

Are the trichomes in corollas of Mutisieae (Asteraceae) really twin hairs?

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Received May 2002; accepted for publication August 2002

The corollas of three species of *Onoseris*, 13 species of *Trichocline* and one species of *Uechtritzia* (Asteraceae, Mutisieae) exhibit trichomes that are morphologically similar to the twin hairs which are traditionally considered exclusive of the cypselas in Asteraceae. Four types of trichomes were found: 1-celled, 2-celled, 3-celled, and 4-celled. The 3-celled and 4-celled corolla hairs are those which most resemble the typical cypselas twin hairs. The ontogeny of the corolla hairs was analysed and coincidences with the ontogeny of the cypselas twin hairs were found. (1) An anticlinal division of the epidermal mother cell originates two hair cells which, in turn, originate the basal cells (sometimes one of them is reduced or similar to the epidermal cells) by oblique or periclinal subdivision. (2) In some cases the basal cell(s) of the 3- or 4-celled corolla hair elongates and reaches the same length as the hair cells. The same kind of trichomes have been demonstrated in cypselas of Mutisieae. (3) The 1- and 2-celled corolla hairs have already been described as variants of the cypselas twin hairs. Based on this evidence we conclude that the corolla hairs of *Onoseris*, *Trichocline* and *Uechtritzia* are twin hairs. It is hypothesized that the 1–4 corolla hairs could be involved in water absorption, as occurs in the cypselas twin hairs. © The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2002, 140, 427–433.

ADDITIONAL KEYWORDS: *Onoseris* – ontogeny – *Trichocline* – *Uechtritzia* – Zwillingshaare.

INTRODUCTION

During a study of the genus *Onoseris* Willd. (Asteraceae, Mutisieae) (G. Sancho, unpubl.), the presence of corolla trichomes that are morphologically similar to cypselas twin hairs was observed. The existence of these distinctive hairs was then also detected on the corollas of other genera of Mutisieae such as *Trichocline* Cass. and *Uechtritzia* Freyn. *Onoseris* (31 species) are perennial herbs or subshrubs that grow from Central America to western Argentina, *Trichocline* (22 species) are perennial herbs from South America, and *Uechtritzia* (three species) are Asiatic perennial herbs.

Twin hairs, also called double hairs and *Zwillingshaare* (Kraus, 1866), are the characteristic trichomes of cypselas of Asteraceae. They represent a synapomorphy of the subfamilies Cichorioideae and Asteroideae, with the third subfamily, the primitive Barnadesioideae, characterized by its barnadesioid

hairs (Bremer & Jansen, 1992; Katinas & Stuessy, 1997).

Traditionally, authors agreed on the exclusive presence of these trichomes in the cypselas of Asteraceae (Hess, 1938; Ramayya, 1962; Roth, 1977). Their morphology and ontogeny were extensively studied in the family (Kraus, 1866; Macloskie, 1883; Hanausek, 1902, 1910; Hess, 1938; Roth, 1977), and Freire & Katinas (1995) analysed particularly the twin hairs in the subtribe Nassauviinae (tribe Mutisieae). Twin hairs basically comprise two triangular or rectangular, short basal cells, one sometimes reduced, and two elongated, cylindrical or elliptical hair cells, completely united with each other along their longitudinal walls.

The basic ontogeny of the twin hairs is represented by an epidermal mother cell that divides by an anticlinal wall and originates two hair cells (Fig. 1A). Next, each hair cell divides by a periclinal or oblique wall (Figs 1B,C). The epidermal mother cell thus becomes subdivided into four daughter cells: two basal cells and two hair cells (Fig. 1D).

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Great variation in twin hair morphology was demonstrated by Hess (1938) and Freire & Katinas (1995) and involves differences in size, length, wall thickness, degree of divergence, and degree of development or reduction of the hair cells and/or the basal cells. Despite this variation, all these trichomes share the same ontogeny.

The hairs found in the corollas of *Onoseris*, *Trichocline* and *Uechtritzia*, most of them with two parallel, long hair cells, resemble the typical cypsela twin hairs. Ontogenetic studies are essential to determine if indeed these corolla trichomes are really twin hairs.

The objectives of this paper are to examine the morphology of mature trichomes in the corollas of species of *Onoseris*, *Trichocline* and *Uechtritzia*, to analyse their ontogeny in buds and mature corollas and to compare it with the ontogeny of cypsela twin hairs.

