uppermost foliage leaf, just below the umbel. No small additional hibernacula (brood buds, bulbils or gemmae, Heslop-Harrison 2004) were found in axils of other foliage leaves.

Shoot morphology and development in *Pinguicula vulgaris*

The hibernaculum of *P. vulgaris* has six to eight bud scales and several young leaves that will form the leaf rosette of the next year, and contains the next season inflorescence, which is at the earliest stage of development. In our material, only the inflorescence meristem is initiated by the end of the vegetation season (Fig. 3a, b). The triangular shape of the inflorescence meristem in Fig. 3a, b indicates the first stages of differentiation of floral meristems. The next order shoot is represented by an undifferentiated meristem. In material collected in late May (i.e., just before the beginning of the vegetation season in the Murmansk region), individual floral meristems or young flowers with differentiating floral organs can be clearly seen (Fig. 3c-f). The fact that different developmental stages are found in the same population and at the same time shows that developmental processes are not synchronous in different individuals. In the material examined developmentally, one to four flowers formed an umbel. Among plants studied at anthesis, umbels
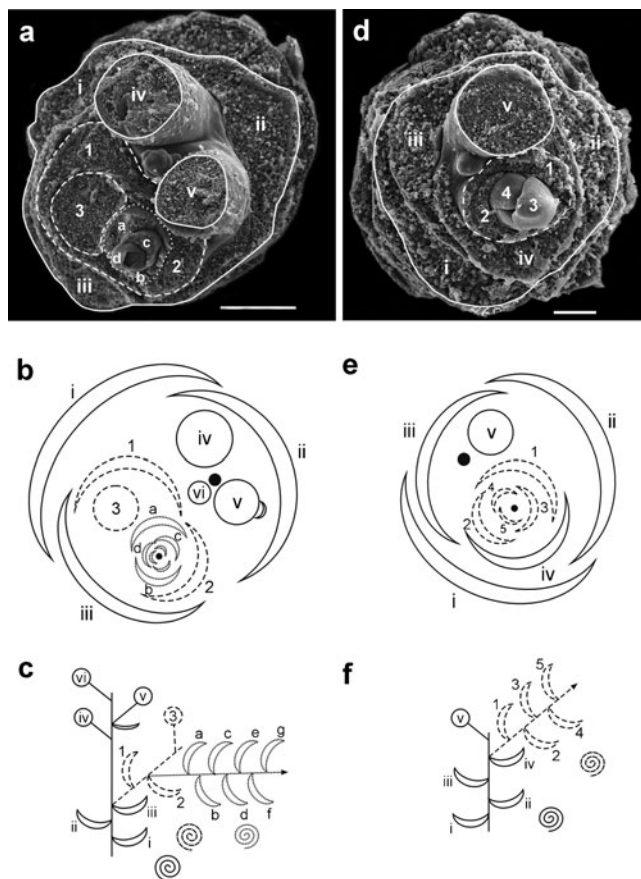

Fig. 2 Shoot branching in *Pinguicula alpina*. Frontal view of shoot apices (**a**, **d**), their diagrams (**b**, **e**) and schematic representation of shoot systems (**c**, **f**). In **a-c** (collected 21 September 2006), leaves i-iii form a clockwise spiral, followed by flowers iv-vi; a lateral shoot with a clockwise spiral (prophylls 1-2 followed by flower 3) is present in the axil of leaf iii; leaves a-g form an anticlockwise spiral and belong to a shoot in the axil of the leaf 2. In **d-f** (collected 1 September 2006), leaves i-iv form an anticlockwise spiral followed by flower v; a lateral shoot with an anticlockwise spiral 1-5 is present in the axil of the leaf iv. Scale bars=500 μm (**a**), 200 μm (**d**)
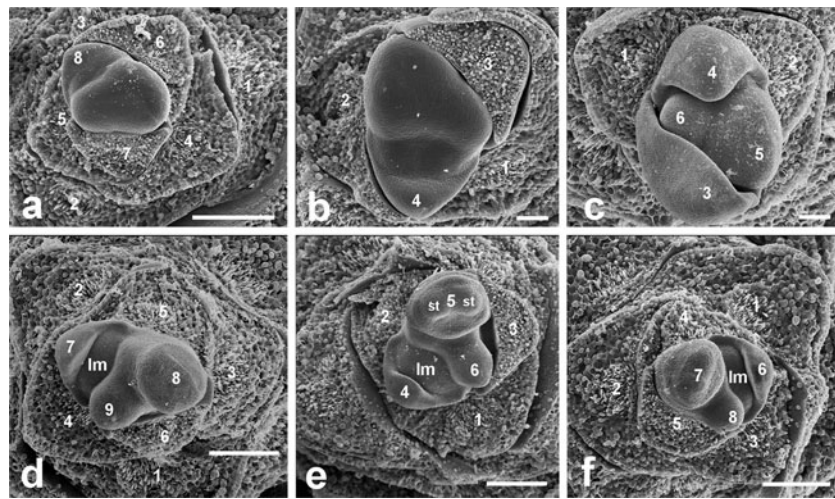
Fig. 3 Early stages of inflorescence development in *P. vulgaris* (material collected in August, September and May). Frontal views of plants with all but very young leaves removed. **a** Plant collected 1 September 2006, with a clockwise spiral of phyllotaxy (eight leaves are visible). The large triangular meristematic bulge in the center will form an inflorescence. **b** Plant collected 11 August 2006, but the developmental stage is similar to that in **a**; an almost undifferentiated lateral meristem is present in the axil of the final foliage leaf (4). **c-f** plants collected 24 May 2006 from the same population in Kirovsk. Phyllotaxy clockwise in **c-e** and anticlockwise in **f**. In **c**, leaves 1-4 are followed by undifferentiated flowers 5 and 6. In **d**, leaves 1-7 are followed by undifferentiated flowers 8 and 9. In **e** and **f**, first-formed flowers (5 and 7, respectively) are at the stage of stamen initiation. Abbreviations: *lm*, lateral meristems in axils of uppermost foliage leaves; *st*, stamen primordium. Scale bars=100 μm (**b**, **c**), 300 μm (**a**, **d**, **e**, **f**)

