Wulfenia 16 (2009): 61–77

Wulfenia
Mitteilungen des
Kärntner Botanikzentrums
Klagenfurt

On the evidence of subunifacial and unifacial leaves: developmental studies in leaf-succulent *Senecio* L. species (Asteraceae)

Ludmila V. Ozerova & Alexander C. Timonin

Summary: The studied leaves initiate as completely bifacial primordia which differentiate into Unterblatt and Oberblatt. The Unterblatt remains bifacial throughout, highly inhibited, and develops to a very short leaf ground. The Oberblatt mostly changes into subunifacial structure due to a prominent thickening towards the apical dome. This thickening concurs with conspicuous widening of Oberblatt's abaxial side whereas its adaxial side nearly retains its original width. Oberblatt's tip becomes really unifacial. It has only an abaxial side and therefore differs from the rest of the Oberblatt. Leaf unifacial structure is thus not a misinterpretation of subunifacial structure *sensu* Hagemann, but a real phenomenon. The subunifacial basal Oberblatt develops into a terete, long cylindrical, spindle-shaped, or sub-ensiform leaf blade or into a petiole and globular leaf blade. All these leaves are called subunifacial because the subunifacial blade (and the petiole if present) highly exceeds both, the very short bifacial leaf ground and very short unifacial tip. The leaves that consist of a bifacial to subunifacial leaf ground and a highly prevailing unifacial rest of the leaf are suggested to be conventionally called unifacial. We conclude that the term 'subunifacial leaf' is neither a synonym nor a substitute of the term 'unifacial leaf'.

Keywords: leaf development, unifacial leaf, subunifacial leaf, terete leaf, ensiform leaf, sub-ensiform leaf, spindle-shaped leaf, globular leaf, Unterblatt, Oberblatt, *Senecio*

A plain bifacial shape is typical of most of the leaves. But many existing leaves and leaf parts, however, show neither external nor internal characters of a bifacial structure. On a theoretical base such leaves / leaf parts have habitually been described as unifacial[1] since 1903 (Čelakovsky 1903; Goebel 1913; Troll 1939; Sitte et al. 2002 etc.). The unifacial leaves are conveniently thought to have lost their adaxial side by (i) (congenital) fusion of both halves of the adaxially folded leaf (Čelakovsky 1903), or by (ii) abaxial outgrowing to substitute an inhibited bifacial Oberblatt (Thielke 1948; Roth 1949), or by (iii) complete rounding of an *ab initio* bifacial leaf primordium (Troll & Meyer 1955).

Unifacial leaf theory thus accepted has been challenged by Hagemann (1970) and Eberwein (1995, 2005, 2007). Hagemann's concept has proceeded from the conclusion that every leaf initiates as completely bifacial primordium. None of its two sides is claimed to be able to disappear during leaf development. Every leaf is thought to retain these two sides lifelong. Both, adaxial and abaxial sides, grow co-ordinately in a typical, obviously bifacial leaf. In a leaf assumed unifacial, the abaxial side is believed to grow longer and wider whereas the adaxial side is considered to grow only longer and to retain its original width. Consequently, the adaxial side becomes narrower during leaf development and quite inconspicuous in the mature leaf which looks then as if it were unifacial and had only an abaxial side. So, the unifacial structure of leaf / leaf part is believed by Hagemann (1970) to be always nothing but an illusion. Accordingly, it's accepted that subunifacial leaves more or less perfectly imitate 'unreal' unifacial leaves.

1) Such leaves were originally called monofacial.

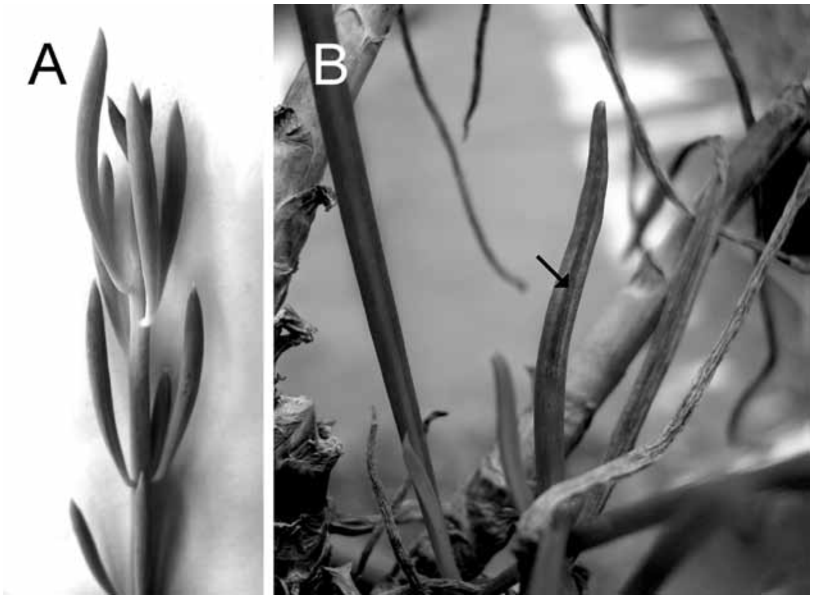


Figure 1. *Senecio talinoides* Sch. Bip. with unifacial leaves (A) and *Senecio acaulis* Sch. Bip. with subunifacial leaves (B). The *arrow* indicates the narrow adaxial side.

Contrary to Hagemann (1970), Eberwein (2007) has more liberally accepted unifacial parts of a leaf. Nevertheless, he manifests that the leaf ground never becomes unifacial. Even if a leaf looks like absolutely unifacial, it always retains in fact a tiny adaxial side at its very base. Such a leaf would erroneously be called unifacial. According to Eberwein (1995) its correct name must be subunifacial. The term 'subunifacial' certainly fits even better the leaves whose reduced adaxial side is easier discernible. Thus, the leaf as a whole is believed to be at most subunifacial.

Though rather different, the two above-mentioned concepts accordingly result in denying the theory of unifacial leaf and substituting it for the theory of subunifacial leaf.

We studied leaf development in leaf-succulent *Senecio* s. ampl. species in order to check whether the unifacial leaf theory has to be demolished in favour of the subunifacial leaf theory. Rather various leaves are inherent in these species, viz clearly bifacial, nearly to genuine peltate, terete to long cylindrical, ensiform, spindle-shaped, and globular with a short petiole. Each variant except the two mentioned first is represented by two types (Fig. 1). Leaves of the first type have a narrow translucent stripe along their upper side from the very base to nearly the tip. The stripe internally concurs with discontinuities of both layers, the sub-epidermal chlorenchyma and the vasculature, as it can be seen in Figure 2 B, C. This stripe has been interpreted as inhibited adaxial side of the leaf. Therefore, such leaves were considered as subunifacial (Timonin & Ozerova 1993; Timonin et al. 2006). Leaves of the second type are uniform opaque all around except for their very bases, where they have a tiny similar stripe. A ring of equidistant vascular bundles and a layer of sub-epidermal chlorenchyma, which is continuous/discontinuous by the bundles, can be seen in cross-sections of the opaque part of the leaf (Fig. 2 A). We considered such leaves to be unifacial (Timonin & Ozerova 1993). The present paper shows the development of subunifacial leaves as mentioned above in 5 *Senecio* species. The development of the considered unifacial leaves was published elsewhere (Timonin et al. 2006).