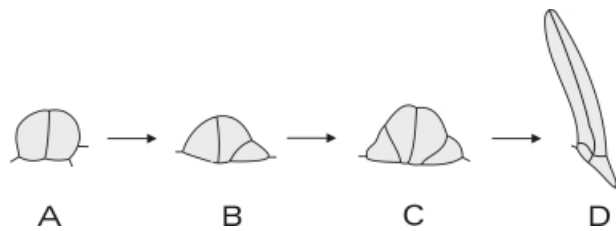


Figure 1. A–D. Ontogeny of the typical twin hair in cypselas of Asteraceae (redrawn from Freire & Katinas, 1995).

MATERIAL AND METHODS

This study is based on specimens from F, LP, MO, US, and WIS herbaria (abbreviation as in Index Herbariorum, Holmgren, Holmgren & Barnett, 1990). A list of specimens investigated with vouchers is given in the Appendix I. All 31 species of *Onoseris*, 21 species of *Trichocline* and one species of *Uechtritzia* were studied. *Trichocline spathulata*, recently transferred to the genus *Amblyosperma* (Hind, 2001), is considered here as species of *Trichocline* and thus included in the analysis.

For microscopic examination, corollas in buds and mature capitula were observed after being boiled in water, then rinsed and stained with 2% safranin. Drawings were made by the authors using an Olympus CH2 microscope with camera-lucida. For scanning electron microscopy (SEM) studies, the material was placed directly on the stubs and coated with gold. The samples were scanned and photographed in a Jeol JSM-T 100 Scanning Electron Microscope.

Descriptive terminology for trichomes follows Ramayya (1962) and Hess (1938). To avoid confusion in the terminology we will call the trichomes analysed here 'corolla hairs', and restrict 'twin hairs' to the trichomes traditionally described for the cypselas of Asteraceae. The terms 'trichome' and 'hair' are used as synonyms.

RESULTS

The type, characteristics, and distribution of corolla hairs, for each of the analysed species are summarized in Table 1. Corolla hairs were found in three of the 31

Table 1. Species of *Onoseris*, *Trichocline* and *Uechtritzia* with corolla hairs

Species	Type of corolla hairs	Short/Long	Distribution in corolla
<i>Onoseris castelnaeana</i>	1-, 2-, 3-, and 4-celled	long	lobes
<i>O. cumingii</i>	2- and 3-celled	long	tube (in a ring)
<i>O. odorata</i>	2- and 3-celled	long	tube (in a ring)
<i>T. catharinensis</i>	3- and 4-celled	long	lower half of the tube
<i>T. caulescens</i>	2-celled	long	tube
<i>T. cineraria</i>	2-celled	short	tube
<i>T. deserticola</i>	2-, 3-, and 4-celled	short	tube (in a ring)
<i>T. dealbata</i>	2-, 3-, and 4-celled	short	under the lobes and tube
<i>T. exscapa</i>	2-celled	long	tube
<i>T. heterophylla</i>	2, 3-, and 4-celled	long	tube
<i>T. incana</i>	4-celled	long	tube
<i>T. linearifolia</i>	3-celled	long	tube
<i>T. maxima</i>	3-, and 4-celled	long	tube
<i>T. reptans</i>	3-celled	long	tube
<i>T. spathulata</i>	2-, 3-, and 4-celled	long	tube
<i>T. speciosa</i>	3- and 4-celled	long	tube
<i>Uechtritzia kokanica</i>	4-celled	long	under the lobes

species of *Onoseris*, in 13 of the 21 species of *Trichocline*, and in the only species of *Uechtritzia* analysed.

POSITION

Onoseris, *Trichocline* and *Uechtritzia* have dimorphic florets. Corolla hairs are found mostly in the middle of the corolla tubes (Table 1) of the central florets in *Onoseris* and *Trichocline*, and near the apex in the marginal corollas of *Uechtritzia*. The trichomes are present on the external epidermis. The longest hairs are adpressed or parallel to the surface with the trichome apex pointing toward the apex of the corolla.