with up to six flowers are found. Every subsequent flower of an umbel is strongly delayed in development, so that a fully performed flower(s), a flower at young stage of development and an undifferentiated floral meristem(s) can be seen in the same inflorescence (Fig. 4b, d). No trace of the

Fig. 4 Young lateral shoots of *P. vulgaris* (material collected in June). Frontal views of plants with all but very young leaves removed. Phyllotaxy is anticlockwise in (**a**, **c**) and clockwise in (**b**, **d**). **a** A lateral shoot is formed in axil of the leaf i, then the main axis has formed flowers ii, iii (removed) and iv (probably abortive). **b** A lateral shoot is present in the axil of the leaf i, flower ii is removed, flower iii is very young. **c** A lateral shoot in the axil of the leaf i is formed, then the main axis has formed flowers ii (removed), iii, iv, v. **d** A lateral shoot in the axil of the leaf vi is formed, then the main axis has formed flowers vii, viii (removed), ix, x. Arabic figures = leaves of lateral shoots. Scale bars=300 μm

flower-subtending bract has been observed at any developmental stage. At anthesis, pedicels of individual flowers elongate, the inflorescence axis remains short, and the inflorescence remains sessile.

The meristem of the second order shoot is similar to the material collected in August, September and May, and contains no obvious leaf primordia, which start to initiate in June (Fig. 4). In our material, chirality of the second order shoot was always the same as the chirality of the first order shoot (Fig. 4). The second order axis forms a terminal hibernaculum during July. One to four small additional hibernacula form in axils of foliage leaves situated below the bud scales of the terminal hibernaculum. By next spring, subtending leaves of additional hibernacula cannot be traced anymore, but the lateral hibernacula remain attached to the base of the much larger terminal hibernaculum.

Flower development in *Pinguicula alpina* and *P. vulgaris*

In both species, flowers are pronouncedly monosymmetric and normally contain five sepals (but see below), five petals, two stamens and two united carpels (Figs. 4, 5, 6, 7, 8). Two sepals are anterior (abaxial), two are lateral, and the fifth sepal is median posterior (adaxial). Flower orientation can be clearly seen in Fig. 5d, where a flower-subtending bract is visible (arrow). The calyx is bilabiate with two sepals united in a lower lip and three sepals united in an upper lip. The two lips are basally united forming a very short calyx tube. The petals alternate with sepals, and the median petal
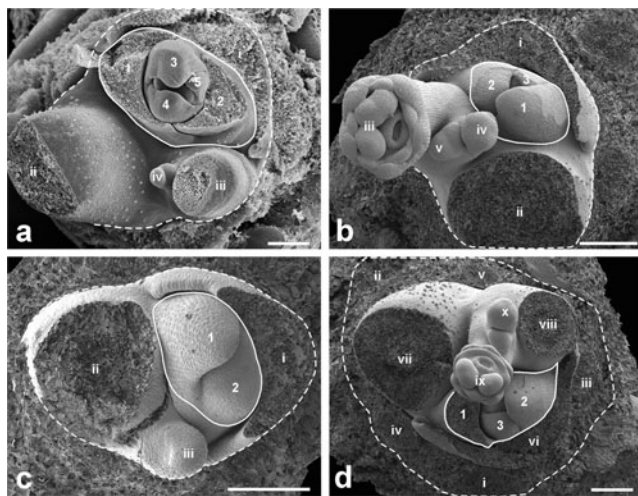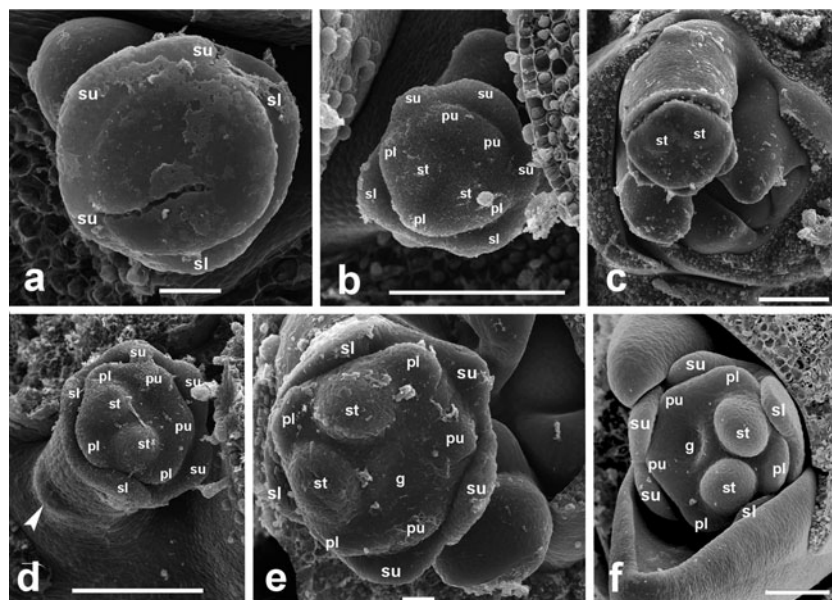
Fig. 5 *Pinguicula alpina*, early flower development. **a** Flower with all five sepals initiated. **b** Flower with calyx, corolla and androecium initiated. Two posterior petals are united with each other and the median abaxial petal is united with lateral ones. Stamen primordia are just initiated. **c** Two flowers and a next order shoot with two prophylls well visible. The larger flower is at approximately the same stage as the flower in **b**, but the pattern of early petal fusion is not the same. Here, all petals except the median abaxial one are united. **d** Slightly later stage with stamen primordia better developed. All petals except the abaxial one are united. *Arrowhead* points to the flower-subtending bract. **e-f** Earliest stage of gynoecium development. The gynoecium is visible as a shallow horseshoe-shaped rim on the radius between the stamens. Abbreviations: *g*, gynoecium; *pl*, lower lip petals; *pu*, upper lip petals; *sl*, lower lip sepals; *su*, upper lip sepals; *st*, stamen. Scale bars=50 μm (**a**, **e**), 100 μm (**f**), 200 μm (**b**, **c**, **d**)

