

Leaf vasculature in four species of *Caputia* B. Nord. & Pelser (Asteraceae, Senecioneae)

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Summary: The investigated species of *Caputia* are leaf-succulent plants. Various leaf types are inherent in these species, namely typical flat (*C. medley-woodii*, *C. scaposa*), terete fusiform (*C. tomentosa*) and terete cylindrical (*C. pyramidata*, *C. scaposa*). The fusiform leaves are morphologically and anatomically very similar to the unifacial leaves which were previously specified for a few species of Senecioneae. However, the arrangement of the main bundles revealed in the leaves under consideration clearly shows that they should all be considered bifacial. The terete leaves are concluded to have evolved from the typical flat, bifacial leaves similar to those in *C. medley-woodii*. Our conclusion is in a good agreement with the molecular-based phylogeny of *Caputia* published elsewhere and the succession of the different leaf types on the developing shoot of *C. scaposa*. The terete leaves evolved by means of arresting marginal growth and increasing thickening growth, the latter having been mostly adaxial in *C. tomentosa* and abaxial in *C. pyramidata*. The origin of the terete leaves is associated with the emergence of the system of peripheral bundles which are circle-arranged. This circle of bundles is continuous in *C. tomentosa* and *C. scaposa* and abaxially discontinuous in *C. pyramidata*. The circle-arranged peripheral bundles mask the bifacial structure of leaf vasculature. The terete leaves of *Caputia* should be attributed to the new ‘cryptic bifacial’ anatomical type of leaves to stress their specificity.

Keywords: plant anatomy, leaf vasculature, unifacial leaf, bifacial leaf, cryptic bifacial leaf, terete leaf, *Caputia*, Asteraceae

Species of the genus *Caputia* had been placed among succulent members of the immense and extremely heterogeneous genus *Senecio* L. for a long time (BREMER 1994) and only in 2012, they were placed into a separated genus *Caputia* B. Nord. & Pelser (NORDENSTAM & PELSER 2012). These species are nested in the basal clade *Senecio medley-woodii*–*Brachyglottis* of the subtribe Senecioninae (PELSER et al. 2007) that is rather distant from both *Senecio* s. str. and other succulent groundsels (TIMONIN et al. 2015), including the members of *Curio* P.V. Heath. At the same time, the species of *Caputia* demonstrate astonishing external similarity with the species of *Curio* in terms of leaf morphology. In the genus *Curio*, the bifacial leaves evolved to subunifacial and unifacial terete leaves (TIMONIN & OZEROVA 1993). Similar leaf evolution could be anticipated in the genus *Caputia*. Unifacial leaves are known to have a characteristic vasculature (TROLL 1939; KAUSSMANN 1963; NAPP-ZINN 1973). The vasculature of leaves of *Caputia* species is still underexplored. Therefore, we anatomically examined leaves of *Caputia medley-woodii* (Hutch.) B. Nord. & Pelser, *Caputia tomentosa* (Haw.) B. Nord. & Pelser, *Caputia pyramidata* (DC.) B. Nord. & Pelser and *Caputia scaposa* (DC.) B. Nord. & Pelser to test our assumption.

Materials and methods

Leaves and shoots of the examined species were collected from living plants grown in the greenhouse of Tsitsin Main Botanical Garden of Russian Academy of Sciences, Moscow, and fixed and stored in 70% ethanol.

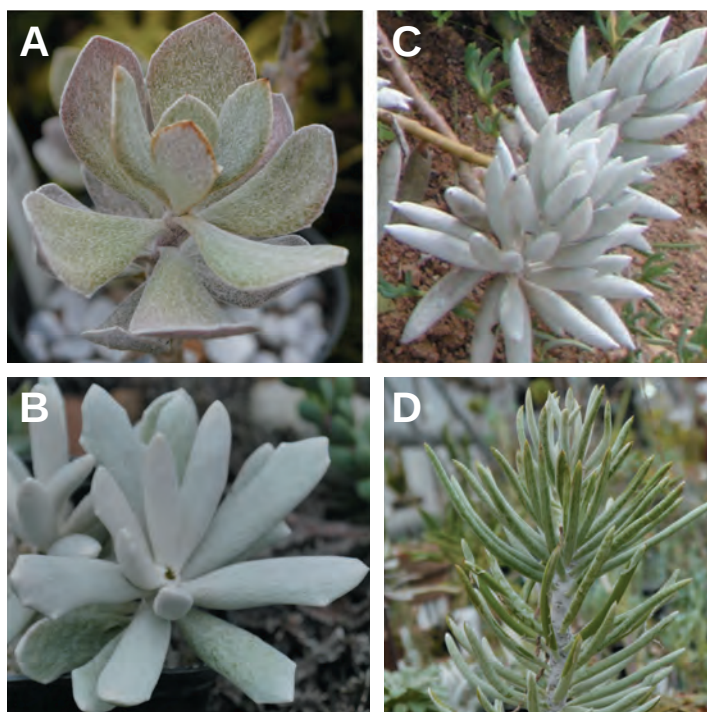


Figure 1. Investigated species. A – *Caputia medley-woodii*; B – *C. tomentosa* with oblanceolate leaves; C – *C. tomentosa* with fusiform leaves; D – *C. pyramidata*.

Serial transverse hand-razor sections were treated with 0.5% alcoholic phloroglucinol and concentrated hydrochloric acid and embedded in glycerin on slides according to BARYKINA et al. (2004). The leaves of *Caputia medley-woodii* were made translucent by processing the total leaf with phloroglucinol and hydrochloric acid. The preparations were analysed under the light microscope. Photographs were taken via light microscope (LM) Nikon eclipse Ci equipped with digital camera Nikon digital sight DS-Vi1. 3D models of leaf vasculature were constructed using Blender 2.8 (Blender Foundation, Amsterdam, Netherlands) on the base of serial leaf cross-sections.