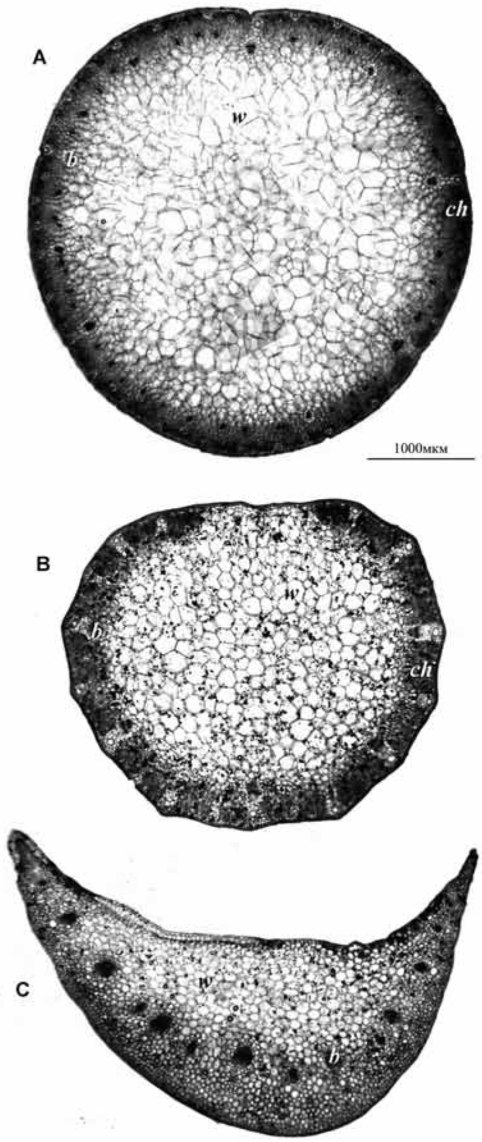
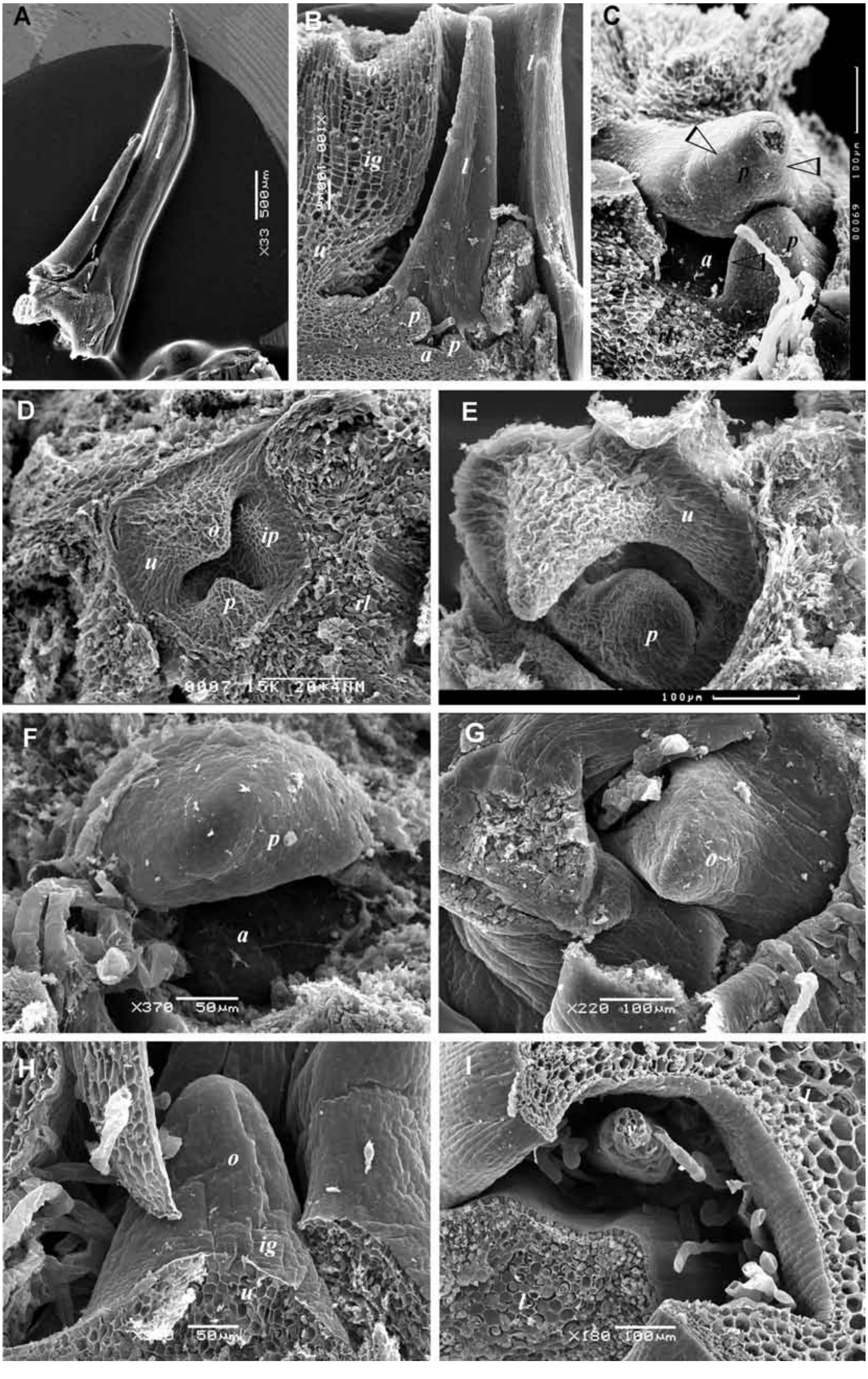


Figure 2. Cross-sections of leaf blades: *Senecio talinoides* (A), *S. acaulis* (B). Cross-section of the leaf ground in *S. acaulis* (C). *b* – vascular bundle; *ch* – chlorenchyma; *w* – water storing parenchyma.

Materials and methods

Plants of *S. acaulis* Sch. Bip., *S. crassissimus* Humbert, *S. hallianus* G.D. Rowley, *S. herreianus* Dinter, and *S. rowleyanus* H. Jacobsen grown in the greenhouse of Tsitsin Main Botanical Garden of Russian Academy of Science in Moscow were used for the present investigation. Tips of growing shoots were picked up, fixed with 70% ethanol for a couple of days, dehydrated in a series of 90% ethanol, absolute ethanol, 50% absolute ethanol & 50% acetone, 100% acetone, 100% acetone for one hour in each, critical-point dried and fastened on stubs. The tips thus prepared were covered with Pt/Pd/Au and examined with SEM Camscan 4LV or Hitachi S405–A.


A
l
l
X33 500µm
B
o
ig
u
l
l
p
a
p
C
p
p
a
100µm
D
u
o
ip
p
rl
E
u
o
p
100µm
F
p
a
X370 50µm
G
o
X220 100µm
H
o
ig
u
50µm
I
v
l
l
X180 100µm

Results

Senecio acaulis has long cylindrical leaves (Fig. 1 B), multi-leaved terminal buds, and slightly convex to slightly concave apical domes (Fig. 3 A–F). The leaf initiates at the periphery of the apical dome as *ab initio* flattish primordium having a discernible margin between its ad- and abaxial sides (Fig. 3 C, D). The abaxial side of the primordium originally elongates more rapidly than its adaxial side, which causes a vaulting of the primordium over the apical dome (Fig. 3 D, E). The base of the primordium then grows much wider than its distal part (Fig. 3 D, E). This indicates the differentiation of the primordium into a wider Unterblatt and narrower Oberblatt, respectively. The former subsequently remains inhibited whereas the latter mostly grows long and becomes straight (Fig. 3 C, F, G). The thickening of the Oberblatt usually accompanies its elongating soon. As a result of this thickening, the Oberblatt's tip changes to be perfectly round in the cross-section lacking a detectable margin (Fig. 3 I). Adaxial and abaxial sides of the tip become indistinguishable after it has rounded. The rounding of the Oberblatt's tip is delayed in a few leaves, however (Fig. 4 A, B). The basal Oberblatt thickens by means of its adaxial rounding meristem (Fig. 4 F) which becomes semicircular to crescent-shaped in cross-section due to suppressed widening of the adaxial side (Figs 3 G; 4 F). The growth of the Oberblatt subsequently concentrates at its boundary with the Unterblatt (Fig. 3 H) and produces a long cylindrical leaf blade with a narrow adaxial side shaped like a shallow furrow (Fig. 4 C–E). The cross-section of the leaf blade is round but the margin is quite visible (Figs 3; 4: *arrowheads*). Besides, the adaxial side of the leaf blade clearly differs from the abaxial one in shape of its epidermal cells and lacking stomata.

The furrow of the adaxial side ends below the leaf tip which is round in cross-section (Fig. 4 C–E). The tip's epidermis consists of fairly uniform cells and clearly differs in cell shape and arrangement from both, adaxial and abaxial epidermises of the leaf blade below, though it shares stomata with the abaxial epidermis (Fig. 4 D). The adaxial epidermis transforms into the tip's epidermis further distally than the abaxial epidermis.