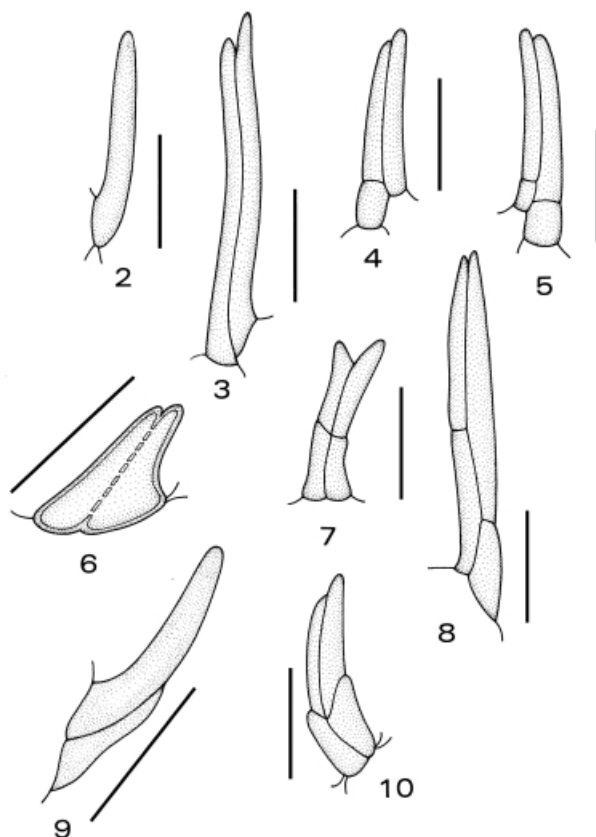
DESCRIPTION

Basal cells: One, two or absent; when present short or long, subtriangular to rectangular, with thick or thin walls. Hair cells: One or two, cylindrical or elliptical, elongated, equal or subequal in length, acute or obtuse at the apex, completely united with each other along their longitudinal walls. The walls are thin or heavily thickened, with or without pits. Length of hairs ranges from 50 μm to 290 μm .

Corolla hairs can be 1-celled (constituted by one hair cell; Figs 2, 12), 2-celled (with two hair cells; Figs 3, 13), 3-celled (with two hair cells and one basal cell distinct from the epidermal cells; Figs 4, 14, 15) and 4-celled (with two basal cells and two hair cells; Fig. 5). For the purpose of discussion, these hairs will be provisionally distinguished as '1-celled corolla hairs', '2-celled corolla hairs', '3-celled corolla hairs', and '4-celled corolla hairs', respectively. The 1-celled corolla hairs are found only in *Onoseris castelnaeana* together with the other three types of trichomes (Table 1).

The 2–4-celled corolla hairs can be divided into two categories: short and long (Table 1). Short hairs (Fig. 6) are 50–90 (max. 110) μm in length, the hair cells are equal in length, obtuse at the apex, and walls are very thick, with many pits. They were found only in three species of *Trichocline* (Table 1). Long hairs (Figs 3–5) are 120–230 (min. 100, max. 290) μm long, with the hair cells generally subequal in length, acute at the apex, and thin walls with no evident pits. The combination of short and long hairs never coexist in the same species. Variation of all these types involves the hair cells slightly diverging at the tips (Fig. 7), septation (Figs 8, 17, 18), one hair cell very short (Fig. 9), and the basal cells long (Fig. 10). Sometimes one basal cell elongates and resembles a hair cell (Fig. 16).

The corolla hairs are commonly accompanied by other types of hairs such as biserial glandular hairs (in most species), oblique-septate-flagellate hairs (*T. maxima*, *T. excapa*), and simple biserial hairs (*T. maxima*, *T. aurea*, *T. humilis* and *T. plicata*). The

