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Development of ensiform leaves in *Senecio crassissimus* Humber and *Curio ficoides* (L.) P.V. Heath (Asteraceae: Senecioneae)

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Summary: Senecio crassissimus and *Curio ficoides* are unique among Asteraceae in their ensiform leaves. However, their leaves differ in both the outline of the leaf blade as well as its faciality and the mode of vertical plane flattening. The leaf blade of *C. ficoides* is unifacial and becomes flattened by adaxial growing. The leaf blade of *S. crassissimus* is subunifacial and becomes flattened by abaxial growing. Therefore, these leaves must have evolved convergently. The ensiform leaves of *C. ficoides* are similar to classic ensiform leaves inherent in Iridaceae. The ensiform leaves of *S. crassissimus* differ from the latter in subunifaciality and flattening mode of their leaf blade. Accordingly, the leaves of *S. crassissimus* should better be categorized as subensiform.

Keywords: leaf development, ensiform leaf, subensiform leaf, unifacial leaf, subunifacial leaf, *Curio*, *Senecio*, Asteraceae

Heliophytic plants are characterized by a variety of adaptations to thrive in sunny arid habitats. Special orientation of their leaves relative to sunlight is one of their most striking adaptations. The leaf blades of heliophytic plants are arranged in vertical plane to expose their edge to the incident sunlight. Such an arrangement of the leaf blade significantly reduces its midday heating and transpiration, which the inhabitants of the arid habitats badly need (Goryshina 1979; Werk & Ehleringer 1984; Smith & Ullberg 1989; James & Bell 2000). A vertical plane arrangement of leaf blades differently forms in different plants. The 90° torsion of the petiole is characteristic of various plant taxa (Werk & Ehleringer 1984; Smith & Ullberg 1989; James & Bell 2000). A much deeper morphogenetic and structural transformation is demonstrated by ensiform leaves which are especially characteristic of Iridaceae. The leaf blades of these leaves result from the disappearance of their adaxial side and high thickening in the median plane to become vertical-plane flattened (Troll 1939; Rudall 1990). Ensiform leaves are the rarest leaf type in Asteraceae. They are reliably known only in two leaf-succulent species, namely *Curio ficoides* (L.) P.V. Heath and *Senecio crassissimus* Humber (Rowley 2002) of the tribe Senecioneae. The genus *Curio* segregated by Heath (1997) mostly corresponds to the section *Rowleyani* C. Jeffrey of the mammoth and heterogeneous genus *Senecio* L. (cf. Jeffrey 1992). However, these genera have recently been shown to be rather distantly related according to molecular phylogenetics data (Pelser et al. 2007). Therefore, these species are unlikely to have inherited their ensiform leaves from a common ancestor. These leaves most likely evolved convergently. Therefore, it is worth investigating the similarity / difference of the organogenesis of such leaves in these distantly related taxa.

Materials and methods

Curio ficoides is a sprawling evergreen shrub more than 1 m tall, widespread in the Lesser Karoo and Eastern Cape of South Africa. It has succulent, cylindrical stems and succulent, bluish-gray, ensiform, wax coated leaves (Fig. 1A).

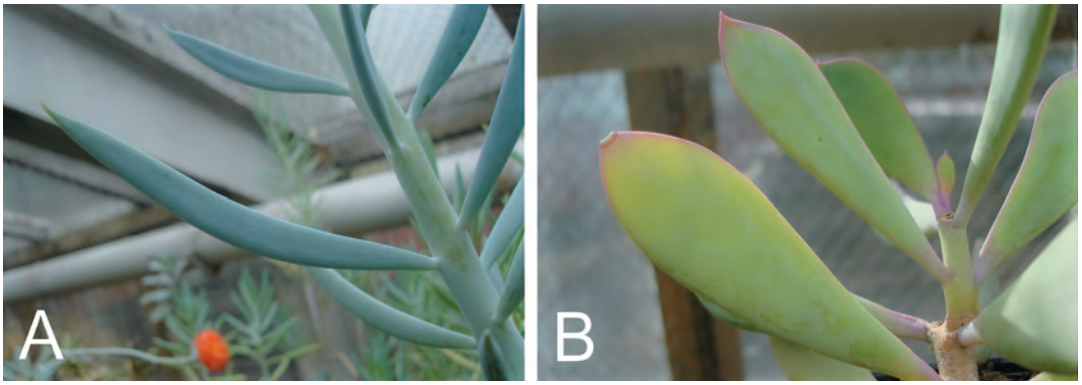

Figure 1. Ensiform leaves of *Curio ficoides* (A) and *Senecio crassissimus* (B).