Senecio hallianus has terete leaves (Fig. 5 A, J), multi-leaved terminal buds (Fig. 5 A), and small, slightly convex apical domes (Fig. 5 B–H), nearly unchangeable during the plastochrone. Leaf initiates as a rounded bulge at the periphery of the apical dome (Fig. 5 C). The bulge soon develops into a dorsiventral primordium (Fig. 5 D–E) which shows a rather discernible margin delimiting its ad- and abaxial sides. The primordium grows longer and wider and starts thickening nearly throughout except its very base (Fig. 5 D). Different thickening of basal and distal parts of the primordium manifests its differentiation into a short thinner Unterblatt and a prevailing thicker Oberblatt (Fig. 5 D). The former mostly grows in width (Fig. 5 H) to become an inhibited leaf ground. The Oberblatt usually curves towards the apical dome during its development (Fig. 5 E, F). Subsequent growth of the Oberblatt concentrates at its boundary with the Unterblatt, which is indicated by distinctly shorter epidermal cells there (Fig. 5 C: left leaf). This intercalary growing results in a straight elongated terete leaf blade (Fig. 5 H–J), but the Oberblatt's tip remains adaxially bent (Fig. 5 A, H–J) even in the mature leaf. Thickening of the Oberblatt causes it to

Figure 3. Terminal buds of *Senecio acaulis*. A – exterior with some outer leaves removed, B – longitudinally sectioned, C–G, I – viewed from above, H – bud with growing leaf viewed from abaxial side. *a* – apex, *ig* – zone of intercalary growing, *ip* – initiating primordium of the leaf, *l* – leaf, *o* – Oberblatt, *p* – leaf primordium, *rl* – removed leaf, *u* – Unterblatt, *v* – Vorläuferspitze; *arrowheads* indicate leaf margins.

<<<

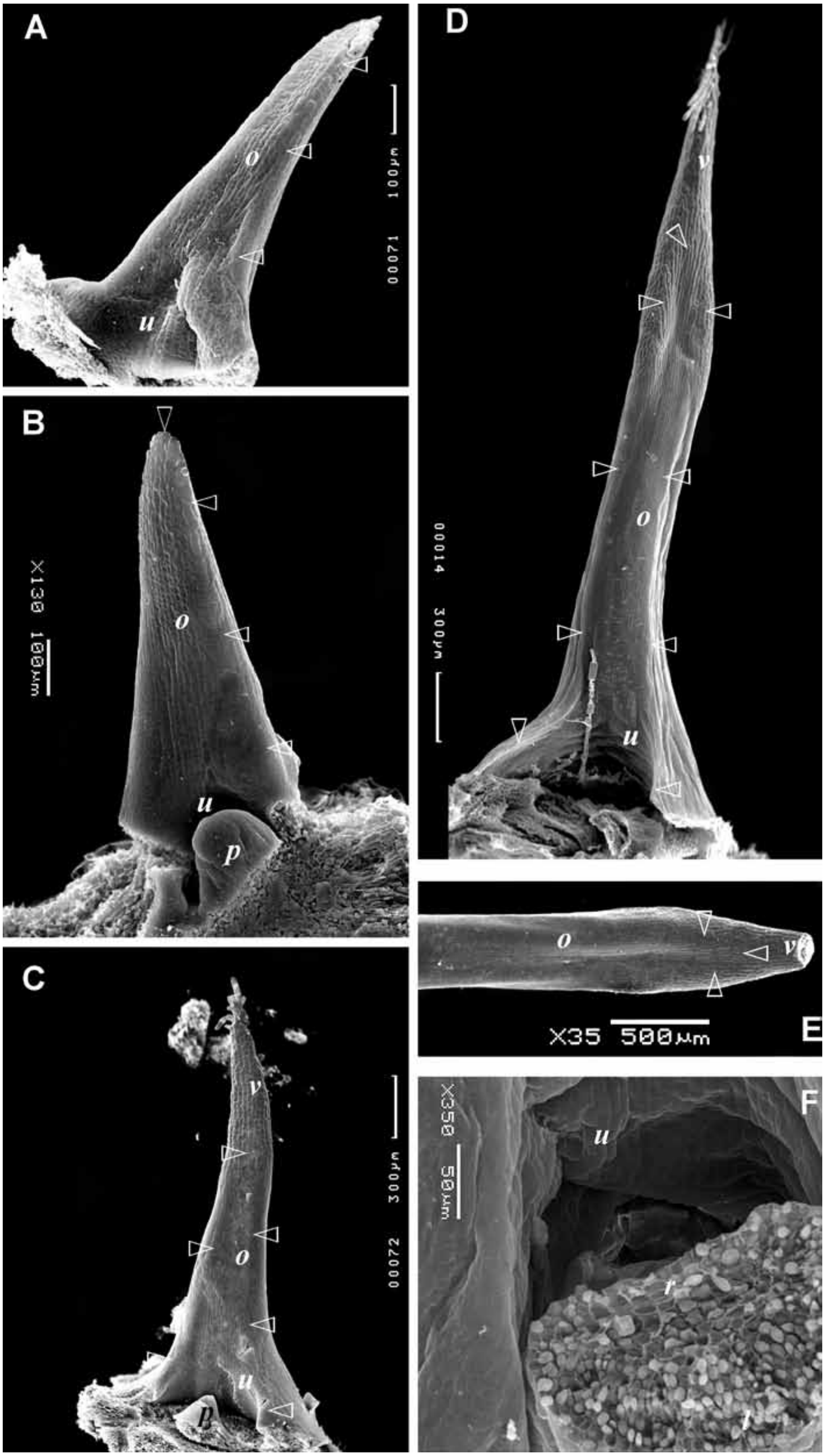


Figure 4. Developing leaves of *Senecio acaulis*. *l* – leaf, *o* – Oberblatt, *p* – leaf primordium, *r* – rounding meristem, *u* – Unterblatt, *v* – Vorläuferspitze; *arrowheads* indicate leaf margins.

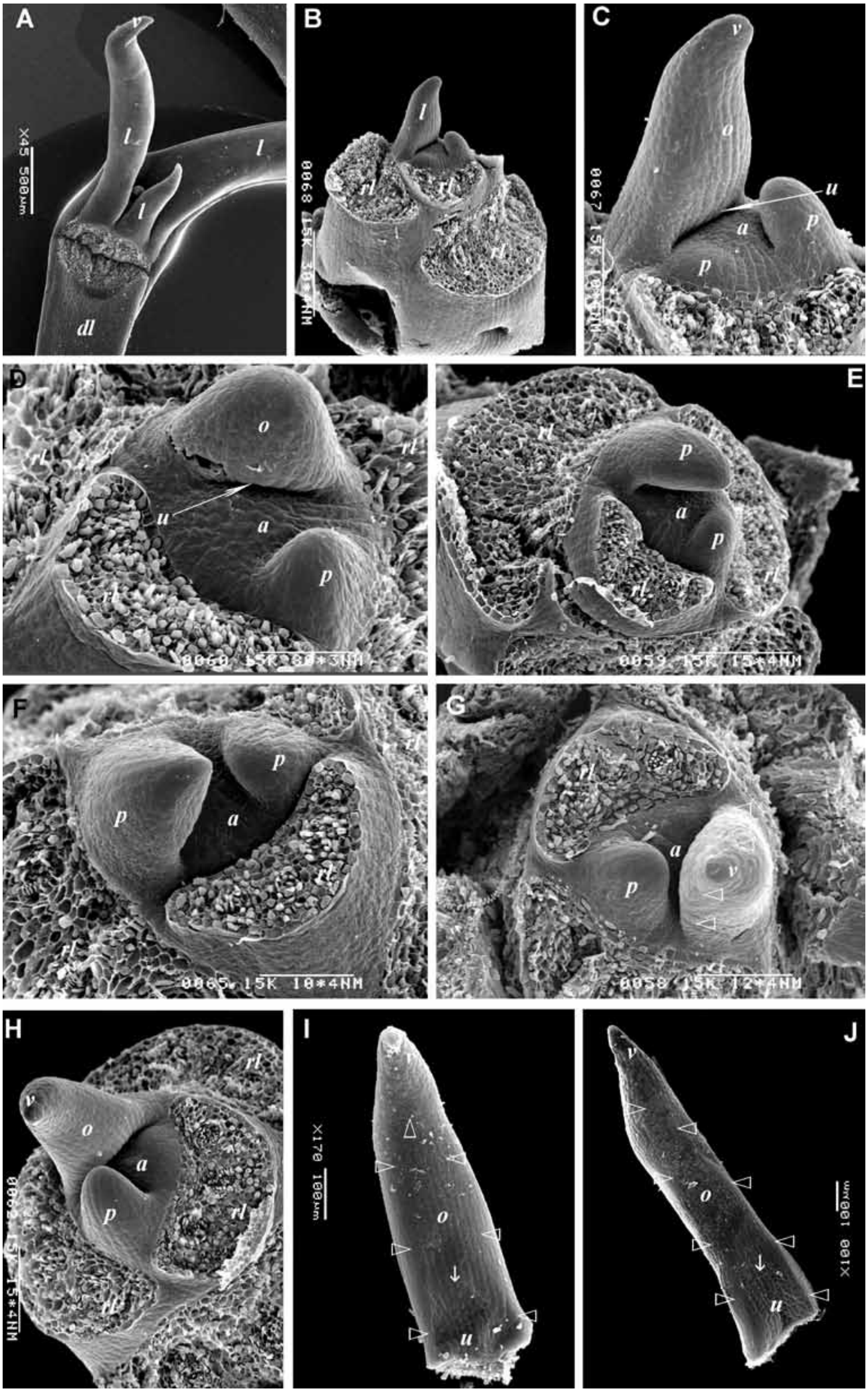


Figure 5. Terminal buds (A–H) and developing leaves (I–J) of *Senecio hallianus*. *a* – apex, *dl* – artificially deflected leaf, *l* – leaf, *o* – Oberblatt, *p* – leaf primordium, *rl* – removed leaf, *u* – Unterblatt, *v* – Vorläuferspitze; *arrowheads* indicate leaf margins, *short arrows* indicate the boundary between Unter- and Oberblatt on the adaxial side of the leaf.