Voucher specimens were deposited at Syreischikov Herbarium of Lomonosov Moscow State University [MW]: MW 0975 108 (*C. medley-woodii*), MW 0975 109 (*C. tomentosa*), MW 0975 110 (*C. pyramidata*) and MW 0975 111 (*C. scaposa*).

Results

Caputia medley-woodii has fleshy, subpetiolate, obovate leaves (Fig. 1A). The petiole is adaxially flattened and abaxially convex (Fig. 2C), both lamina sides are flattened (Fig. 2D).

The petiole vasculature consists of five main bundles (Figs 2C; 3A): the median (*m*) and two pairs of lateral ones, (*l1* and *l2*) respectively. The median and inner lateral bundles *l1* regularly branch off minor bundles, which branch further on and anastomose each other to form a plexus. Minor bundles are in a plane somewhat displaced towards the adaxial side in relation to the main bundles (Fig. 2D). The number of the minor bundles is highly changeable and varies with the leaf blade width. The outer lateral bundles *l2* continue through the petiole and merge with a marginal plexus of minor bundles in the petiole-lamina transition zone (Fig. 2B). Anastomosing

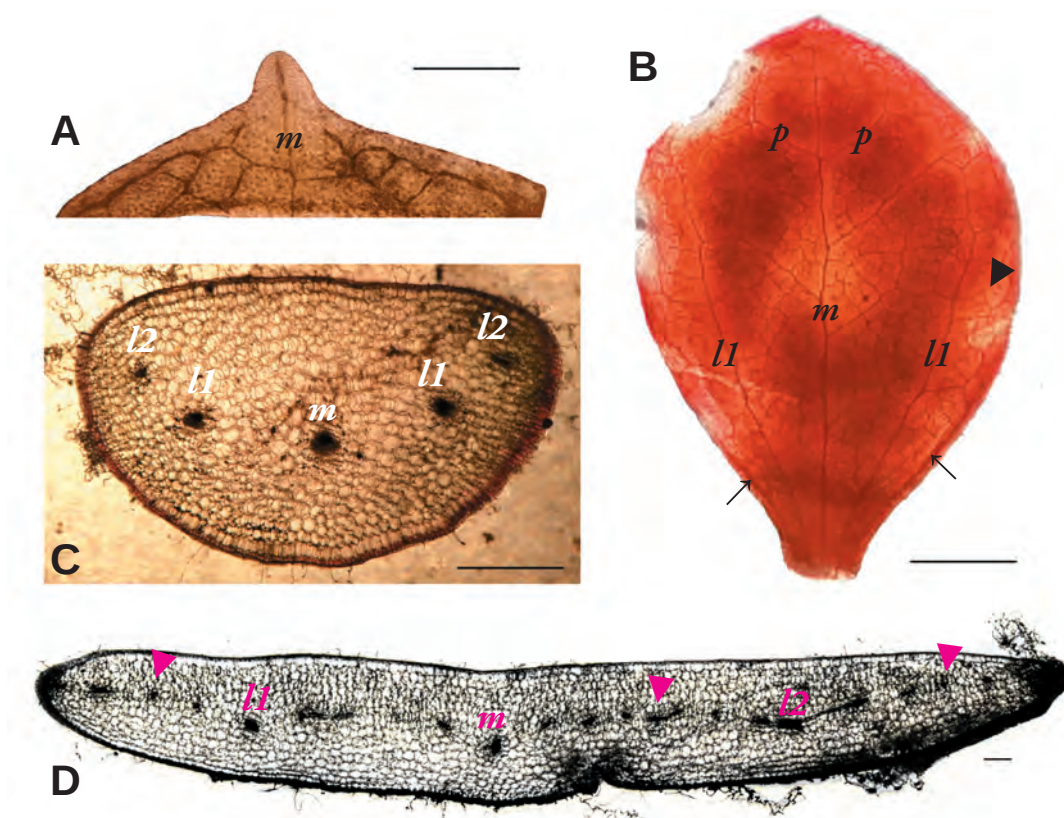


Figure 2. Leaf of *C. medley-woodii*. A – lamina tip; B – leaf venation; C – petiole, cross section; D – lamina, cross section. *l1* – inner lateral bundle; *l2* – outer lateral bundle; *m* – median bundle; *p* – pectinal bundle; arrow – outer lateral bundle; arrow head – vascular plexus. Scale bars = 0.25 cm (A); 1 cm (B); 0.1 cm (C, D).

of bundles prevail over branching off minor bundles in the distal half of the lamina. All minor bundles gradually integrate towards the leaf tip to fuse with the lateral main bundles, the latter integrate with the median bundle. This bundle is observable to the very tip of the leaf, where it terminates blindly (Figs 2A; 3B).

The median bundle gives rise to a pair of the pectinal bundles (*p*) *sensu* SPICER (1986) in the distal third of the lamina (Fig. 2B). These bundles arc acropetally to fuse with the terminal plexus of minor bundles and disappear there. Both inner lateral bundles *l1* run practically $\frac{3}{4}$ of the leaf blade, where they arc acropetally and merge with the pectinal bundles.

Caputia tomentosa has thick leaves, which are different in typical plants and cultivars. The former have terete fusiform leaves (Fig. 1C), whereas the latter have subpetiolate oblanceolate (Fig. 1B) ones. The leaf base is acroscopically concave and basiscopically convex in both types (Fig. 4A). The leaf blade of oblanceolate leaves is 0–4-toothed, sometimes asymmetrical (Fig. 1B). It is semicircular to cordate in cross section with a slightly convex to furrowed acroscopic side (Fig. 4C). The fusiform leaves are circular in cross section (Fig. 4D, E); the acroscopic furrow is sometimes absent. The leaf tip is dorsiventrally flattened in both leaf morphological types (Fig. 4B).