Senecio crassissimus is an erect evergreen shrub up to 60 cm tall, endemic to the central part of Madagascar. It has succulent, purple stems and succulent, wax coated, obovate leaves flattened in the vertical plane (Fig. 1B).

Material was taken from living plants grown in the greenhouse of Tsitsin Main Botanical Garden of the Russian Academy of Science, Moscow, Russia.

The tips of growing shoots were cut and after removal of all leaves exceeding 1 mm were fixed in 70% ethanol for 3 days. The fixed shoot tips were treated as follows. All leaves shielding the apex were removed under 70% ethanol with syringe needles and sharp-end tweezers under a stereoscopic microscope MBS-9. The material thus prepared was dehydrated in a liquids series: 96% ethanol, 100% ethanol, 100% ethanol : 100% acetone (1 : 1), 100% acetone. The material was kept three times for at least 2 hours in each liquid. The dehydrated material was dried at the critical point, mounted on stubs and coated with a mixture of Pt, Pd, Au and Ag in various combinations depending on availability. The preparations were examined under SEMs Camscan 4DV and Hitachi S405-A.

Results

Curio ficoides has small-capacity terminal buds with only two or three developing leaf primordia therein (Fig. 2A, B). A flat or slightly concave shoot apex forms flattened, bilateral leaf primordia on its periphery. Each leaf primordium soon differentiates into the basal *Unterblatt* (lower leaf zone) and distal *Oberblatt* (upper leaf zone) (Fig. 2B). The *Unterblatt* subsequently hardly elongates, but significantly expands laterally. Therefore, the leaf mostly consists of the *Oberblatt* already at an early developmental stage (Fig. 2E). *Oberblatt* thickens and rounds up blurring the edge between its ad- and abaxial sides. The rounding especially progresses in the primordium tip, which differentiates into the unifacial *Vorläuferspitze* (forerunner tip) bearing more or less tiered epidermal cells (Fig. 2B, C). The basal part of the *Oberblatt* also becomes unifacial.

Elongation of the unifacial *Oberblatt* is further on concentrated at its base, where it adjoins the *Unterblatt*. The intercalary elongating part of the *Oberblatt* gives rise to the leaf blade. Subsequently, it does not only lengthen, but also significantly thickens at the side facing the apex (Fig. 2D). The leaf resultantly becomes characteristically flattened in the median plane (Fig. 1A). Thus, the ensiform leaf blade starts developing almost immediately after differentiation of the *Oberblatt*, during the intra-bud growth of the leaf.