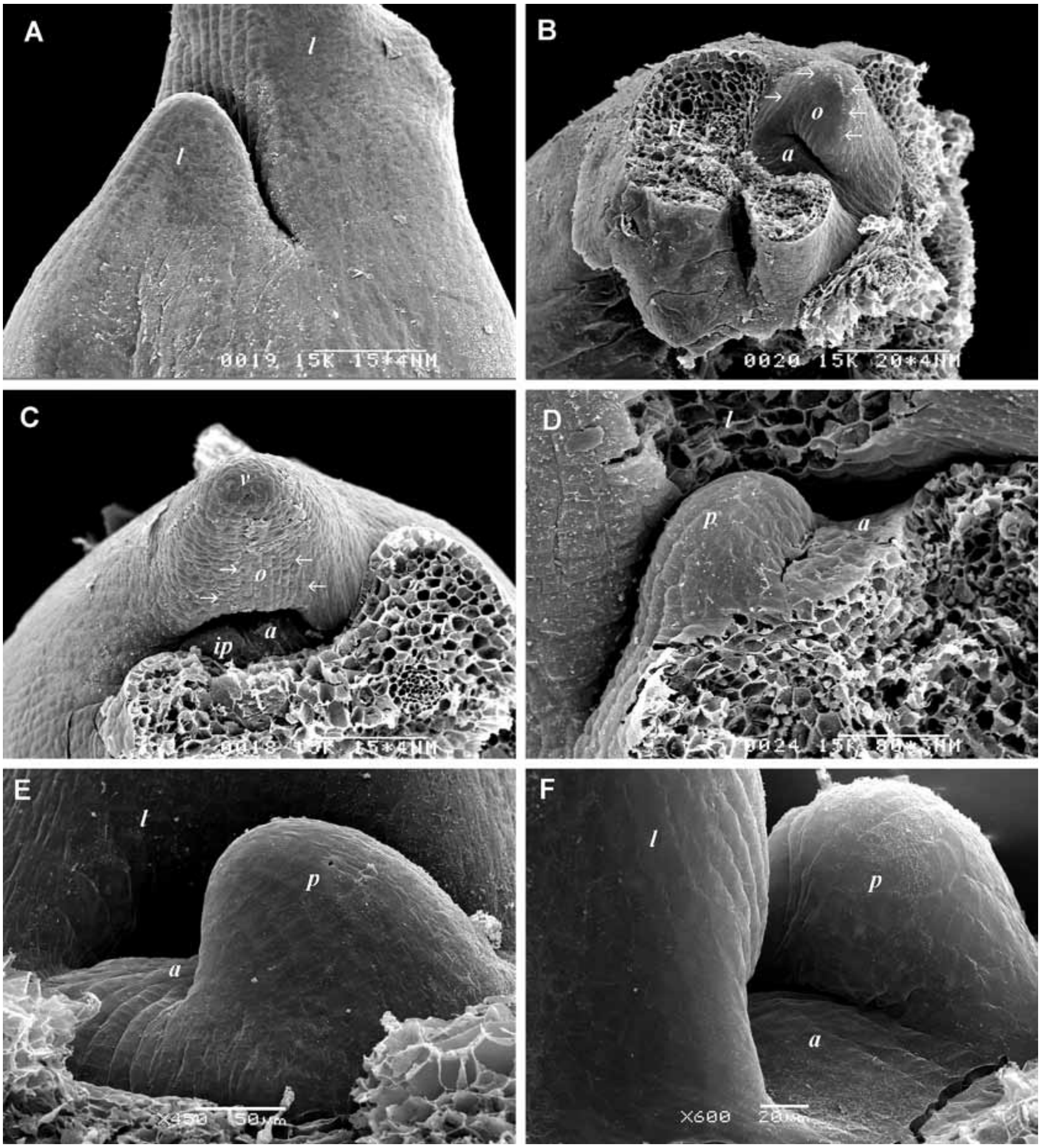


Figure 6. Exterior (A) and uncovered (B–D) terminal buds and the leaf primordium viewed from outside (E) and from inside (F) of the bud of *Senecio herreianus*. *a* – apex, *ip* – initiating primordium of the leaf, *l* – leaf, *o* – Oberblatt, *p* – primordium, *rl* – removed leaf, *v* – Vorläuferspitze; *arrows* indicate leaf margins.

grow more round in cross-section (Fig. 5 G, H). Nevertheless, the Oberblatt's adaxial side is still detectable in the rather advanced leaf primordium due to its flat surface and less regularly arranged smaller epidermal cells of the bordering leaf margin. Comparisons of differently developed leaf primordia show that thickening of the Oberblatt concurs with widening of its abaxial side (Fig. 5 E: right primordium and 5 G).

The Oberblatt's tip, which had arisen before the intercalary growing of the Oberblatt started, thickens to become perfectly round in cross-section (Fig. 5 G–H). Its epidermal cells are all alike and they are orientated in transverse rings (Fig. 5 H) rather than in longitudinal rows which are