is abaxial. The median petal is basally spurred and distally bifid. The other petals are entire; they are narrower than the median petal. Three petals form a lower lip, while two petals form an upper lip. The two lips are united in a well-developed corolla tube. In *P. alpina*, the petals are white; the median petal is much larger than the lateral ones and has

a yellow spot that is highly variable in size and form; lower corolla lip with a palate; tube short, broadly funnel-shaped; spur cylindrical, more or less curved, as long as the corolla tube; in *P. vulgaris*, the petals are lilac or blue-violet; lower corolla lip without palate; corolla tube is funnel-shaped; spur is cylindrical, acute, longer than the corolla tube and

Fig. 6 *Pinguicula alpina*, late flower development. **a** Stage with ring-shaped gynoecium primordium. **b-e** Flowers with calyx aestivation visible. **f** Flower with lower lip sepals removed to show young spur of corolla. Abbreviations: *g*, gynoecium; *pl*, lower lip petals; *pu*, upper lip petals; *s*, spur, *sl*, lower lip sepals; *su*, upper lip sepals; *st*, stamen. Scale bars=100 μm (**a**), 200 μm (**b**), 300 μm (**e**), 500 μm (**c**, **d**), 1,000 μm (**f**)
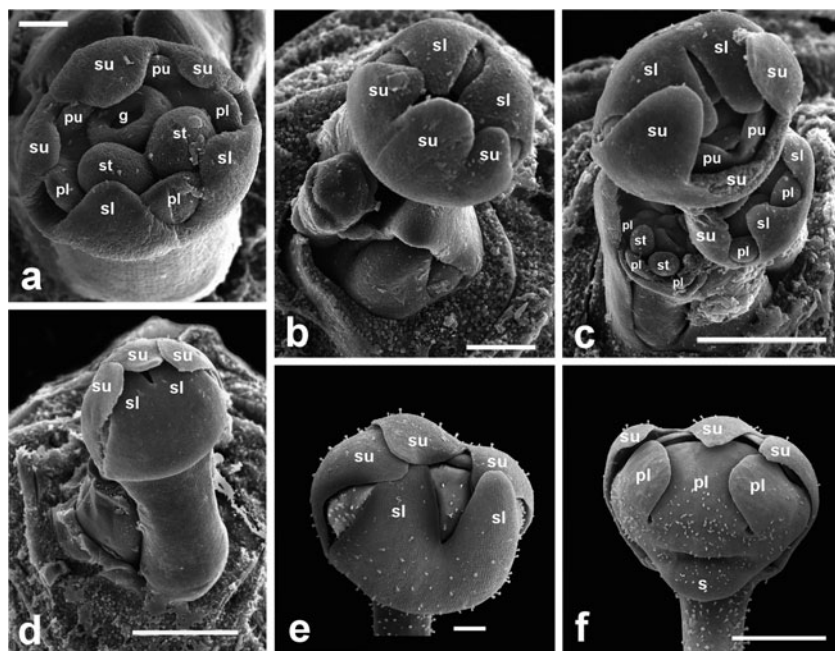
Fig. 7 *Pinguicula vulgaris*, early flower development. **a** The earliest stage with a very narrow calyx rim marked by *arrows*. **b,c** Initiation of calyx and androecium; the two massive stamen primordia appear just before corolla initiation. **d-e** Flowers with median abaxial petal initiated. **f-i** Further development of corolla. **f** and **i** Different views of the same flower, while **g** and **h** are different views of another flower. In **f** no connection between the median lower lip petal and lateral lower lip petals observable, but in **i** at the same young flower (as well as in another flower in **g** and **h**) it is clearly visible. **h-i** All petals are united by a rim. At this stage, the gynoecium is not visible. Abbreviations: *pl*, lower lip petals; *pu*, upper lip petals; *s*, spur, *sl*, lower lip sepals; *su*, upper lip sepals; *st*, stamen. Scale bars=200 μm (**a**, **b**, **c**, **f**, **g**, **h**), 300 μm (**d**, **e**. **i**)
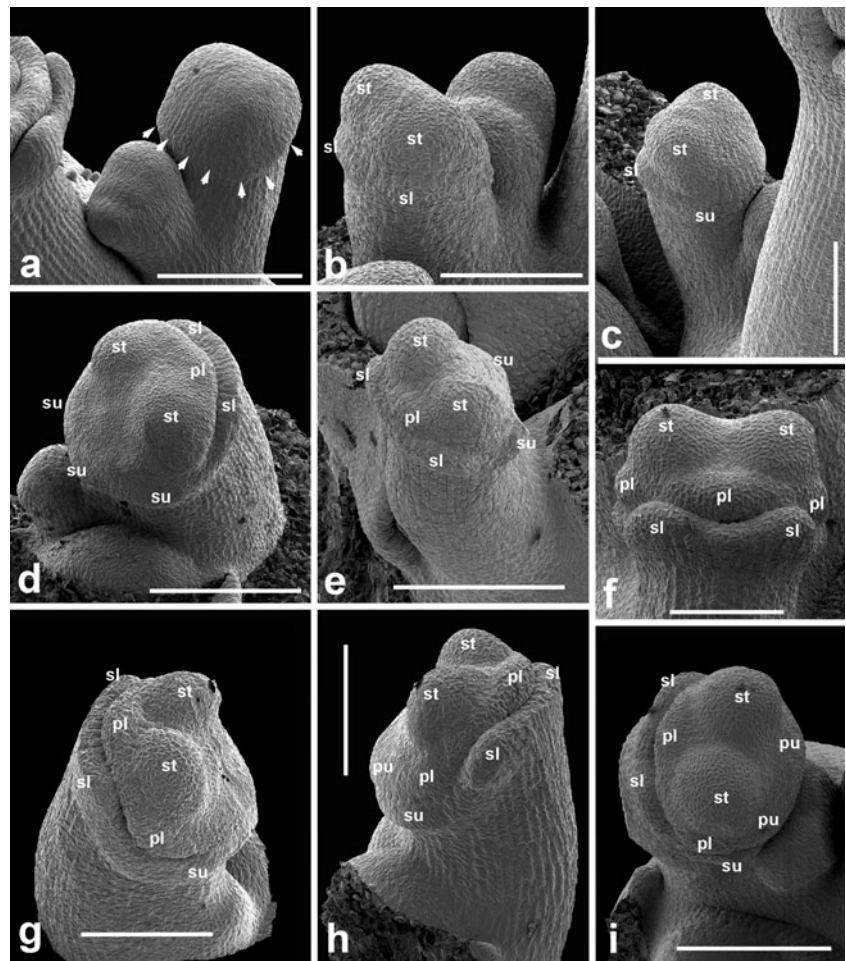
does not form an angle with the tube. The two stamens lie on the same radii as the two lower lip sepals. The two carpels are united in a unilocular gynoecium with a free central placenta (Fig. 8i).