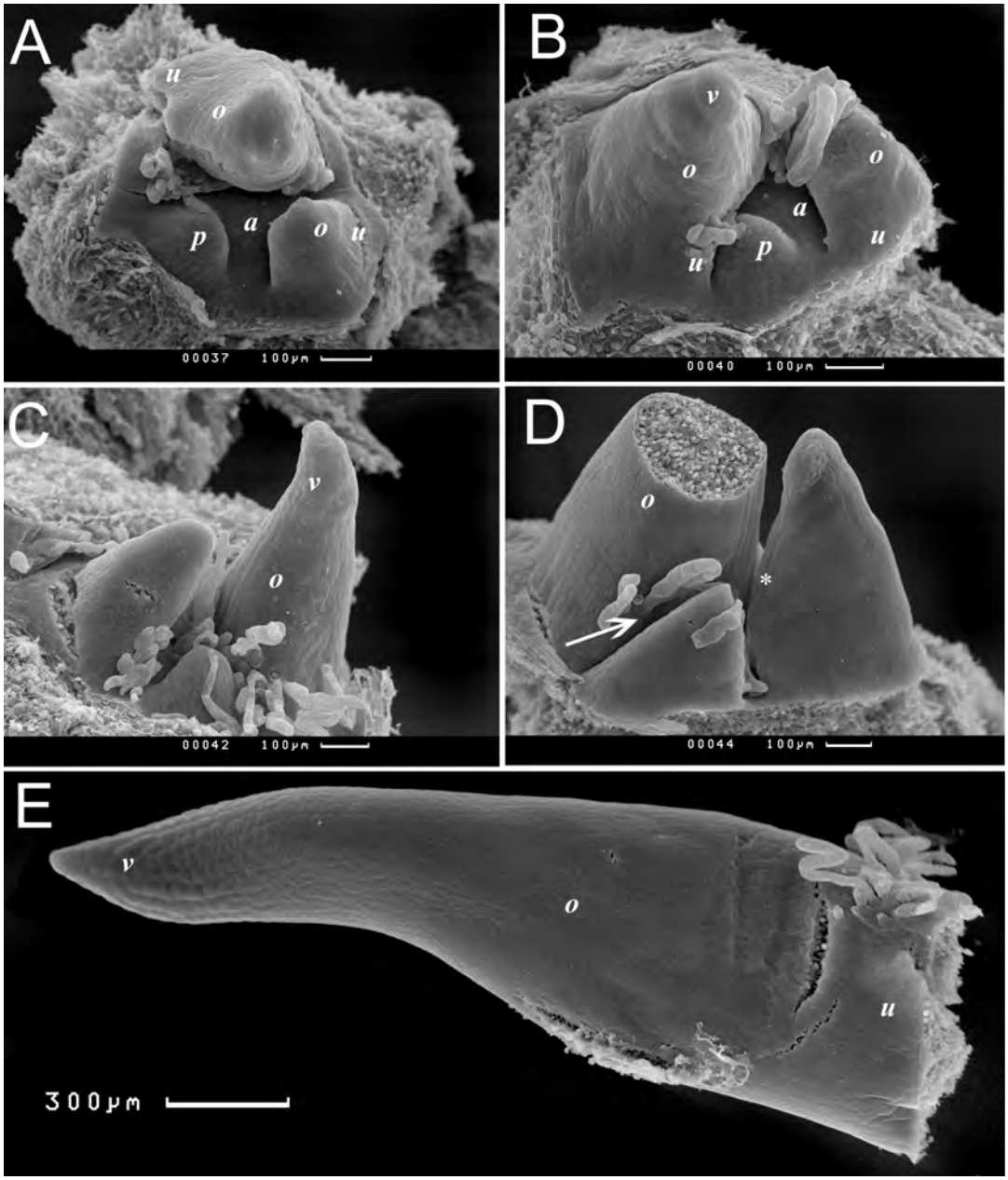

Figure 2. Developing leaves of *Curio ficoides*. A, B – terminal bud and developing leaf primordia; C – *Vorläuferspitze*; D – thickening *Oberblatt* of young leaf; E – intercalary elongating leaf. *a* – apex; *p* – leaf primordium; *o* – *Oberblatt*; *u* – *Unterblatt*; *v* – *Vorläuferspitze*; *arrow* – adaxial side of the *Unterblatt*; *asterisk* – thickening adaxial side.

Senecio crassissimus has small-capacity terminal buds and a flattish apex (Fig. 3A, C). The leaf initiates as a flattened, bifacial primordium at the periphery of the apex (Fig. 3A). The abaxial side of the leaf primordium initially outgrows its adaxial side in longitudinal direction causing the primordium to bend over the apex (acrovergence). The bent primordium differentiates into the short basal *Unterblatt* and the distal *Oberblatt* (Fig. 3A). The former one expands laterally (Fig. 3C). The latter one mostly grows longitudinally. Elongation of its adaxial side intensifies to straighten the primordium nearly throughout except for its very tip. The distalmost part of