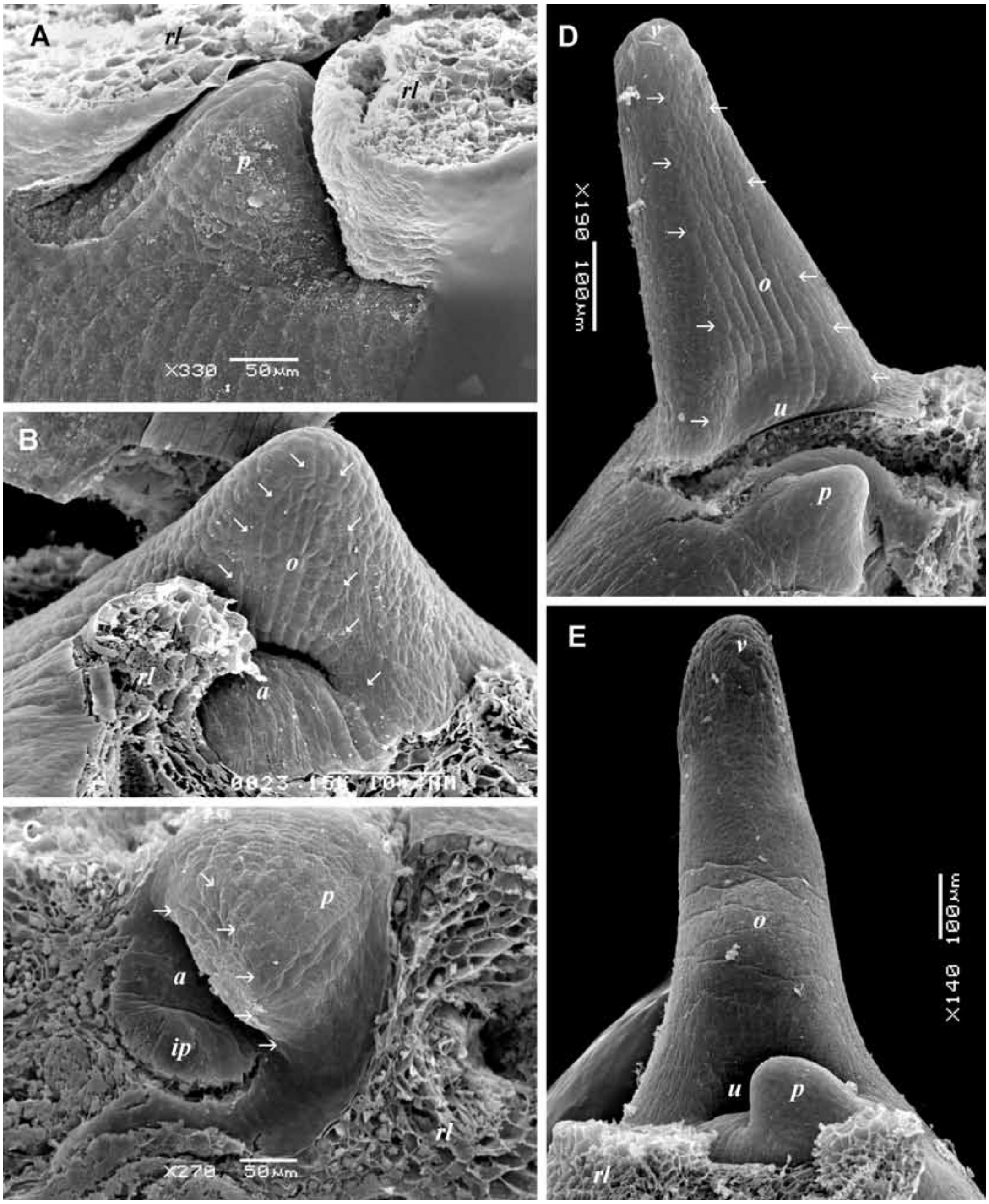


Figure 7. Terminal buds of *Senecio herreianus*. *a* – apex, *ip* – initiating primordium of the leaf, *o* – Oberblatt, *p* – leaf primordium, *rl* – removed leaf, *u* – Unterblatt, *v* – Vorläuferspitze; *arrows* indicate leaf margins.

typical of most epidermal cells of the rest of the Oberblatt. Therefore, the adaxial and abaxial sides of the tip are absolutely indistinguishable. The tip's epidermis clearly differs from the abaxial epidermis of basal Oberblatt and more sharply from the adaxial epidermis (Fig. 5 J).

Senecio herreianus has spindle-shaped leaves, 2- to 4-leaved terminal buds (Fig. 6 A–B), and slightly convex to slightly concave apical domes (Figs 6 B–F; 7 B–C, E). Leaf initiates at the periphery of

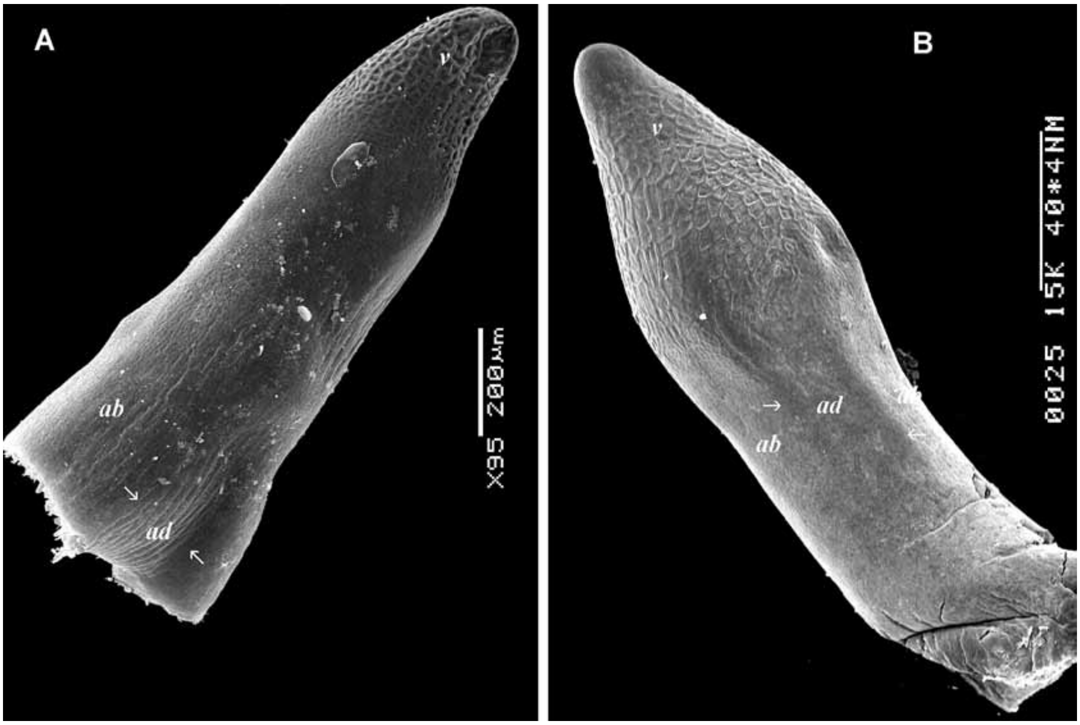


Figure 8. Developing leaves of *Senecio herreianus*. *ab* – abaxial side, *ad* – adaxial side, *v* – Vorläuferspitze; *arrows* indicate leaf margins.

the apical dome (Figs 6 C; 7 C) as a flattish primordium which acquires distinguishable ad- and abaxial sides though the bordering margin is indistinct (Fig. 6 D–F). The primordium grows straight (Fig. 7 D), soon highly thickens distally towards the apex and thus partly overhangs the apical dome (Figs 6 B; 7 B–C). It differentiates into a thinner inhibited Unterblatt and a progressing Oberblatt. The latter is *ab initio* bifacial throughout (Figs 6 B; 7 A–C) though its margins soon look like a smoothly folded surface. The adaxial side of the Oberblatt differs from the abaxial one in clearer longitudinal rows of the epidermal cells (Fig. 7 B). These rows disappear near the Oberblatt's tip, however.

The marginal folding of Oberblatt's surface completely disappears during the growth of the Oberblatt (Fig. 6 C). Nevertheless, its ad- and abaxial sides remain still recognizable due to differences in shapes and arrangements of their constituting cells. Advanced thickening of the Oberblatt concurs with a widening of its abaxial side and an illusory narrowing of its adaxial side (Fig. 6 B, C).

It is the Oberblatt's tip, however, whose thickening results in the absolute disappearance of distinction between its adaxial and abaxial sides, viz all cells of the tip's epidermis are fairly uniform and tend to be arranged in transverse rings in the more developed primordium (Fig. 6 C). Such an arrangement of the tip's epidermal cells somewhat resembles that of cells of the abaxial epidermis of the basal Oberblatt. Notwithstanding, the latter are really in transverse rings and longitudinal rows (Fig. 7 C).

Subsequent growth of the Oberblatt concentrates at its boundary with the Unterblatt to develop a terete leaf blade (Fig. 7 E). In a dehydrated blade, the adaxial side curves inwards to look like a