The vasculature is identical in both morphological types. The leaf is supplied by three bundles, the median (*m*) and two lateral ones (*l*) (Figs 3C, E; 4A). The xylem of these bundles

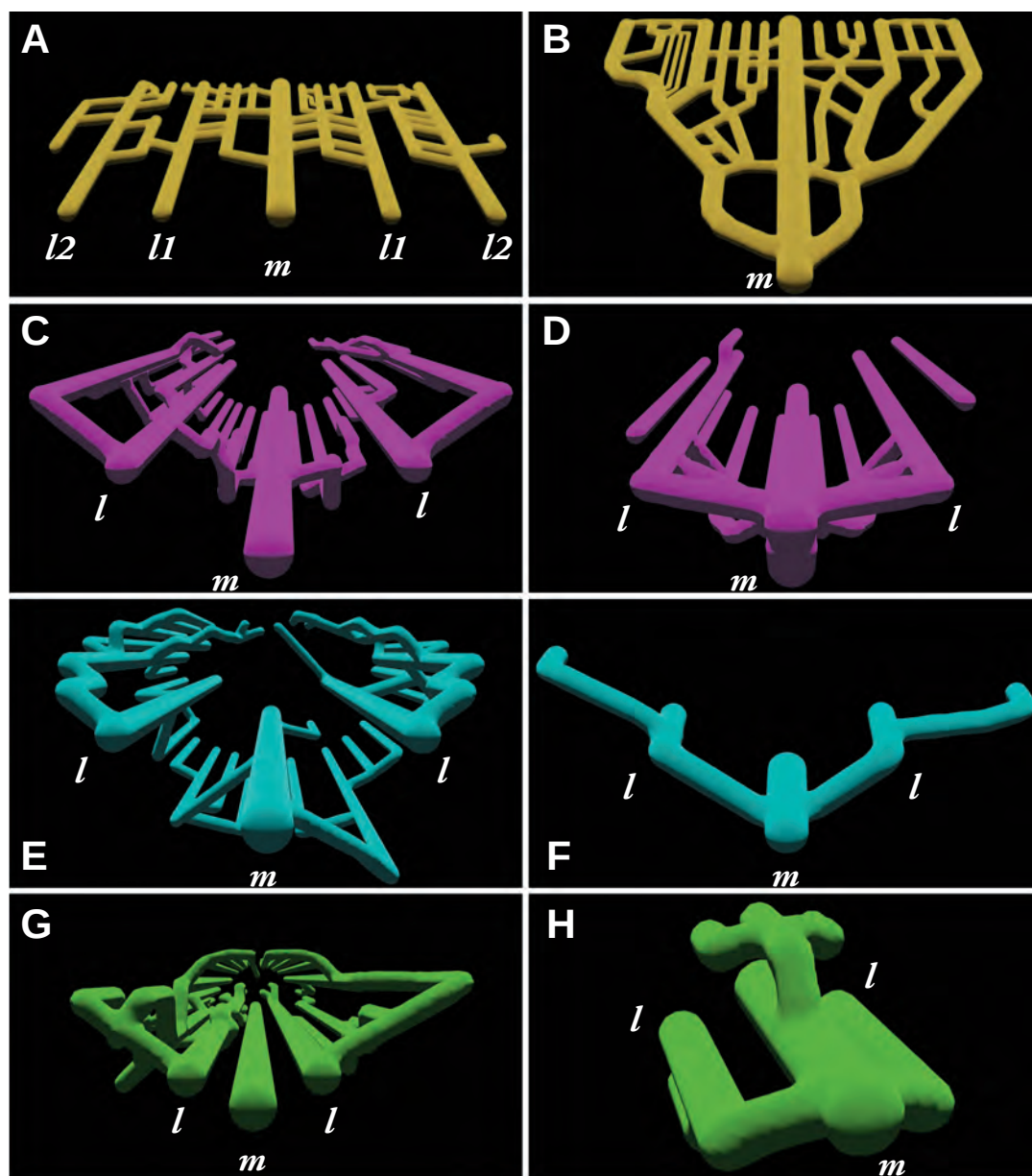


Figure 3. 3D reconstructions of leaf vasculature. A, B – *C. medley-woodii*; C, D – *C. tomentosa*, oblanceolate leaf; E, F – *C. tomentosa*, fusiform leaf; G, H – *C. pyramidata*. A, C, E, G – basal parts viewed from the node; B, D, F, H – the distalmost parts viewed from the tip. *l* – lateral bundle; *l1* – inner lateral bundle; *l2* – outer lateral bundle; *m* – median bundle.

the acroscopic side and their phloem faces the basiscopic side. Disposition of these bundles is V-shaped in cross-section (Figs 3C, E; 4C–E). These bundles run through the leaf as its main bundles up to the very tip, where they merge into one bundle (Figs 3D, F; 4F). From the second quarter of leaf, these bundles irregularly branch off smaller bundles (Fig. 4D, E). The median bundle derivatives mostly run to the basiscopic side, but few run laterally. Most of lateral bundle derivatives run laterally and a few ones run to the acroscopic or basiscopic side of leaf. Toward the leaf tip, the derivatives of main bundles rearrange to an acroscopically discontinuous circle