In all studied young flowers of both species with recognizable sepals, a calyx tube was already visible. Thus, the sepals show early congenital fusion. The calyx tube is attached to the receptacle at a slightly lower level between the future lower and upper calyx lip, so that in a top view of a flower the false impression may arise that the tube is absent from these regions (Fig. 5a, c). In oblique views (e.g., Fig. 7), the calyx tube can be seen along the entire circumference of a flower. Figure 7a shows the earliest stage, with a very narrow calyx rim marked by arrows.

In *P. alpina*, stamens appear simultaneously with petals (Fig. 5b-d). In *P. vulgaris*, the two massive stamen primordia appear just before the first evidence of corolla initiation (Fig. 7b). In our material of *P. alpina*, petals initiate simultaneously. In *P. vulgaris*, the median abaxial sepal appears slightly earlier than the rest of the corolla (Fig. 7d, e). When all five petals are initiated, in both species, they are already all connected into a corolla tube, so that we interpret petal fusion as early congenital (early sympetaly, Erbar 1991), or

at least some petals are united with each other. For example, it is not possible to trace boundaries between individual lower lip petals in Fig. 5b. In the flowers illustrated in Fig. 5d, f, no boundaries can be seen between the lateral lower lip petals and the two upper lip petals. In the flower illustrated in Figs. 7h, i, all petals are united by a rim, and it is really impossible to see any boundary, for example, between the two upper lip petals. When deciding about the presence or absence of a connection between petals, it is important to remember that one and the same structure may look different when viewed from different angles. For example, Figs. 7f and 7i show the same young flower. In 7f no connection between the median lower lip petal and lateral lower lip petals can be seen, but it is clearly visible in Fig. 7i. The continuous nature of the corolla is also clear in later developmental stages. For example, no boundary between the two upper lip petals is visible in the flowers illustrated in Figs. 8a-c (see also Figs. 9g, i). Only in late stages, each petal develops its individual blade (Figs. 8h, 9f). Even later, a spur of the corolla becomes recognizable (Fig. 6f).