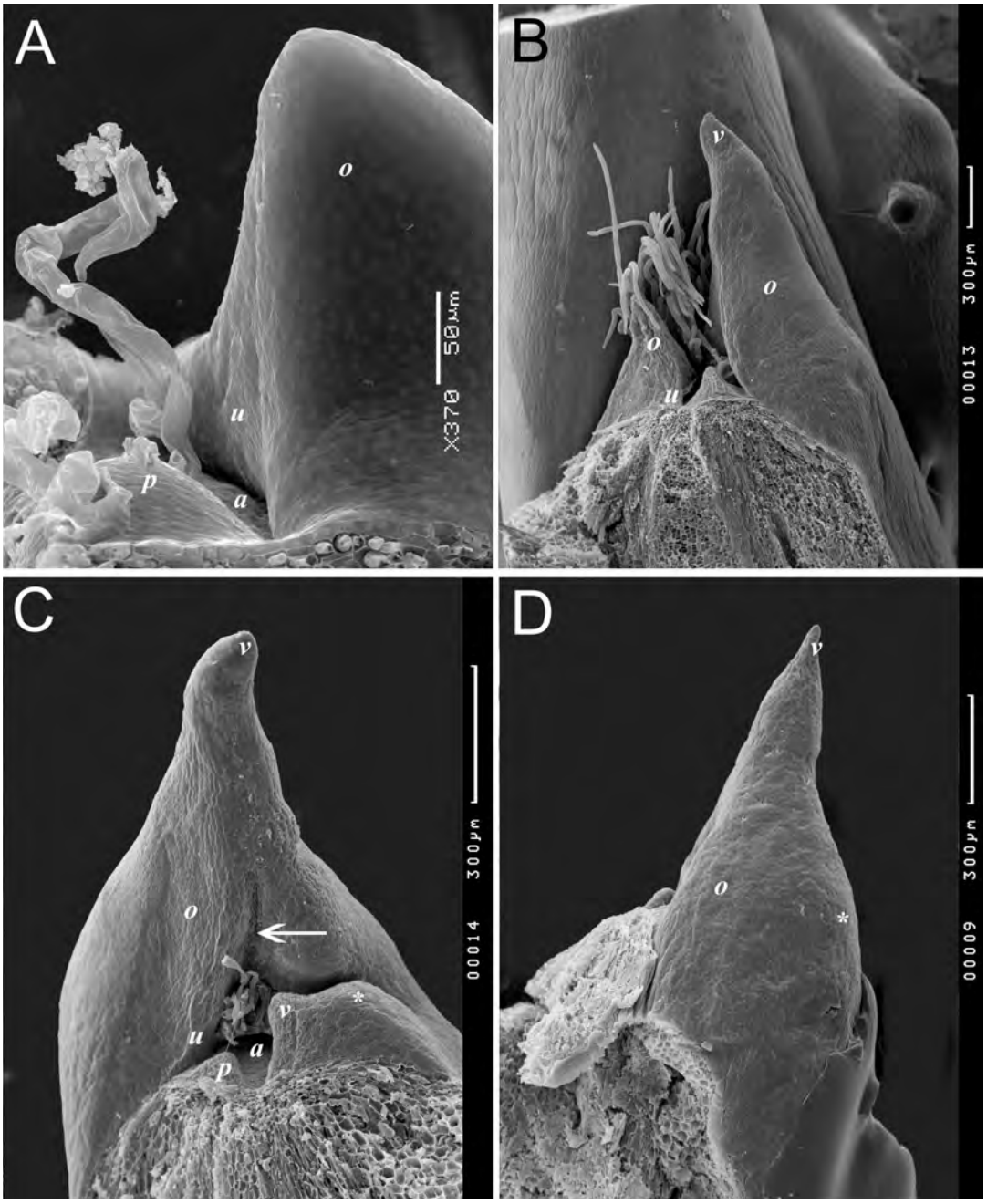

Figure 3. Developing leaves of *Senecio crassissimus*. A – terminal bud and initiated leaf primordium; B – terminal bud and leaf primordia; C – *Vorläuferspitze* and subunifacial leaf blade; D – abaxially growing young leaf. *a* – apex; *p* – leaf primordium; *o* – *Oberblatt*; *u* – *Unterblatt*; *v* – *Vorläuferspitze*; *arrow* – adaxial side of the *Oberblatt*; *asterisk* – thickening abaxial side.

Oberblatt differentiates into the unifacial *Vorläuferspitze* bearing more or less tiered epidermal cells (Fig. 3B, C). The basal part of the *Oberblatt* remains bifacial. It elongates intercalarily at its very base near the border to the *Unterblatt*. While elongating, the *Oberblatt* also thickens throughout on its abaxial side (Fig. 3D). This abaxial thickening forms a longitudinal dorsal ridge which further on gives rise to most of the leaf blade. The abaxial side of the developing leaf blade greatly

widens with this dorsal growing, whereas the adaxial side nearly retains its original width. It looks like a strip, gradually tapering as the leaf blade grows (Fig. 3C).

Discussion

Both studied species are characterized by an identical leaf development from the initiation of the leaf primordium up to the differentiation of a short unifacial *Vorläuferspitze*, which differs well from the proximal part of the *Oberblatt* in shape and tiered arrangement of its epidermal cells. The species under consideration share a leaf blade formation by means of the basal intercalary growing of the *Oberblatt*. However, the vertical plane flattening of this intercalary growing *Oberblatt* is not identical in the two species.