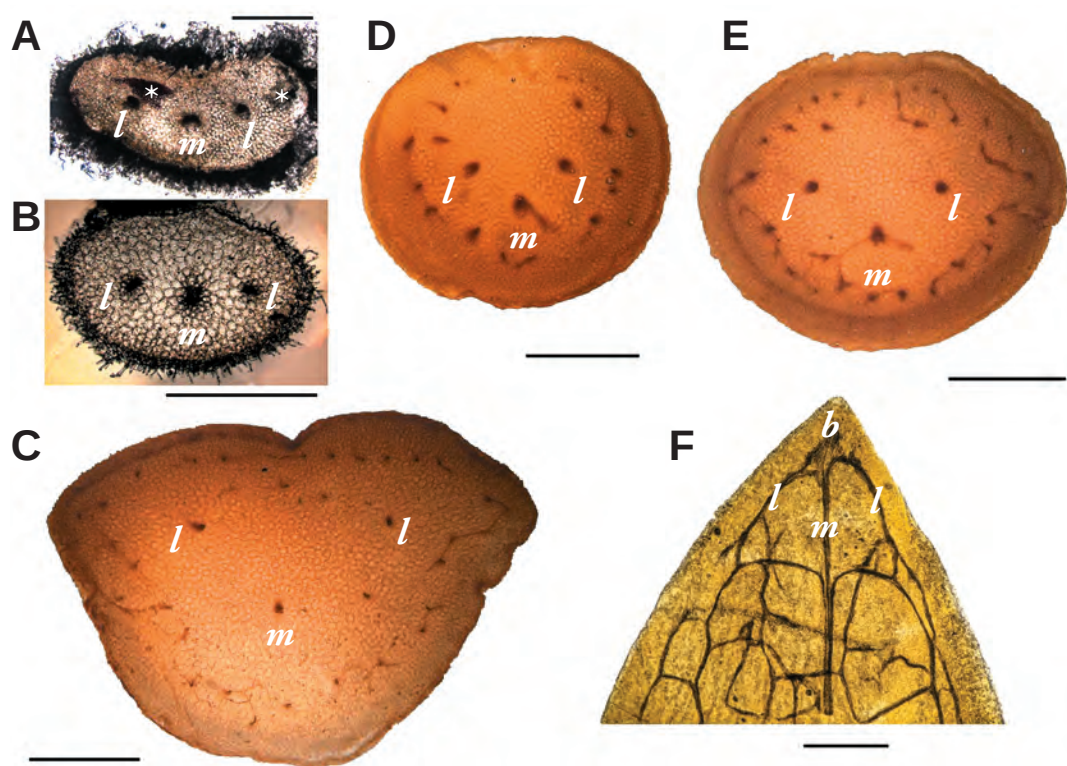


Figure 4. Leaf of *C. tomentosa*. A – petiole; B, F – lamina tip; C – lamina of oblanceolate leaf; D, E – lamina of fusiform leaf; A–E – cross sections; F – translucent. *b* – body of barrel tracheids; *l* – lateral bundle; *m* – median bundle; *asterisk* – sclerified parenchyma. Scale bars = 0.1 cm.

(Fig. 4D) and further on to continuous one (Fig. 4C, E). These bundles constitute a loose vascular plexus. Thus, the leaf vasculature consists of three inner main bundles and a peripheral vascular plexus. At the very tip, the bundles of plexus merge the main bundles. The body of barrel tracheids (*b*) terminates three main bundles (Fig. 4F).

Caputia pyramidata has long, terete, cylindrical leaves (Fig. 1D) with a very short basal part indistinctly delimited from a long, terete, distal part. The basal part is acroscopically flattened and basiscopically convex (Fig. 5A); the distal part is circular in cross section, with a deep narrow, basiscopic furrow (Fig. 5C).

Vasculature of the basal part consists of the median (*m*) and two lateral bundles (*l*) which are arranged in nearly one plane and have typically arranged tissues (Figs 3G; 5A). These bundles continue into the distal part as its three main bundles (Fig. 5B). The median bundle runs unchanged up to the leaf tip (Fig. 5D). The lateral bundles shift basiscopically (Fig. 5A–C) and turn exoscopic sensu MELO-DE-PINNA et al. (2014). They fuse with the main bundles in the leaf tip (Fig. 5E). The lateral bundles (*l*) irregularly branch off peripheral bundles, which run mostly laterally and toward the basiscopic side. Thus, a discontinuous $\cap$ -shaped disposition of the peripheral bundles in cross-section forms at the middle of lamina (Figs 3G; 5B). Further on to the leaf tip, some most peripheral branches run outward to the acroscopic side (Fig. 5B).

Resultantly, $\cap$ -shaped disposition of the peripheral bundles in cross-section turns into an Ω -shaped one in a distal part of the leaf blade (Fig. 5C). Most peripheral bundles are exoscopic,