The gynoecium can first be seen as a horseshoe-shaped primordium on the abaxial (anterior) side of the floral center
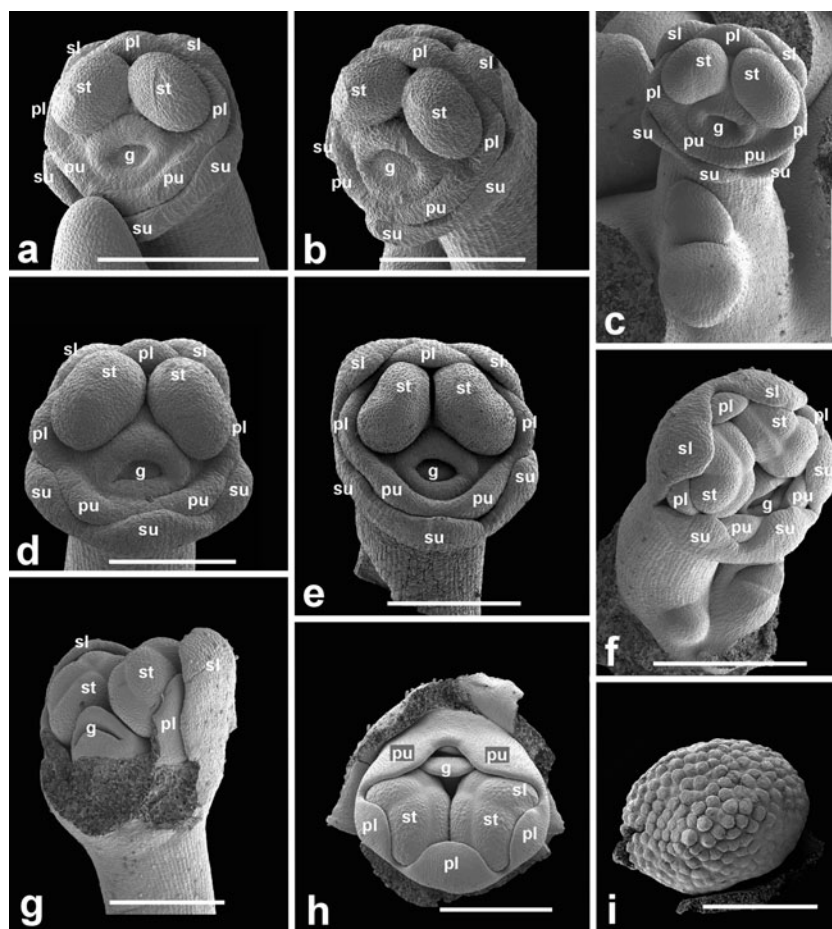
Fig. 8 *Pinguicula vulgaris*, late flower development. **a-e** Flowers with ring-shaped gynoecium primordium. **a-c** Flowers with all petals united in a tube and no boundary between the two upper lip petals visible. **d** Flower at a stage similar to those in **a-c**, but with individual upper lip petals well recognizable, though united by a shallow corolla tube. **e** Flower at a slightly later developmental stage than in **d** (indicated by anthers with thecae just starting to appear and a deeper gynoecium orifice), but with upper lip petals well united. **f** Flower with anthers having thecae and microsporangia recognizable, but the gynoecium orifice yet open. **g** Flower at a further developmental stage with upper lip sepals and petals removed to show a gynoecium with its orifice closed and abaxial side more developed than the adaxial one. **h** Flower with sepals removed to show corolla with each petal possessing its individual blade. **i** Placenta with ovules. Abbreviations: *g*, gynoecium; *pl*, lower lip petals; *pu*, upper lip petals; *s*, spur, *sl*, lower lip sepals; *su*, upper lip sepals; *st*, stamen. Scale bars=300 μm (**a**, **b**, **d**, **i**), 400 μm (**c**), 500 μm (**f**, **g**, **h**)

(Fig. 5e, f). The gynoecium primordium soon becomes complete on the adaxial side and thus has a nearly symmetrical ring-shaped form (Figs. 6a, 8a-e). The bicarpellate nature of the gynoecium is not detectable during these early stages.

In late developmental stages, the lower and upper calyx lips can be easily recognized (Figs. 6b-f; 7, 8, 9a-e). The two lips are nearly equal in length. In *P. alpina*, in most cases, the upper lip covers the lower lip in the flower bud (Fig. 6b-d). In *P. vulgaris*, the lower lip typically covers the upper lip (Figs. 9a, b). In both species, there are exceptions from the typical condition. For example, in the flower of *P. alpina* illustrated in Fig. 6e, one of the lower lip sepals covers an upper lip sepal, while another lower lip sepal is covered by the upper lip sepals; a similar situation is illustrated for *P. vulgaris* in Fig. 9d.