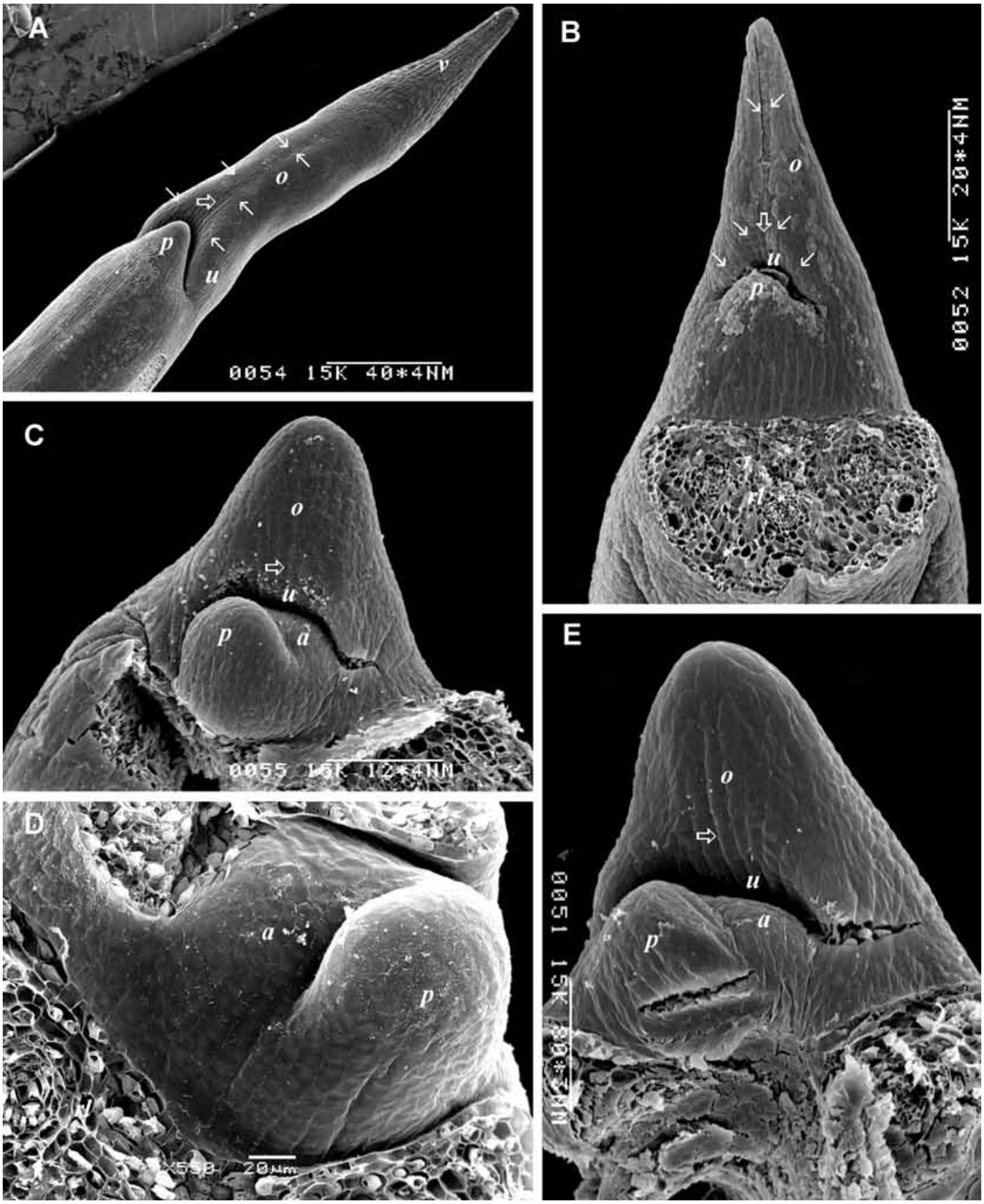


Figure 9. Terminal buds of *Senecio rowleyanus*. *a* – apex, *o* – Oberblatt, *p* – leaf primordium, *rl* – removed leaf, *u* – Unterblatt, *v* – Vorläuferspitze; *arrows* indicate leaf margins, *double arrows* indicate the boundary between Unter- and Oberblatt on the adaxial side.

shallow furrow (Fig. 8) which evidently ends nearby the Oberblatt's tip. The latter remains round in cross-section and shows highly uniform epidermal cells all around (Fig. 8 A). These cells differ from both, the adaxial and the abaxial epidermis cells of the terete leaf blade (Fig. 8 B). The tip remarkably has stomata similar to the abaxial side of the blade.

Later the terete leaf blade changes into a spindle-shaped leaf by thickening of its middle part.

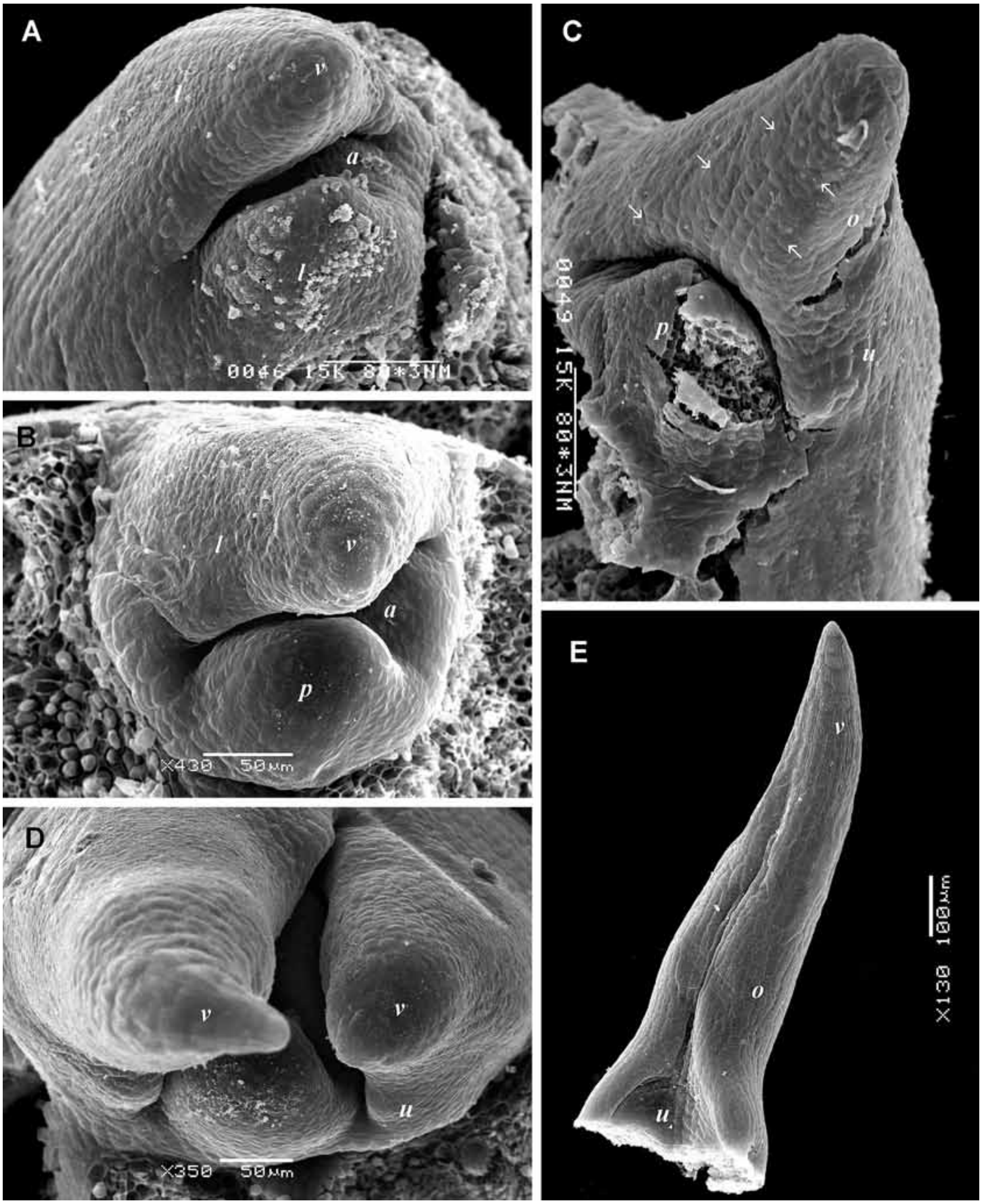


Figure 10. Terminal buds (A–D) and developing leaf (E) of *Senecio rowleyanus*. *a* – apex, *l* – leaf, *o* – Oberblatt, *p* – leaf primordium, *u* – Unterblatt, *v* – Vorläuferspitze; *arrows* indicate leaf margins.

Senecio rowleyanus has short-petiolate globular leaves, 2- to 3-leaved terminal buds (Figs 9; 10), and slightly convex apical domes (Fig. 9 C–E). Leaf initiates at the periphery of the apical dome as a completely bifacial primordium (Figs 9 D–E; 10 A). Its flat adaxial side is easily distinguishable from the outwardly curved abaxial side in spite of the indistinct blunt margin (Figs 9 C; 10 B). The primordium grows straight differentiating into an inhibited Unterblatt and a progressing Oberblatt (Fig. 9 C, E). The former grows a bit wider, its margin becomes sharper (Fig. 9 E). The