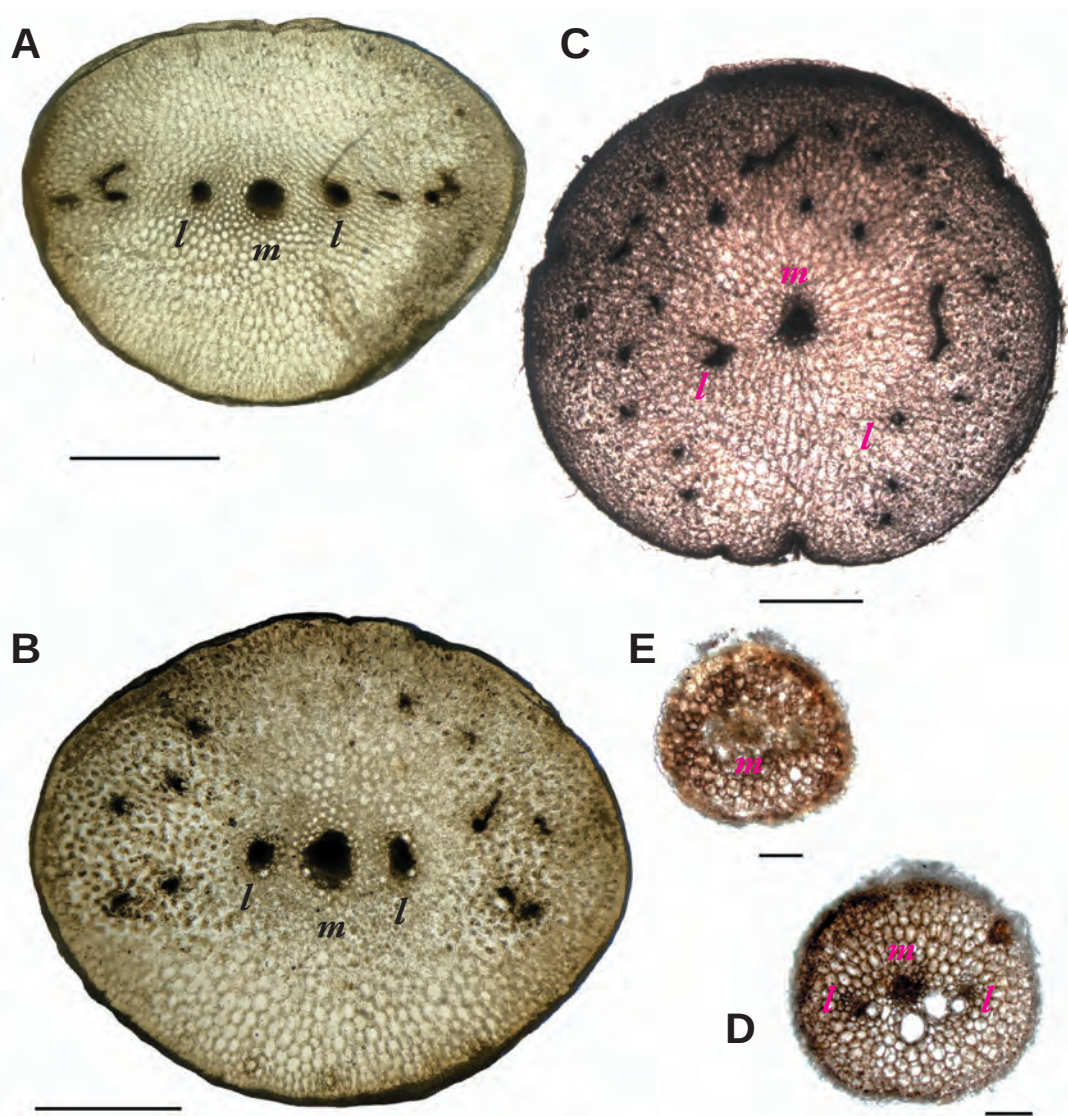


Figure 5. Leaf of *C. pyramidata*, cross sections. A – petiole; B – petiole-lamina transitional zone; C – lamina; D, E – lamina tip. *l* – lateral bundle; *m* – median bundle. Scale bars = 0.1 cm (A–C), 0.02 cm (D, E).

but few of them show an unstable arrangement of their xylem and phloem. The peripheral bundles gradually fuse with each other and with lateral bundles, the latter merging with the median bundle in the leaf tip (Figs 3H; 5E).

Caputia scaposa (Fig. 6A) has thick leaves of three morphological types, which form a regular sequence in each annual shoot (Fig. 6B). The basal leaves of the annual shoot are the shortest ones. They are thick and oblanceolate. The middle leaves of the annual shoot are in average twice longer and terete. The distal leaves of the annual shoot differ from middle ones by flattened tip.

Leaves of all three types are not differentiated into petiole and lamina. All three morphological leaf types have an oval leaf base in cross-section (Fig. 7A). The vasculature of the three morphological types is basically similar. Five bundles, namely, the median (*m*) and two pairs of laterals (*l1* and *l2*), supply the leaves (Figs 7A; 8A, C). In the basal leaves, these five main bundles run through



Figure 6. Appearance (A) and leaf series (B) of *C. scaposa*. arrow – flattened tip.

the whole leaf up to the very tip (Fig. 8B). The xylem of these bundles is directed acroscopically and their phloem is directed to the basiscopic side. The main bundles are located in one plane equidistant from both leaf sides in the lamina basal third (Fig. 7A), further to the leaf tip these bundles shift to the basiscopic side (Fig. 7B). In the leaf tip (Fig. 7C, D), five main bundles gradually merge with each other to the single median bundle, which terminates blindly (Fig. 8B).

In the basal part of the leaf, the outer lateral bundles (*l2*) branch off smaller bundles (Fig. 7E). Derivatives of *l2* branch off further on and form a vascular plexus, which gradually fills the acroscopic side of the lamina (Figs 7F; 8A). A few bundles branch off from *l1* and *m* (Fig. 7B). These bundles deviate towards the basiscopic side (Fig. 7F). The vascular plexus is most developed on the third quarter of the lamina (Fig. 7G). In the distal part of the leaf, most of the plexus bundles gradually merge each other and the main bundles, a few terminate blindly.

Only three of five bundles, *viz.* median (*m*) and inner laterals (*l1*) continue unchanged to the leaf tip in two other leaf morphological types (Fig. 8D). The outer lateral bundles disintegrate into a plexus of peripheral bundles at the basal part of the leaves (Fig. 7H). Plexus gradually fills the acroscopic side. There are anastomoses between the peripheral vascular plexus and inner lateral bundles (Fig. 7I). A few median bundle derivatives contribute to the basiscopic part of the vascular plexus (Fig. 7I).

Discussion

The leaves of *C. medley-woodii* are undoubtedly bifacial as evidenced by its distinct margins and characteristic pattern of its vasculature. The main bundles are in one plane and the minor bundles are a little bit displaced adaxially. The conductive tissues are arranged typically in all leaf bundles.

The basal leaves of *C. scaposa* are also certainly bifacial and very similar to those of *C. medley-woodii* in distinct margins and vasculature pattern, but the minor bundles are more displaced adaxially.