The *Oberblatt* in *C. ficoides* becomes a unifacial structure with completely indistinguishable margins of the ad- and abaxial sides of the former leaf primordium. This unifacial structure widens **adaxially** to form the vertical plane flattened, ensiform leaf blade. Such leaves are quite similar in their shape and unifaciality to the typical ensiform leaves characteristic of Iridaceae. However, the ensiform leaf blade of Iridaceae either develops as an outgrowth on the abaxial side of the primoridum, which replaces its primary apex (Thielke 1948; Roth 1949), or results from the adaxial thickening succeded by the 'marginal' growth of both sides of the primordium (Rudall 1990; Sajo & Rudall 1999). Thus, the ensiform leaves of *C. ficoides* are developmentally very similar, but not identical with the classic ensiform leaves of Iridaceae.

The *Oberblatt* in *S. crassissimus* retains its adaxial side which extends up to the very *Vorläuferspitze*. The vertical plane flattening of the *Oberblatt* results from its **abaxial** growth. Such a growth causes the abaxial side of the *Oberblatt* to widen greatly, whereas its adaxial side is unaffected. Therefore, the adaxial side becomes relatively narrower during the widening of the ensiform leaf. The definitive ensiform leaves in this species are resultantly subunifacial and differ from the classic ensiform leaves not only in obovate shape of their leaf blade, but also in their subunifaciality and the mode of vertical plane flattening. That is why these leaves are worth being termed 'sub-ensiform'.

Conclusions

The ensiform leaves in *Curio ficoides* and *Senecio crassissimus* sharply differ in the modes of vertical plane flattening. These are adaxial growth in the former and abaxial growth in the latter. Besides, the ensiform leaf blades in *S. crassissimus* are subunifacial contrary to their unifacial counterparts in *C. ficoides*. These differences corroborate a convergent origin of the ensiform leaves in the species concerned.

The leaves of *C. ficoides* are very similar, although not identical to the classic ensiform leaves of Iridaceae in their development and structure. The leaves of *S. crassissimus* are more distinct and deserve to be categorized as subensiform leaves.

The development of ensiform leaves in the two species under consideration shows both common characters (initiation as a bifacial primordium, differentiation of *Unter-* and *Oberblatt*, unifacial *Vorläuferspitze*, overdeveloped abaxial side of the leaf blade) and essential differences (complete vs incomplete abortion of the adaxial side; adaxial vs abaxial growth to become vertically flattened). Different evolutionary transformations of a common ancestral gene network, which determines

leaf development, are thereof concludable. If so, these two species may turn out to be valuable model objects for studying the evolutionary rearrangements of gene networks in higher plants.

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References

Goryshina T.K. (1979): Ekologia rastenij [Plant ecology]. – Moscow: Vysshaja shkola. [In Russian]

James S.A. & Bell D.T. (2000): Leaf orientation, light interception and stomatal conductance of *Eucalyptus globulus* ssp. *globulus* leaves. – Tree Physiol. **20**: 815–823.

Jeffrey C. (1992): The tribe Senecioneae (Compositae) in the Mascarene Islands with an annotated world check-list of the genera of the tribe. – Kew Bull. **47**: 49–110.

Heath P.V. (1997): Three new generic names in Asteraceae: part 1. – Calyx **5**: 136.

Pelser P.B., Nordenstam B., Kadereit J.W. & Watson L.E. (2007): An ITS phylogeny of tribe Senecioneae (Asteraceae) and a new delimitation of *Senecio* L. – Taxon **56**: 1077–1104.

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

Rowley G.D. (2002): *Senecio*. – In: Eggli U. [ed.]: Illustrated handbook of succulent plants: Dicotyledons: 29–43. – Berlin, Heidelberg: Springer.

Rudall P.J. (1990): Comparative leaf morphogenesis in Iridaceae. – Bot. Jahrb. Syst. **122**: 241–260.

Sajo M.G. & Rudall P.J. (1999): Systematic vegetative anatomy and ensiform leaf development in *Xyris* (Xyridaceae). – Bot. J. Linn. Soc. **130**: 171–182.

Smith M. & Ullberg D. (1979): Effect of leaf angle and orientation on photosynthesis and water relation in *Silphium terebinthinaceum*. – Amer. J. Bot. **76**: 1714–1719.

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

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

Werk K.S. & Ehleringer J. (1984): Non-random leaf orientation in *Lactuca serriola* L. – Pl. Cell Environm. **7**: 81–87.

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