Several abnormalities have been found in the material of *P. vulgaris*. On five occasions, additional sepals (or sepal lobes?) have been found. All these cases are illustrated in Fig. 9c, d, e, h, i. In one of them (Fig. 9h), a structure that resembles an extra sepal (arrowhead) in fact represents a part of a prophyll of the lateral shoot. In the latter case, the first prophyll of the lateral shoot (which is situated in the axil of the uppermost foliage leaf) is congenitally united by its dorsal surface with the flower pedicel. Only the distal most part of the prophyll is free; it is located at the same level as the sepals. Adjacent upper lip sepals seem to be moved apart to provide a space for the prophyll tip. No abnormalities in the corolla, androecium or gynoecium structure can be seen despite the highly unusual calyx structure. In one flower, two staminodes were found (Fig. 9g) on the radii of the upper lip lateral sepals. In one plant, a
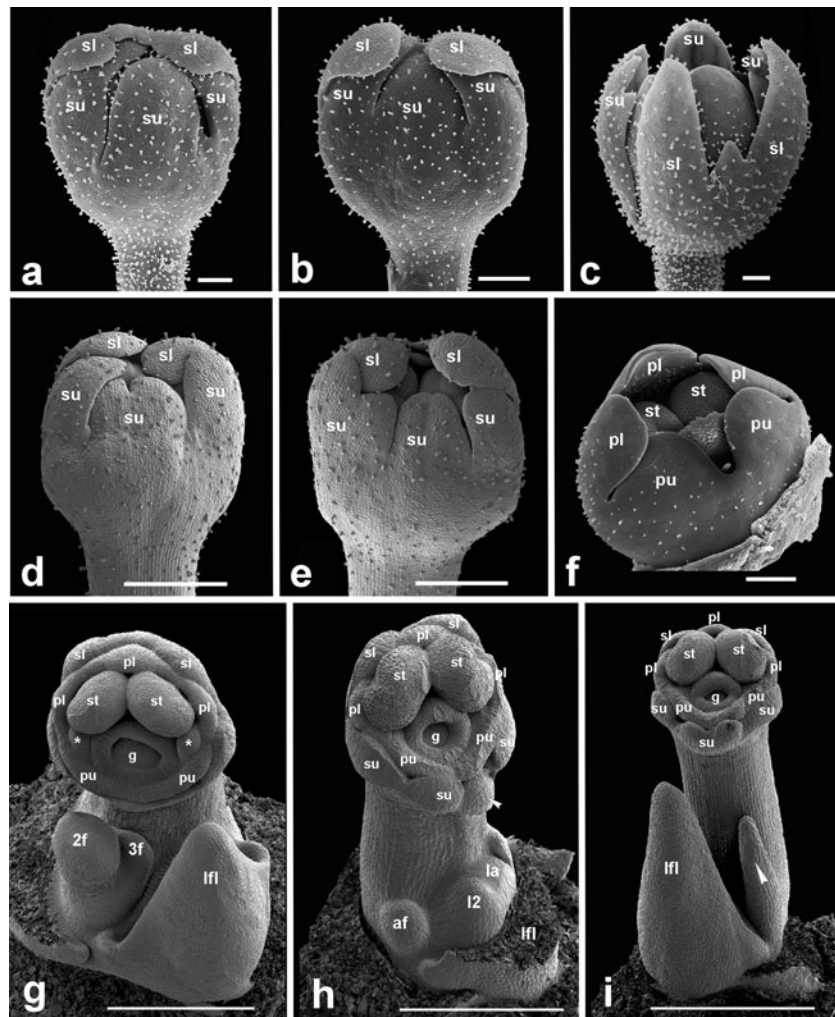
Fig. 9 *Pinguicula vulgaris*, calyx and corolla aestivation and various abnormalities in floral morphology. **a-e** Calyx morphology in flower buds. **a-b** The lower lip sepals cover the upper lip sepals (a typical condition). **c-e** Abnormalities with additional sepal or sepal lobes. **f** Corolla aestivation (calyx removed). **g** The only flower observed in our material that possessed two staminodes (*asterisks*). **h** Flower with a meristematic structure (*arrowhead*) that resembles an additional sepal primordium but in fact represents a distal-most portion of the first prophyll of a lateral shoot. This prophyll is congenitally united by its abaxial surface with the flower pedicel. **i** Shoot tip with a filamentous structure (marked with *arrow*) formed after the last foliage leaf and a flower. Note a bifid median adaxial sepal in the flower. The filamentous structure is developed in a position where a second flower is present in two-flowered inflorescences of *Pinguicula*. Abbreviations: *af*, aborted second flower; *2f*, the second flower; *3f*, the third flower; *g*, gynoecium; *l2*, second leaf of the lateral axis; *la*, apex of lateral shoot; *lfl*, last foliage leaf; *pl*, lower lip petals; *pu*, upper lip petals; *sl*, lower lip sepals; *su*, upper lip sepals; *st*, stamen. Scale bars=300 μm (**a, b, c, f**), 500 μm (**d, g, h, i**)

filamentous structure was found in place of a second flower, i.e., in a position where another flower could be expected (Fig. 9i), a phenomenon that sporadically occurs in various angiosperms (Sokoloff et al. 2006; Lock et al. 2009).