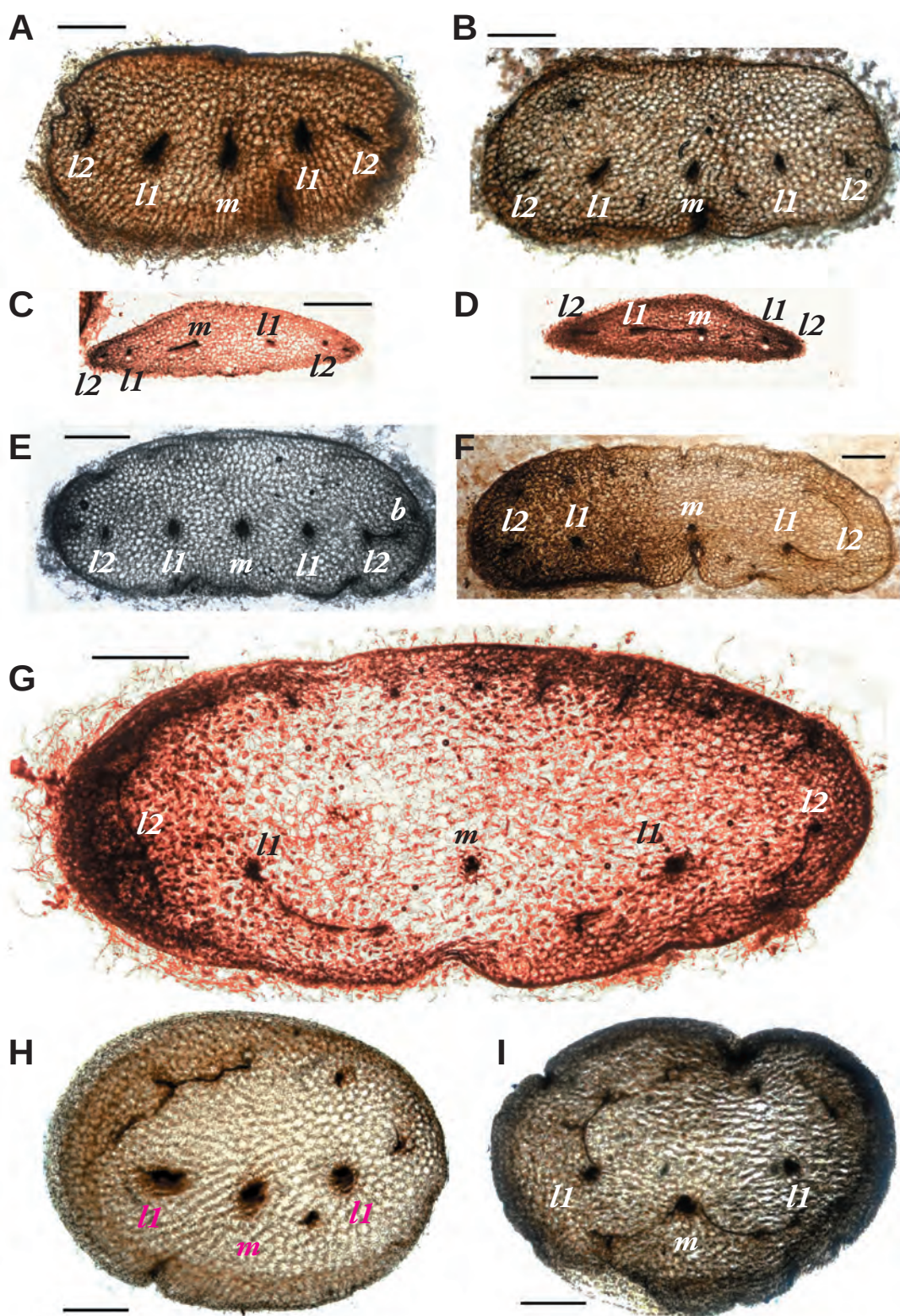


Figure 7. Leaf of *C. scaposa*, cross sections. A – basal part of a leaf; B, E, F, G – lamina of basal leaf; H, I – lamina of intermediate/distal leaf; C, D – lamina tip. *b* – branching of *l2* bundle; *l1* – inner lateral bundle; *l2* – outer lateral bundle; *m* – median bundle. Scale bars = 0.1 cm.

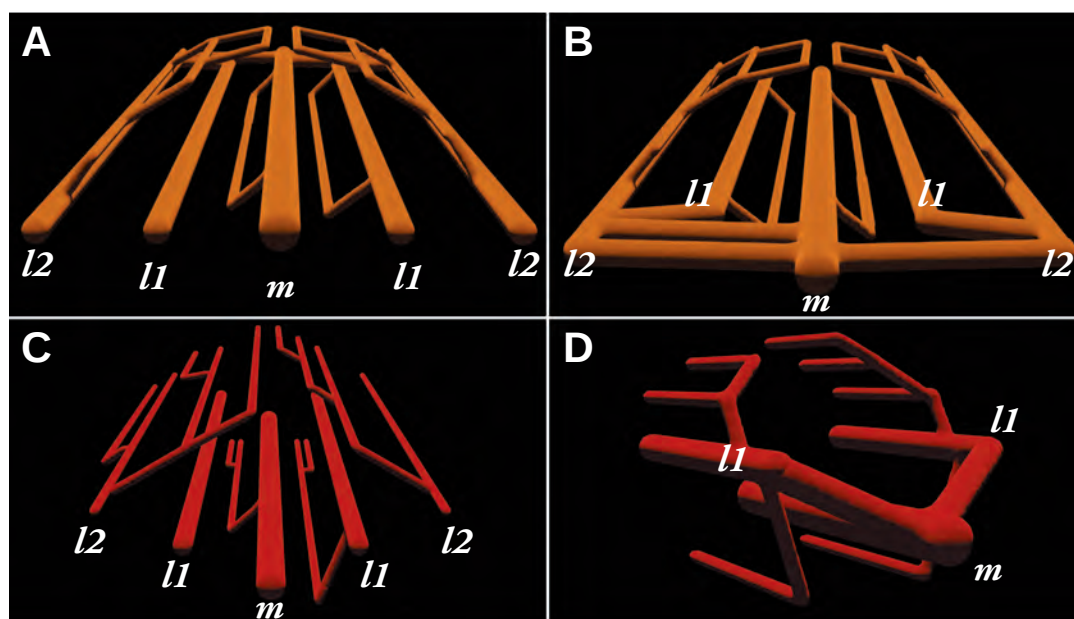


Figure 8. 3D reconstructions of leaf vasculature of *C. scaposa*. A, B – basal leaf; C, D – intermediate/distal leaf; A, C – basal parts viewed from the node; B, D – the distalmost parts viewed from the tip. *l1* – inner lateral bundle; *l2* – outer lateral bundle; *m* – median bundle.