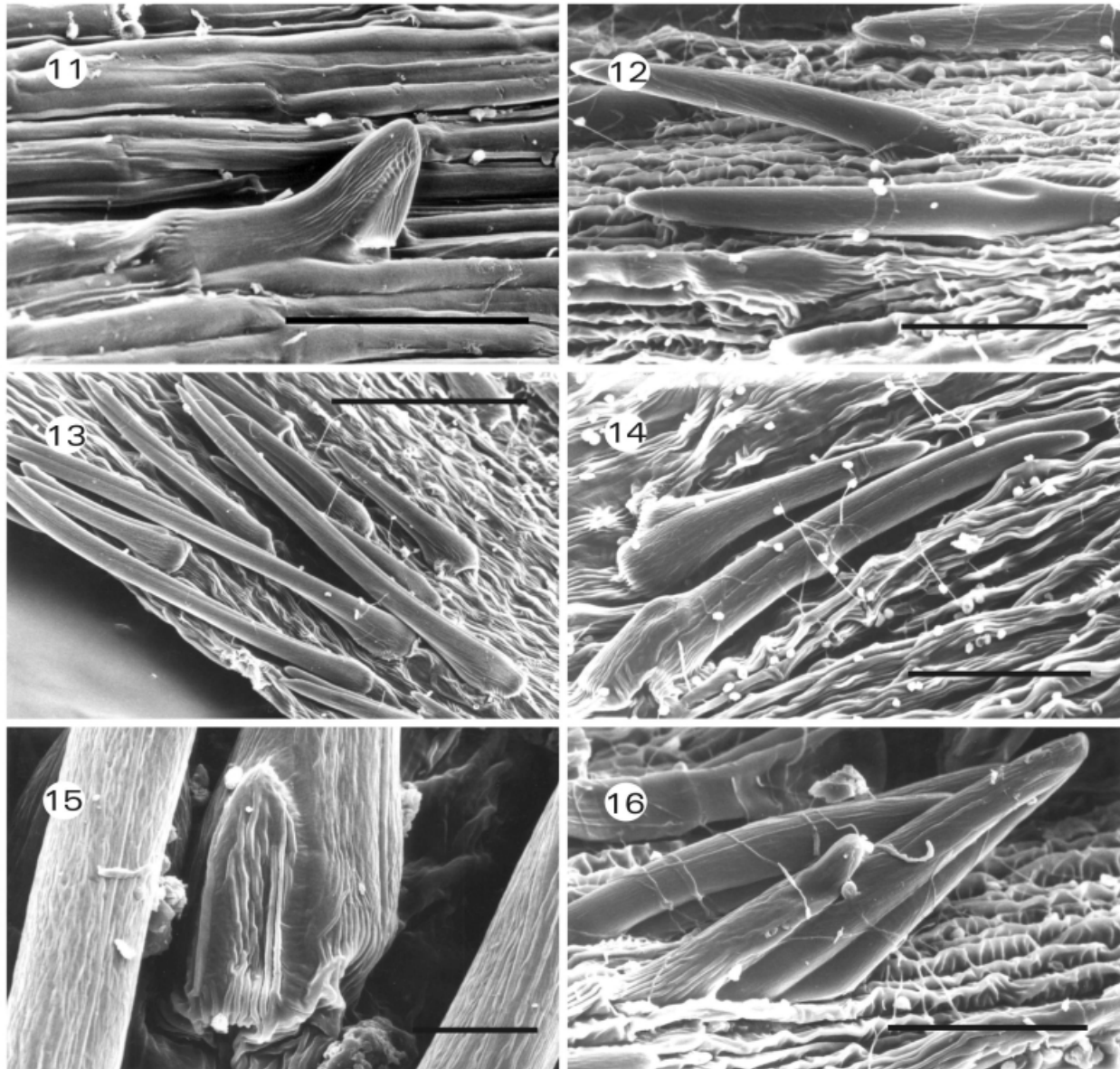


Figures 2–10. Corolla hairs in *Onoseris*, *Trichocline* and *Uechtritzia*. Scale bars = 100 μm . Fig. 2. 1-celled hair. *O. castelnaeana*. Coll. Vargas 403, LP. Fig. 3. 2-celled hair. *O. odorata*. Coll. López *et al.* 7387, LP. Fig. 4. 3-celled hair. *T. catharinensis*. Coll. Pereira and Pabst 7720, LP. Fig. 5. 4-celled hair. *T. catharinensis*. Coll. Pereira and Pabst 7720, LP. Fig. 6. Short 2-celled hair. *T. dealbata*. Coll. Ruiz Leal 1192, LP. Fig. 7. Divergent and septate 2-celled hair. *O. castelnaeana*. Coll. Vargas 403, LP. Fig. 8. Septate 2-celled hair. *T. heterophylla*. Coll. Gallinal *et al.* 2810, LP. Fig. 9. 2-celled hair with one hair cell very short. *O. castelnaeana*. Coll. Vargas 403, LP. Fig. 10. 4-celled hair with long basal cells. *U. kokanica*. Coll. Zaprjagaev s.n., WIS.

few-celled simple biserial hairs can occasionally resemble the corolla hairs, but the former are different because they have strongly stained cells with dense content and a visible nucleus.