Discussion

Flower development

Cieslak et al. (2005) revealed important correlations between phylogeny and growth patterns in *Pinguicula*. Our data support the conclusions of Cieslak et al. (2005) highlighting important differences between the rhythmic patterns of development in *P. alpina* and *P. villosa* belonging to different clades of *Pinguicula*. In *P. alpina*, organ initiation on the floral meristem takes place during the season before anthesis. In *P. vulgaris*, this process takes place during the season of anthesis. Our observations on *P. vulgaris* agree with the data of Dickson (1869). Since Dickson has collected his material from an entirely different region, the rhythmic patterns of development seem to be stable at the level of species. It will be interesting to understand the timing of flower organ initiation in other temperate *Pinguicula* species to see if there is a correlation with their ecology.
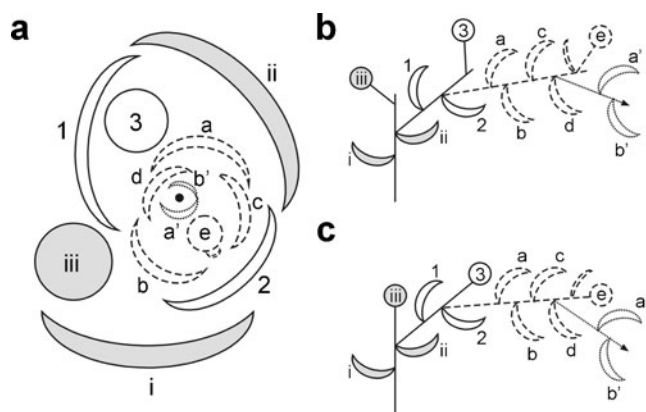
Fig. 10 Diagram (**a**) and schematic representations (**b**, **c**) of shoot system in *Pinguicula moranensis* based on fig. 2c in Grob et al. (2007). Abbreviations as in Fig. 2 of the present article. **b** Our preferred interpretation. **c** Our understanding of the interpretation adopted by Grob et al. (2007)

Pinguicula alpina generally differs in calyx aestivation compared to the two other species studied with this respect, *P. moranensis* (Grob et al. 2007) and *P. vulgaris* (Dickson 1869; this study). In these two latter species, lower lip sepals covered the upper lip sepals in the bud. In *P. alpina*, the upper lip sepals cover the inner lip sepals. The growth of two abaxial sepals is accelerated in *P. moranensis* (Grob et al. 2007). In contrast, no significant difference in sepal length is found in young flowers of *P. alpina* and *P. vulgaris*. Future studies will show whether the pattern of sepal aestivation is of taxonomic significance in Lentibulariaceae. This study already revealed a variation in calyx morphology in both *P. alpina* and *P. vulgaris*. Easier cases of variation include deviations from the typical patterns of aestivation. More complex cases include multiplication (or lobing) of sepals in *P. vulgaris*. Interestingly, these deviations in calyx morphology (even the teratological insertion of a distal part of a prophyll of a lateral shoot) do not affect the number and position of subsequent floral organs. This may mean that pre-patterning of petal, stamen and carpel positions takes place before pre-patterning of sepal positions in early flower development.

Our data show that the corolla tube appears quite early in the flower development of *P. alpina* and *P. vulgaris*. This mode of petal fusion resembles the 'early' sympetaly as defined by Erbar (1991). The occurrence of 'early' vs. 'late' sympetaly is considered to be of phylogenetic significance (Leins & Erbar 1997, 2010; Erbar & Leins 2011). Most families of the order Lamiales are characterized by 'late' sympetaly. Therefore, our observation of 'early' sympetaly in *Pinguicula* is important. Erbar (1991) reported 'early' sympetaly, together with an intermediate type, for members of the family Acanthaceae. Interestingly, Acanthaceae might be the closest phylogenetic relatives of Lentibulariaceae (Soltis et al. 2011,

though bootstrap support <50%). Also, Schönenberger and Endress (1998) did not find 'early' sympetaly in the members of Acanthaceae they examined.

An interesting feature of flower development in *Pinguicula* is relatively late corolla initiation. At least in *P. vulgaris*, the corolla is initiated after the androecium. As in flowers of other members of Lamiales bearing two stamens (*Veronica*: Erbar 1991; *Heliohebe*: Bello et al. 2004; Calceolariaceae: Mayr and Weber 2006), stamen primordia are massive in *Pinguicula*. Small rudiments of two posterior stamens reported for young flowers of *P. vulgaris* (Dickson 1869) are missing in *P. alpina* and probably in *P. moranensis* (Grob et al. 2007). In our material of *P. vulgaris*, only one flower with staminodes was found.