The oblanceolate leaves of *C. tomentosa* also have distinct margins. Their vasculature is rather specific being differentiated into two subsystems of main and peripheral bundles. The main bundles are V-shaped arranged in the leaf cross-section. Their xylem is always oriented to the acroscopic side of the leaf and phloem is oriented to the basiscopic one. This arrangement of the conductive tissues is typical of a bifacial leaf (NAPP-ZINN 1973). Peripheral bundles are arranged circularly. Most of them have a xylem facing the acroscopic side of the leaf, but a few have a xylem oriented basiscopically. Thus, the arrangement of conductive tissues in peripheral bundles drastically differs from genuine unifacial leaf (NAPP-ZINN l. c.). Therefore, the anatomy of the oblanceolate leaf of *C. tomentosa* fits more the criteria of the bifacial leaf (TROLL 1939; NAPP-ZINN 1973).

The terete leaves (middle and distal leaves in *C. scaposa*, fusiform in *C. tomentosa*, cylindrical in *C. pyramidata*) differ from the above-mentioned leaves in their indiscernible margins. They look like unifacial leaves. Indeed, the terete leaves are usually unifacial or inverse unifacial (TROLL 1939; NAPP-ZINN 1973). Unifacial leaves have only the abaxial side and no primary margins and circularly arranged endoscopic bundles (TROLL l. c.; NAPP-ZINN l. c.). Inverse unifacial leaves have only the adaxial side and no primary margins and circularly arranged exoscopic bundles (NAPP-ZINN 1973).

The vasculature of *Caputia* terete leaves differs from both genuine unifacial and inverse unifacial leaves. Vasculature of *C. tomentosa* fusiform leaves and both middle and distal *C. scaposa* leaves seems to be identical. It consists of three main bundles and a circular plexus of peripheral bundles. Orientation of conductive tissues in both main and peripheral bundles is similar to that in oblanceolate leaves of *C. tomentosa*. Main bundles arrangement is V-shaped in cross-section. The specificity of *C. pyramidata* leaves is that their arrangement of main bundles is Λ -shaped in cross-section. Other traits such as general vasculature organisation and arrangement of conductive

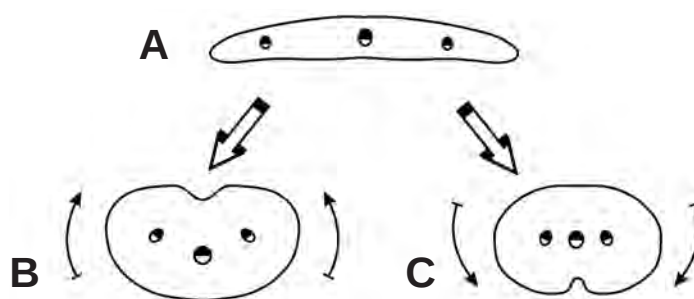


Figure 9. Presumable evolution of leaves in the genus *Caputia*. A – *C. medley-woodii* type; B – *C. tomentosa* type; C – *C. pyramidata* type.

tissues are similar to other terete leaves mentioned above. Thus, the vasculature of *Caputia* terete leaves is more similar to oblanceolate bifacial *C. tomentosa* leaves than to both unifacial and inverse unifacial leaves. But they have indiscernible margins and thus are not distinctly bifacial either. Therefore, these leaves are worth being considered ‘cryptic bifacial’.

GUÉDÈS (1979) considered terete leaves to be phyllodia. The terete leaves of *Caputia* species consist of two radically different parts in their vasculature. Only the much shorter basal part is nearly identical to the genuine petiole of *C. medley-woodii* in its oval cross-section and vasculature pattern. Therefore, this leaf part should be attributed to the petiole of these terete leaves. Consequently, the much longer distal part is worth being considered as leaf blade.

The leaf of *C. medley-woodii* seems to be the least altered, because this species is nested as early divergent clade in the *Caputia* cladogram (PELSER et al. 2007; OZEROVA et al. 2017). We recognised it close to the ancestral type (Fig. 9A). The leaf vasculature tends to become 3-dimensional, as the minor veins are slightly displaced toward the adaxial side. Such a 3D arrangement of the vascular bundles is reported to be typical of succulent leaves (GRIFFITHS 2013; MELO-DEPINNA et al. 2014, 2016).

The basal leaves of *C. scaposa* are thicker and narrower than the leaves of *C. medley-woodii*. Main bundles are further displaced acroscopically. That is why we believe the concerned leaves could have evolved via a light narrowing and acroscopical thickening of ancestral *C. medley-woodii*-like leaves.

The oblanceolate leaves of *C. tomentosa* could have evolved from the ancestral ones via narrowing and thickening of their laminae, too. The lamina thickening seems to have dramatically affected the leaf vasculature to cause its differentiation into the inner main bundles and peripheral bundles. The latter are likely to have displaced outward to form the vascular plexus near the lamina surface for efficient supplying of the most active peripheral chlorenchyma. The adaxial thickening of the lamina should have prevailed, because the most peripheral bundles are above the main ones. However, rather many peripheral bundles are below the main ones, thus indicating the abaxial thickening of the lamina. The main bundles should have altered their original flat arrangement into the V-shaped one. We believe that some previous folding of the lamina towards the adaxial side (involution) (Fig. 9B) could cause this alteration. The occasional furrow on the adaxial side of the oblanceolate leaves confirms this hypothesis. Progressive narrowing and thickening of the lamina should have resulted in the loss of discernible margins and in the origin of the terete leaves. Such leaves are usually thought to be formed only by the ‘Rundungsmeristem’, which maintains

adaxial thickening of the leaf (BÜNNING & GÄUMANN 1956). This is not the case with the terete leaves concerned, however.

The terete leaves of *C. tomentosa* have the same vascular pattern as its oblanceolate leaves. Therefore, arrested marginal growth, prevailing acroscopic thickening – all must have been accompanied by some acroscopic folding of the lamina to evolve the terete leaf in this species.

We believe that similar changes could have happened in the evolution of *C. scaposa*'s both middle and distal leaves.