ONTOGENY

- (1) One-celled corolla hairs: one epidermal mother cell elongates and differentiates into a hair cell.
- (2) Two-celled corolla hairs: one epidermal mother cell divides by an anticlinal wall, both cells elongate and differentiate into two hair cells.

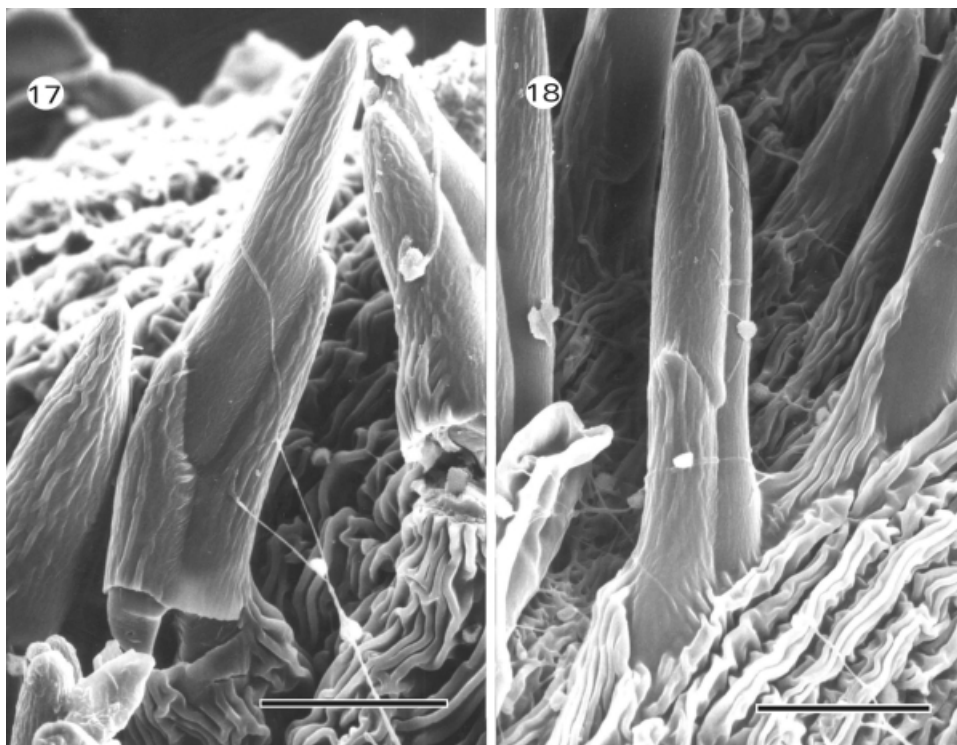


Figures 11–16. Fig. 11. First step of the ontogeny of 2-, 3- and 4-celled corolla hairs, showing the anticlinal division of the epidermal mother cell. *Onoseris odorata*. Coll. Ferreyra 6353, LP. Scale bar = 50 μm . Fig. 12. 1-celled hairs. *O. castelnaeana*. Coll. Vargas 403, LP. Scale bar = 50 μm . Fig. 13. 2-celled hairs. *O. odorata*. Coll. Ferreyra 6353, LP. Scale bar = 100 μm . Fig. 14. 3-celled hairs, note the long basal cell. *O. odorata*. Coll. Ferreyra 6353, LP. Scale bar = 50 μm . Fig. 15. 3-celled hair, detail of the basal cell. *O. odorata*. Coll. López *et al.* 7387, LP. Scale bar = 20 μm . Fig. 16. 3-celled hair with one basal cell very elongated. *O. castelnaeana*. Coll. Vargas 403, LP. Scale bar = 50 μm .

(3) Three-celled corolla hairs: one epidermal mother cell divides by an anticlinal wall (Fig. 11), both cells elongate and differentiate into two hair cells. When the hair cells have elongated, one of them divides by an oblique or periclinal wall and originates one basal cell. (4) Four-celled corolla hairs: the epidermal mother cell divides by an anticlinal wall, both cells elongate and differentiate into two hair cells. When the hair cells

have elongated, both cells divide by an oblique or periclinal wall originating two basal cells.