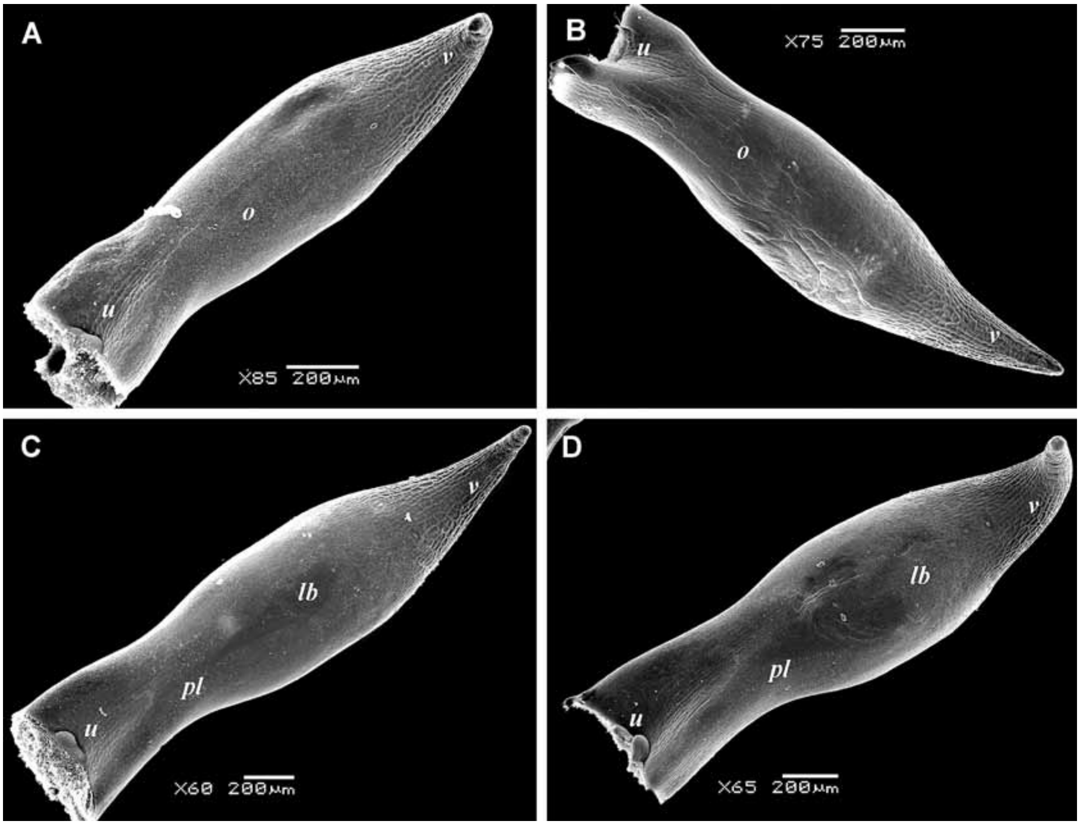


Figure 11. Developing leaves of *Senecio rowleyanus*. *lb* – leaf blade, *o* – Oberblatt, *pl* – petiole, *u* – Unterblatt, *v* – Vorläuferspitze.

latter grows longer, thickens towards the apex and projects over the apical dome (Fig. 9 C, E). Thickening of the Oberblatt causes its margin to become blunter. It remains quite recognizable, however, due to a more irregular arrangement of its epidermal cells which contrasts with the longitudinal cell rows of both, adaxial and abaxial epidermises (Figs 9 E; 10 A: upper leaf). Moreover, the flat adaxial side is still clearly distinguishable from the curved abaxial side of the Oberblatt.

Later the Oberblatt's tip becomes perfectly round in cross-section (Fig. 10 A–D). Besides, its epidermal cells resemble neither the adaxial nor the abaxial epidermis of the rest of the Oberblatt, though being a little bit more similar to the abaxial epidermis. They tend to be arranged in transverse rings. As a result the tip's margin and its both sides become absolutely indiscernible (Fig. 10 D).

The growth of the Oberblatt then concentrates at its boundary with the Unterblatt. Thickening of the basal Oberblatt concurs with a considerable widening of its abaxial side (Fig. 10 C–D) and thus results in a terete Oberblatt which has a narrow adaxial side curving inwards to become a shallow furrow if dehydrated (Figs 9 B; 10 E).

After reaching a length of about 1 mm, the Oberblatt distally thickens (Fig. 11) to form a globular leaf blade, whereas its basal part remains much thinner and changes into a distinct petiole (Fig. 11 C–D).

Senecio crassissimus has sub-ensiform[2] leaves, multi-leaved terminal buds, and a flat apical dome (Fig. 12 A–H). Leaf initiates as flattish recognizably bifacial primordium (Fig. 12 B–C). First its abaxial side longitudinally outgrows its adaxial side, thus causing the primordium to curve over the apical dome (Fig. 12 F: upper leaf). Then the primordium differentiates into the shortest Unterblatt of all studied species and the Oberblatt. The former exceedingly grows wider (Fig. 12 C, F–G). The latter mostly elongates and straightens up throughout but its very tip. Contrary to the Unterblatt, the Oberblatt considerably thickens towards the apex and thus partly overhangs the apical dome (Fig. 12 C, E: left leaf). Excessive dorsal thickening makes the primordium look like humpy (Fig. 12 C: right leaf). This dorsal thickening leads to a longitudinal dorsal ridge (Fig. 12 F) and causes the typical flattening of the median-plane of the developing leaf.

Both, dorsal and apexwards thickenings of the Oberblatt, concur with a great widening of its abaxial side, whereas the adaxial side nearly retains its original width. The latter remains quite recognizable throughout the Oberblatt (Fig. 12 B). Then the tip of the Oberblatt grows perfectly round in cross-section (Fig. 12 C: upper leaf, F: lower leaf, G: front leaf). The tip's epidermal cells are uniform all around and arranged in transverse rings. Therefore, the adaxial and abaxial sides are absolutely indistinguishable in the tip of the Oberblatt (Fig. 12 C, F–G).

Subsequent growth of the primordium concentrates at the Oberblatt's base to produce a sub-ensiform leaf blade terminated with a short conical tip. The narrow adaxial side of the blade ends by the tip (Fig. 12 H–I). It is curved inwards in a dehydrated leaf. The tip's epidermis essentially differs from both, adaxial and abaxial epidermises, in shape and in the arrangement of its constituting cells. It has stomata like the abaxial epidermis of the Oberblatt.

Discussion

The leaves of all studied *Senecio* species initiate as tangentially flattish, completely bifacial primordia. This is typical of any Spermatophyte's leaf. The prominent thickening of the Oberblatt towards the apex (which coincides with great dorsal thickening along the whole primordium in *S. crassissimus*) is a distinctive difference between the discussed *Senecio*-leaves and the typical leaves of Spermatophytes. The thickening causes the Oberblatt's margin to grow more round and indistinct, but the bifacial structure of the Oberblatt is surely detectable by a set of really discernible characters: (1) Though indistinct, the margin is indeed distinguishable because its epidermis differs from that of the abaxial side and even more from that of the adaxial side in shapes and more irregular arrangements of the constituting cells. (2) The adaxial side of the Oberblatt is flat and thus differs from its curved abaxial side. (3) The adaxial side becomes depressed to a narrow furrow in dehydrated leaves and makes the Oberblatt's margin more evident. A comparison of leaves in progress shows that the abaxial side grows much wider during the leaf thickening whereas the adaxial side mostly retains its original width. Therefore, the adaxial side looks as if it is reduced in advancing leaf, but by no means it disappears. Accordingly, most of the Oberblatt grows into a subunifacial leaf blade. This development fits well Hagemann's (1970) concept.

The Oberblatt's tip contrasts to the rest of the Oberblatt inasmuch as it becomes perfectly round in cross-section at the stage of intercalary growing, however. Having thus changed, the tip shows

2) Leaves of this species differ from typical ensiform ones in their obovate shape, although they are flat in their median plane just like every ensiform leaf. That is why these leaves are assigned to the ensiform type. Because of their peculiarity they are further called 'sub-ensiform'.