Flat arrangement of the main bundles makes acroscopic folding of the lamina unlikely in evolving terete leaves of *C. pyramidata*. Such leaves would be improperly considered a result of the typical 'Rundungsmeristem' activity, because most of their peripheral bundles are below the main ones and Ω -arranged in leaf cross-section. The Ω -arrangement of the vascular bundles rather indicates the abaxial thickening and adaxialisation of the leaf (i.e. reduction of its abaxial portion) (Fig. 9C) quite contrary to the leaf abaxialisation caused by the rounding meristem.

Leaf adaxialisation is a very rare deviation, which usually affects only the petiole of hypopeltate/hypoascidiate leaves¹ (FRANK 1976; DUPUY & GUÉDÈS 1979; UNNIKRISSNAN & HEMA 1990; MCCONNELL & BARTON 1998; FUKUSHIMA & HASEBE 2013). However, the structure of the adaxialised leaf of *Caputia pyramidata* does not indicate any reasons to consider it as a petiole of hypopeltate/hypoascidiate leaf.

The adaxialised leaves of *C. pyramidata* are anatomically similar to the adaxialised leaves of *Calycadenia truncata* DC. (Asteraceae), *Austrocylindropuntia subulata* (Muehl.) Backeb., *Opuntia ficus-indica* (L.) Mill. and *Maihuenia* spp. (all Cactaceae), which also cannot be credited as the petioles of the hypopeltate/hypoascidiate leaves. DUPUY & GUÉDÈS (1979) regarded those leaves as congenitally merged hypoascidiate laminae. However, the basiscopic sector of the terete leaves of *A. subulata* is not vascularised and differs from the rest of the leaf in mesophyll structure (BAILEY 1968; OZEROVA & TIMONIN 2020). Therefore, this basiscopic sector should not be considered the basiscopic portion of the ascidiate lamina, which is congenitally merged with its acroscopic portion. There is one more reason to regard this sector as a genuine abaxial portion of the epeltate (sub)terete leaf. The terete leaves of Cactaceae members certainly became adaxialised by means of narrowing of their abaxial side up to its complete disappearance (BAILEY 1968). However, such a narrowing of the abaxial portion of the lamina is consistent neither with the presence of an abaxial longitudinal furrow nor with Ω -arranged vascular bundles in the leaves of *Caputia pyramidata*.

As to the adaxialised leaves of *Calycadenia truncata*, CARLQUIST (1959) interpreted them as an acme of evolutionary out-rolling of the margins of epeltate leaf (lamina revolution), whose preceding stages are observable in leaves of *Calycadenia multiglandulosa* DC. Evolutionary outrolling of the leaf margins in *Caputia pyramidata*, if admitted, would be quite consistent with their abaxial longitudinal furrow, but not with the Ω -arrangement of their vascular bundles.

Some revolution of the lamina could have taken place in the evolution of terete leaves in *Caputia pyramidata* (Fig. 9C), but this process must have been supplemented by the basiscopic thickening in two separate submarginal sites.

¹ The model mutations commonly explored cause partial or complete adaxialisation of the abaxial epidermis and leave the mesophyll and vasculature unaffected (JUAREZ et al. 2004; HIBARA et al. 2009). These mutants' leaves are obviously incompatible with the concerned adaxialised leaves of *C. pyramidata*.

Thus, *C. medley-woodii* seems to have retained the least altered or ancestral leaves of the genus *Caputia*. The terete leaves of *C. pyramidata* and *C. tomentosa* are of specific cryptic bifacial type. However, they differ in a set of traits and therefore represent two different evolutionary lines (Fig. 9).

Caputia scaposa strikingly differs from other *Caputia* species in its leaf polymorphism. Both middle and distal leaves are quite comparable to *C. tomentosa* fusiform leaves, whereas the basal *C. scaposa* leaves seem to be a transitional type between flat *C. medley-woodii* leaves and clearly thickened *C. tomentosa* oblanceolate leaves. However, molecular phylogenetics shows this species to be the most advanced in *Caputia* (OZEROVA et al. 2017). Therefore, these basal leaves are conceivable to be an evolutionary reversion. If so, these leaves would have three main bundles like the terete leaves of the investigated species. But they are supplied by five main bundles just as presumable ancestral leaves of *Caputia*. Such a complete reversion seems unlikely. Moreover, basal leaves antecede the terete ones on the annual shoot. The antecedent structures are often believed to be ancestral according to Haeckel's 'biogenetic law' (HAECKEL 1866; NELSON 1978; OLSSON et al. 2017). Accordingly, the basal leaves of *C. scaposa* are worth being considered as ancestral rather than derivative. Leaf polymorphism in *C. scaposa* thus shows heterobathmy *sensu* TAKHTAJAN (1959).

Conclusion

The initial leaf type in the genus *Caputia* was probably a slightly thickened typical bifacial leaf similar to the leaves of extant *C. medley-woodii*. Evolutionary suppression of marginal growth and increase of leaf thickness resulted in the appearance of terete, cryptic bifacial leaves very similar to the unifacial leaves of other Senecioneae. The terete leaves of *C. tomentosa* have evolved through acroscopic thickening and involution of the lamina. Those of *C. pyramidata* appeared as the result of basiscopic thickening and revolution of the lamina.

Assumed evolution of leaves in these *Caputia* species are in agreement with results of published molecular phylogeny of this genus. *C. scaposa* has dimorphic leaves sequentially developing on an annual shoot. The basal oblanceolate leaves could be compared to thickened leaves of ancestral type with more suppressed marginal growth. The distal leaves are anatomically similar to terete leaves of *C. tomentosa*. *Caputia scaposa* leaves look like an intermediate evolutionary stage from the ancestral leaf type to terete leaf type of *C. tomentosa*. Such an interpretation fits well the data presented and Haeckel's 'biogenetic law'. However, the location of this species in *Caputia* cladogram rather indicates an evolutionary reversion of *C. scaposa* leaves to the ancestral leaf type. This contradiction agrees with ANTONOV's (2003) idea about the partial mismatch of molecular and morphological evolution in plants.

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