In summary, two lines of modification (Fig. 19) explain the variation of the corolla hairs. (A) One epidermal mother cell, which does not undergo division, originates the 1-celled trichomes; and (B) one epidermal mother cell originates a 2-celled trichome by an anticlinal division, which in turn can: (1) remain as a



Figures 17–18. Septate 2-celled corolla hairs. *Onoseris castelnaeana*. Coll. Vargas 403, LP. Scale bars = 25 μm . Fig. 17. One hair cell shorter at the right, and the septum at the left. Fig. 18. One hair cell slightly shorter at the back, and the septum at the front.

mature 2-celled trichome; (2) one hair cell by further division originates a 3-celled trichome; (3) the remaining hair cell also divides and originates a 4-celled trichome.

DISCUSSION

Corolla hairs are similar in morphology and ontogeny to the typical cypsela twin hairs of Asteraceae and to some of their variants, and therefore we conclude that hairs found in corollas of *Onoseris*, *Trichocline* and *Uechtrizia* are twin hairs. The ontogenetic process and the morphology of the twin hairs and of the corolla hairs are similar because: (1) in the 3–4-celled hairs a first anticlinal division of the epidermal mother cell originates two hair cells, and a further oblique or periclinal subdivision of them originates the basal cells (sometimes one of them is reduced or is similar to the epidermal cells; Fig. 19B); (2) sometimes the basal cell(s) of the 3- or the 4-celled corolla hair elongates and becomes as long as the hair cells (Fig. 16). The same kind of trichome, called ‘crenate hairs’, was found in cypselas of Mutisieae (e.g. *Acourtia nana*, *Leibnitzia occimadrensis*, *Chaptalia pringlei*) and was established as a variation of the typical twin hair (Freire & Katinas, 1995: 134, fig. 2C); and (3) the 1-

and 2-celled corolla hairs (Figs 2,3), that show a departure from the typical twin hair, were also established as a variation of the typical twin hairs (Hess, 1938: 465, figs 7d,h).

Twin hairs in corollas were recently reported for some species of *Encelia* (Asteraceae, Heliantheae) (Carpenter & Clark, 1999; Carpenter, 1999; our own observations), a genus that inhabits desert environments of North and South America. In *Encelia*, the twin hairs (2–4-celled) were found only in the tube of central corollas, adpressed to the surface with the trichome tip pointing toward the apex, as in most of the species analysed here.

Twin hairs in corollas can be viewed as an ontogenetic ‘mistake’ with no direct adaptive value distinct from, for example, corolla uniseriate hairs. However, some adaptive value may be suggested for corolla twin hairs. Hess (1938) postulated that water absorption is an important function of the cypsela twin hairs, mainly for those trichomes with thickened walls. According to him, the abundance of pits leads to a quick and uniform distribution of the absorbed humidity. Thus, corolla hairs also could help water absorption, especially taking into account that most species of *Trichocline*, *Onoseris castelnaeana*, *O. cumingii*, *O. odorata*, *Uechtrizia kokanica* and *Encelia* grow in