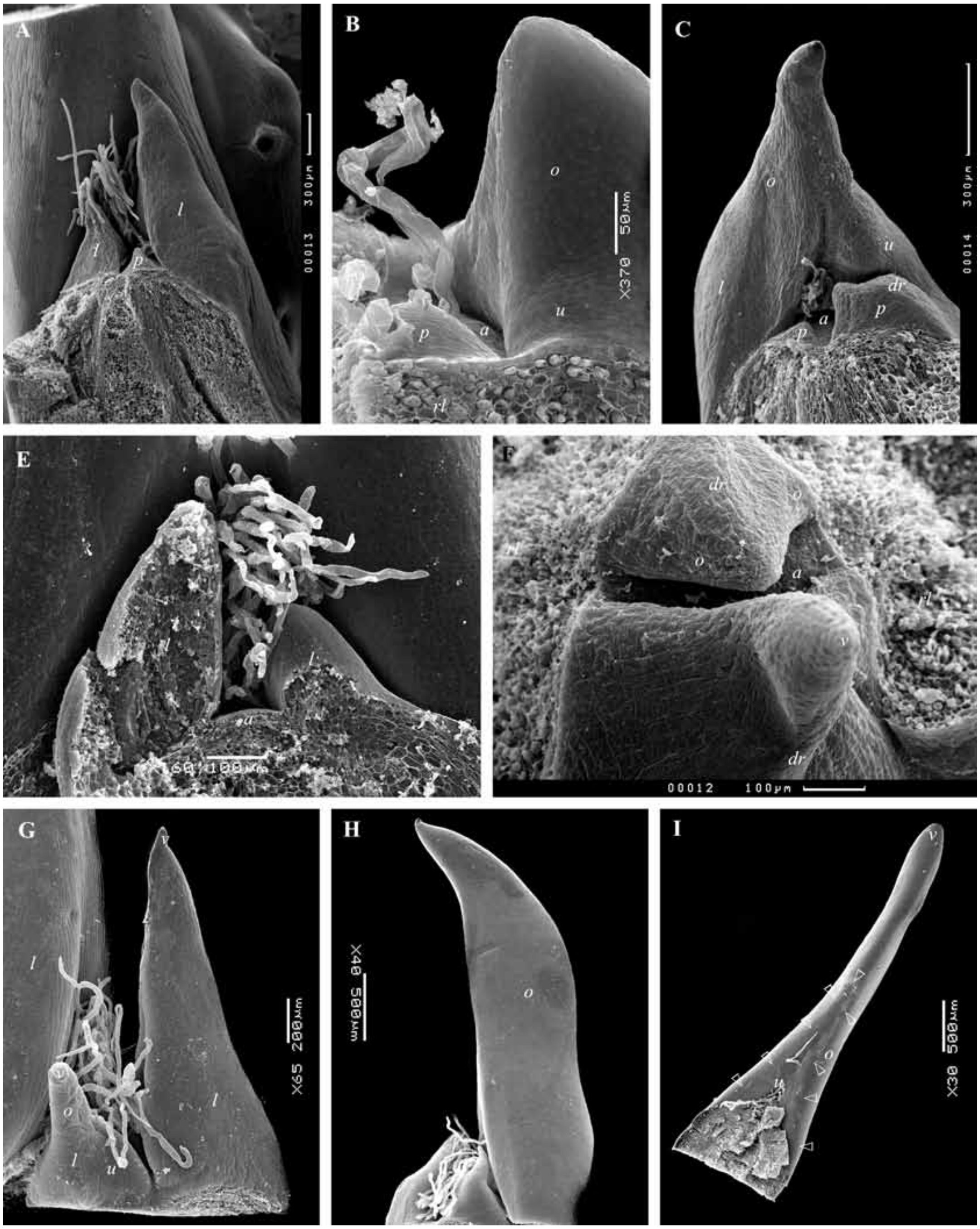


Figure 12. Terminal buds and developing leaves of *Senecio crassissimus*. *a* – apex, *dr* – dorsal ridge, *l* – leaf, *o* – Oberblatt, *p* – leaf primordium, *rl* – removed leaf, *u* – Unterblatt, *v* – Vorläuferspitze; *arrowheads* indicate leaf margins.

no sign of a margin, even if dehydrated. Besides, the epidermal cells and their arrangements are quite uniform all around the tip. As a result, it is impossible to distinguish the adaxial side from the abaxial one. So, how can it be supposed that this tip has a bifacial structure, if there is not one discernible character of its presumed sides and margins? In this case a bifacial structure can only be argued in order to conserve the theory of leaf sides. Leaf sides are by no means an energy, or mass, or momentum. We do not accept their conservation without proofs. We believe that it is much better to adjust a theory to a discernible phenomenon than to construct a morphological phantom in order to support the theory. Accordingly, we think that the bifacial structure of a leaf should be accepted only if there is a difference between its adaxial and abaxial sides or a detectable margin bordering the sides. Otherwise, the leaf / leaf part should be considered unifacial irrespective of being bifacial earlier. So, we follow Troll & Meyer (1955) in accepting that the bifacial structure of a leaf always arises by its initiation but can really disappear during its development. Thus, in the studied species the real bifacial distalmost part of the Oberblatt develops into a real unifacial tip. It has not been revealed, which side remains in the tip. The epidermis of the tip resembles neither adaxial nor abaxial epidermises, but it has stomata similar to the abaxial epidermis. Moreover, dehydrated leaves show that there is a depressed adaxial side that ends by the leaf tip. Both facts indicate that the only side of the unifacial tip is the abaxial side.

Thus, the studied succulent leaves of *Senecio* species evidence that a unifacial leaf-structure does exist which is in contrast to the subunifacial interpretation sensu Hagemann (1970). Therefore, the term 'subunifacial' according to Hagemann is not a correct substitute of the term 'unifacial' in the usual conception. Completely unifacial leaves have not really been revealed so far, because every leaf thoroughly investigated is bifacial at its very base (Eberwein 2005). This fact is an inadequate reason to reject the term 'unifacial', nevertheless. We have shown that the ratio of unifacial part to bifacial–subunifacial part considerably varies in different leaves. For instance, the unifacial tip comprises 5% or less of the length of the mature subunifacial leaf in all studied *Senecio* species. There are leaf-succulent *Senecio* species, however, whose leaves are unifacial except for the shortest leaf ground which hardly comprises 1% of the length of the mature leaf (Timonin et al. 2006). Leaves of these taxa are strikingly different. Obviously, they are worth being differently denominated. That is why we suppose to use the term 'subunifacial' only for leaves whose inhibited adaxial side comprises most of the total length of the leaf. Leaves which have a short bifacial leaf ground, a unifacial blade and petiole (if existing) are suggested to be conventionally denominated 'unifacial' to avoid establishing a new term.

References

Čelakovsky L. J. (1903): O listech monofaciálnich. – Razpr. Česke Akad. Cisaře Františka Josefa Tř. 2, Math. Prir. **12**: 1–40.

Eberwein R. K. (1995): Bau und Ontogenese unkonventioneller Blätter des Typus 'unifaziale Phyllome' und deren Beitrag zur Theorie des Spermatophytenblattes. – Aachen: PhD Dissertation, Rheinisch-Westfälische Technische Hochschule Aachen.

Eberwein R. K. (2005): Blatt oder nicht Blatt – eine einfache Frage? – In: Harlan V. [Hrsg.]: Wert und Grenzen des Typus in der botanischen Morphologie: 149–162. – Nümbrecht: Martina Galunder-Verlag.

Eberwein R. K. (2007): Leaf development in Angiosperms: the problem of unifaciality. – In: Novikov V. S. et al. [Eds]: Proc. Confer. plant morphology and taxonomy dedicated to 300th anniversary of Carl Linnaeus: 221–222. – Moscow: KMK Scientific Press Ltd.

Goebel K. (1913): Organographie der Pflanzen insbesondere der Archegoniaten und Samenpflanzen. 2. Aufl. 1. Teil. – Jena: Gustav Fischer.

Hagemann W. (1970): Studien zur Entwicklungsgeschichte der Angiospermenblätter. Ein Beitrag zur Klärung ihres Gestaltungsprinzips. – Bot. Jahrb. Syst. **90**: 297–423.

Roth I. (1949): Zur Entwicklungsgeschichte des Blattes, mit besonderer Berücksichtigung von Stipular- und Ligularbildungen. – Planta **37**: 299–336.

Sitte P., Weiler E. W., Kadereit J. W., Bresinsky A. & Körner C. (2002): Strasburger's Lehrbuch der Botanik. 35. Aufl. – Heidelberg, Berlin: Elsevier GmbH, Spektrum Akademischer Verlag.

Thielke C. (1948): Beiträge zur Entwicklungsgeschichte unifazialer Blätter. – Planta **36**: 154–177.

Timonin A. C. & Ozerova L. V. (1993): Structure, origin and evolution of the terete leaves in section *Rowleyani* C. Jeffrey of genus *Senecio* L. (Asteraceae). – Proc. Russian Acad. Sci. Ser. Biol. **3**: 393–401. [In Russian]

Timonin A. C., Ozerova L. V. & Remizowa M. V. (2006): Development of unifacial leaves in *Senecio* L. s. lat. (Asteraceae). – Wulfenia **13**: 217–227.

Troll W. (1939): Vergleichende Morphologie der Höheren Pflanzen. 1. Band: Vegetationsorgane. Teil 2. – Berlin: Gebrüder Borntraeger.

Troll W. & Meyer H.-J. (1955): Entwicklungsgeschichtliche Untersuchungen über das Zustandekommen unifazialer Blattstrukturen. – Planta **40**: 286–360.

Addresses of the authors:

Dr Ludmila V. Ozerova
Department of Tropical and Subtropical Plants
Tsitsin Main Botanical Garden of Russian Academy of Science
Botanicheskaya ul. 4
127276 Moscow
Russia
E-mail: lyozerova@yandex.ru

Prof. Dr Alexander C. Timonin
Department of Higher Plants
Faculty of Biology
Lomonosov Moscow State University
Vorobyevy Gory 1 (12)
119992 Moscow
Russia
E-mail: timonin58@mail.ru