Inflorescence structure and flower symmetry

Our data on flower arrangement in *P. alpina* and *P. vulgaris* fully agree with the hypothesis that the perennial shoot systems in *Pinguicula* are sympodial, and flowers form a terminal inflorescence represented by a sessile umbel, which is often reduced to a single flower (Wydler 1857; Dickson 1869; Eichler 1875; Troll 1964; Brunaud and Turlier 1971; Fischer et al. 2004).

After a careful morphological analysis of *P. alpina* and *P. vulgaris*, all the variants of inflorescence structure can be arranged in a morphological series from a terminal many-flowered umbel to a terminal one-flowered umbel. This morphological series can be seen at the level of infraspecific variation. Although the flowers in the one-flowered umbels of *P. vulgaris* and *P. alpina* look terminal, the existence of this morphological series indicates their pseudoterminal position.

According to the interpretation of Grob et al. (2007), the flower position is terminal in *P. moranensis*, though all other details of shoot morphology are closely similar to what is described here for *P. alpina* and *P. vulgaris*. The interpretations for *P. moranensis* and other species differ in the character called axiality (Notov and Kusnetzova 2004). Plants of *P. moranensis* are described as monoaxial (the first order axis is terminated by a flower), while the plants of *P. alpina* and *P. vulgaris* are biaxial. Axiality is generally a stable taxonomic character in angiosperms (reviewed in Notov and Kusnetzova 2004), and it is unlikely that this parameter varies among species of *Pinguicula*. We believe that flower position in *P. moranensis* fully corresponds to that in one-flowered umbels of *P. vulgaris* and *P. alpina*, though the flower-subtending bract is normally reduced in *P. moranensis* (Fig. 10). Besides, Grob et al. (2007) rarely observed a scale at the base of a floral scape in *P. moranensis* and interpreted it as the very last leaf on the main axis, which is formed before of the development of the terminal flower. In our view, the structure and position of this scale

correspond to the reduced flower-subtending bracts that we documented in *P. alpina*.

We assume that flowers in *P. moranensis* occupy a pseudoterminal rather than purely terminal position. If so, *P. moranensis* has a reduced one-flowered umbel, representing the final stage of a morphological series illustrating the progressive reduction of inflorescence. The closest relatives of *Pinguicula*, *Genlisea* and *Utricularia*, possess open racemes, which could be positioned at the beginning of this morphological series.

The question on flower position in *P. moranensis* (terminal vs. pseudoterminal) allows discussing a broader topic on a correlation between patterns of flower symmetry and patterns of flower arrangement in angiosperms. It is well known that sporadically occurring terminal flowers or flower-like structures in racemose inflorescences are either polysymmetric or asymmetric due to their unstable morphology, even in species where lateral flowers are pronouncedly monosymmetric (e.g., Rudall and Bateman 2003; Bull-Hereñu and Claßen-Bockhoff 2011). We speculate that this phenomenon represents a manifestation of a more general rule: in angiosperms, stable monosymmetry takes place only in lateral flowers bearing not more than two phyllomes (prophylls or bracteoles) on their pedicels (or rarely up to three phyllomes: Weber 2004). For example, flowers of a raceme or a thyrse can all be uniformly monosymmetric, whereas flowers of botryoids, thyrsoids and panicles cannot be uniformly monosymmetric across an inflorescence (inflorescence terminology after Endress 2010). We do not know examples of angiosperm species with stable monosymmetry of clearly terminal flowers on shoots bearing more than three phyllomes. As a conclusion, the presence of a terminal flower in *P. moranensis* is unlikely because the flower is monosymmetric. We hypothesize the occurrence of a cryptic flower-subtending bract in those cases when we do not see any visible traces of a phyllome associated with a flower in *Pinguicula*.

Endress (1999) assumed the presence of two developmental gradients responsible for monosymmetry expressed in early flower development in angiosperms: (1) the suppressing gradient of the main shoot and (2) the suppressing gradient of the subtending bract. In the case of pseudoterminal flowers of *Pinguicula*, the main shoot is not developed above the flower primordium, and the flower-subtending bract is highly reduced. One could think this will result in a loss of the abaxial-adaxial gradient and a loss of the monosymmetric nature of the flower. However, this is not the case. Though often not visible externally throughout the flower development, the presence of a (cryptic) flower-subtending bract must have an important morphogenetic effect in all *Pinguicula* species. This hypothesis can be tested in the future by studies of gene expression patterns.

Among the members of Lamiales, the families Oleaceae and Tetrachondraceae share the occurrence of polysymmetric (or disymmetric) flowers and paniculate inflorescences, in which lateral flowers can be preceded by more than two phyllomes (Sehr 2005; see also Troll 1969; Endress 2010). These families occupy a basal position in the molecular phylogenetic trees of Lamiales (e.g., Soltis et al. 2011). It is possible that polysymmetric flowers are plesiomorphic in Oleaceae and Tetrachondraceae, and monosymmetric flowers likely represent a synapomorphy of a large clade within Lamiales that does not include these families, with a number of subsequent reversals (e.g., Donoghue et al. 1998). It is tempting to propose that an evolutionary shift to monosymmetric flowers was associated with a transformation of paniculate inflorescences to thyrses and racemose inflorescences in Lamiales.

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