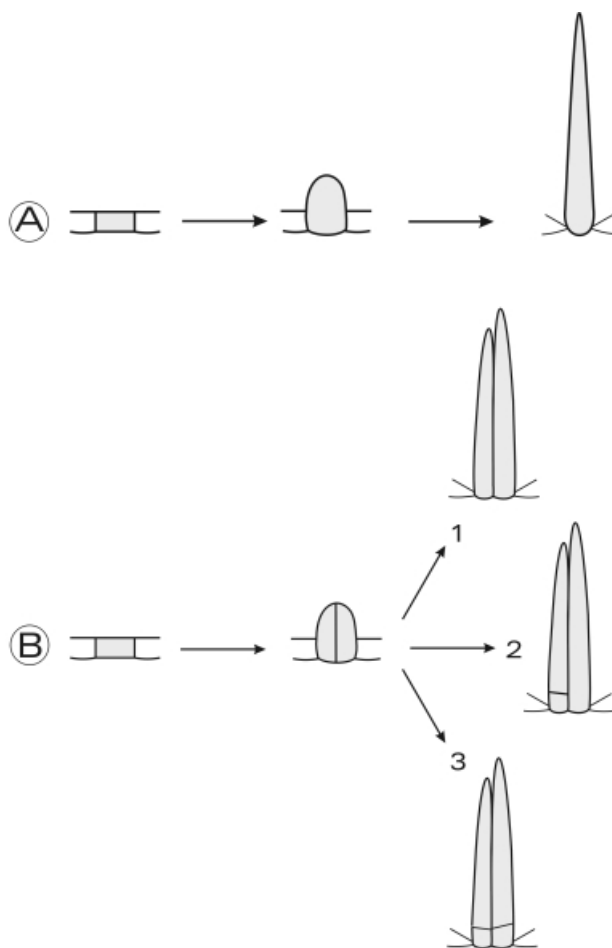


Figure 19. Two lines of modification in the ontogeny of corolla hairs. (A) One epidermal mother cell originates the 1-celled hairs. (B) One epidermal mother cell originates, after the first anticlininal division, 2-, 3- and 4-celled hairs.

dry and semiarid environments. The distribution of hairs in the central florets (except *Uechtrizia*) would be more efficient in humidity retention than if they were distributed in the more exposed marginal florets.

Trichocline and *Uechtrizia* belong to the *Gerbera*-complex (*Chaptalia*, *Gerbera*, *Leibnitzia*, *Perdicium*, *Trichocline* and *Uechtrizia*) (Zardini, 1975; Hansen, 1990; Bremer, 1994; Katinas, 1998), a group of genera mainly distinguished by their scapose habit. Within the complex, *Trichocline* and *Uechtrizia* share dimorphic florets, the marginal florets with well-developed staminodes, and cypselas truncated at the apex. Since none of the remaining genera of the complex exhibit corolla twin hairs, their presence in *Trichocline* and *Uechtrizia* becomes a new character that relates both genera.

Onoseris have been associated with *Trichocline* (Ferreyra, 1944; Hansen, 1991), although *Urmenetea*

is currently considered the closest genus to *Onoseris* (Hansen, 1991; Bremer, 1994; G. Sancho, unpubl.). *Onoseris* and *Trichocline* share the radiate capitula, female marginal florets with developed staminodes, bilabiate corollas with limbs abaxially pubescent, and central florets with papillose anther filaments. The corolla twin hairs found *Onoseris* and *Trichocline* represent another feature shared by both genera.

The presence of corolla twin hairs in two phylogenetically distant tribes of Asteraceae such as Mutisieae (*Onoseris*, *Trichocline* and *Uechtrizia*) and Heliantheae (*Encelia*) would suggest convergent evolution as a response to similar environmental characteristics. More studies in genera of other tribes are necessary to address to what extent the twin hairs in corollas are distributed in the family.

ACKNOWLEDGEMENTS

The authors thank Susana E. Freire and one anonymous reviewer for helpful suggestions on the manuscript, and to the curators of F, LP, MO, US, and WIS who let us examine the material. We also thank Víctor H. Calveti for designing the illustrations. This work was supported by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina, Smithsonian Institution, and the National Geographic Society (Grant 5776–96).

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APPENDIX 1

REPRESENTATIVE SPECIMENS EXAMINED

Onoseris

O. acerifolia Kunth (Hutchinson 1395, US; López *et al.* 4076, LP); *O. alata* Rusby (Cabrera *et al.* 14525, LP; Jiménez 28, LP); *O. albicans* (D. Don) Ferreyra (Sagástegui 3748, LP; Sánchez Vega 233, LP); *O. amplexicaulis* Ferreyra (Ferreyra 7600, LP; Macbride and Featherstone 131, F); *O. annua* Less. (Ferreyra 7376, US; Pennell 15408, MO); *O. brasiliensis* Cabrera (Hatschbach 34719, LP); *O. cabrae* Ferreyra (Ferreyra and Acleto 15339, MO; Hutchinson and Wright 5448, MO); *O. castelnaeana* Wedd. (Vargas 403, 404, LP; Gentry *et al.* 23341, MO); *O. chrysactinoides* Sagást. et Dillon (Sagástegui 14025, US; Sagástegui and Telles 12704, MO); *O. costaricensis* Ferreyra (Valerio s.n., U; Pittier 10596, US); *O. cumingii* Hook. et Arn. (Haught 30, US); *O. donnell-smithii* (Coul.) Ferreyra (Calderón 2018, F, US, Standley 19701, US); *O. drakeana* André (Uribe 5355, US); *O. fraterna* S. F. Blake (Fournet 472, US; Wasshausen and Wood 2203, US); *O. gnaphalioides* Muschl. (López and Sagástegui 5177, LP; López *et al.* 4075, LP); *O. hastata* Wedd. (Castellanos 20218, LP; Cabrera *et al.* 18286, LP); *O. hyssopifolia* Kunth (King 6648, US; Alonso Ortiz

330, US); *O. humboldtiana* Ferreyra (Ferreyra 846, MO); *O. linearifolia* Sagást. (Sánchez Vega *et al.* 956, US); *O. lopezii* Ferreyra (Hudson 1073, US; King and Bishop 9124, F); *O. macbridei* Ferreyra (Smith and Blas 4914, US; Sánchez Vega 325, LP); *O. minima* Domke (Weberbauer 7440, US); *O. odorata* (D. Don) Hook. et Arn. (Ferreyra 2513, 6353, LP; López *et al.* 7387, LP); *O. onoseroides* (Kunth) B. L. Robinson (Haught 3937, LP; Allen 5893, US); *O. peruviana* Ferreyra (Soukup 2501, US; Dudley 11487, US); *O. purpurea* (L. f.) S. F. Blake (García Barriga 12134, US; Pérez Arbelaez and Cuatrecasas 8315, F); *O. sagittata* (Rusby) Rusby (Fosberg 28652, 28604, US); *O. salicifolia* Kunth (Haught 3318, LP; King 6607, US); *O. silvatica* Greenm. (Idrobo and Schultes 569, F; Tonduz 13597, F); *O. speciosa* Kunth (Wurdack 1097, LP; Díaz *et al.* 3469, US); *O. weberbaueri* Ferreyra (Gentry *et al.* 61362, MO; Hutchinson and Wright 3522, F).

Trichocline

T. aurea (D. Don) Reiche (Barros 1707, LP; Looser 677, LP; Ruiz s/n, LP); *T. auriculata* (Wedd.) Hieron. (Hurrell 689, LP; Okada 3099, LP); *T. boecheri* Cabrera (Cabrera *et al.* 24526, 24428, LP); *T. catharinensis* Cabrera (Mondin 819, LP; Pereira and Pabst 7720, LP); *T. caulescens* Phil. (Navas 2073, LP; Ricardi *et al.* 35, LP); *T. cineraria* (D. Don) Hook. et Arn. (Ruiz Leal 4865, 8549, LP); *T. dealbata* (Hook. et Arn.) Griseb. (Ruiz Leal 1192, 7194, LP); *T. deserticola* Zardini (Martin 449, LP; Zöllner 670, LP); *T. exscapa* Griseb. (Maldonado 2962, LP; Sleumer and Vervoorst 3007, LP); *T. heterophylla* (Spreng.) Less. (Chebataroff 1722, LP; Gallinal *et al.* 2810, LP); *T. humilis* Less. (Biraben 5147, LP; Cabrera 12361, LP); *T. incana* Cass. (Biraben 24, LP; Chebataroff 2818, LP); *T. linearifolia* Malme (Ferreira 196, LP; Kumarov 198, LP); *T. macrocephala* Less. (Klein 4913, LP; Smith and Klein 11409, LP); *T. macrorhiza* Cabrera (Cabrera *et al.* 26403, LP; Fabris *et al.* 5427, LP); *T. maxima* Less. (Chebataroff 9112, LP); *T. plicata* Hook. et Arn. (Cabrera *et al.* 24886, 24889, LP); *T. reptans* (Wedd.) B. L. Robinson (Cabrera *et al.* 24099, LP; Meyer *et al.* 21165, LP); *T. sinuata* (D. Don) Cabrera (Cabrera 5667, 6680, LP); *T. spathulata* (A. Cunn. ex DC.) J. H. Willis (Pritzel 140, LP); *T. speciosa* Less. (Montes 10969, LP; Pedersen 3091, LP).

Uechtritzi

Uechtritzi kokanica (Regel et Schmalh.) Pobed. (Zaprjagaev s.n., WIS).

Encelia

Encelia farinosa A. Gray (Rose 45325, LP; Henrickson 1220, LP).