

Achene hairs and their diversity in the genus *Chaetanthera* Ruiz & Pav. (Mutisieae, Asteraceae)

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Summary:

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A detailed and comprehensive survey of the achenes belonging to 35 of the 42 accepted species of the South American genus *Chaetanthera* Ruiz & Pav. revealed new micro-morphological characters. In particular the achene hairs yielded important and taxonomically significant characters. Three achene hair types were distinguished: “Zwillingshaare” (in various forms), filiform hairs, and single-celled papillae. Glabrous achenes were also recorded; the lack of achene hairs was species specific and, not unexpectedly, was not a useful discriminator for bigger groups. Within a species the hair types were consistent. The diversity of hair types and their distribution throughout the genus was compared to the traditional sub-generic structure proposed by CABRERA (1937). The achenes of those taxa belonging to the current subgenera *Proselia*, *Euchaetanthera*, *Tylloma* and *Glandulosa* are never glabrous and have very similar “Zwillingshaare” (90–120 µm long, obovate to elliptic or lanceolate in outline). Achenes of the subgenus *Oriastrum* show consistent variations of spherical or conical-deltoid “Zwillingshaare” (10–50 µm in length) while achenes of taxa in the subgenus *Carmelita* are glabrous or have tiny (7–15 µm in length) spherical “Zwillingshaare”. Achenes of the subgenus *Egania* are mostly glabrous, with a couple of taxa showing single-celled papillae thereon, and two taxa long filamentous (but not “Zwillingshaare”) hairs (approx. 450 µm in length). Based on the hair types, clear divisions within the genus can be seen. However these need to be supported by correlating characters. A revision of the genus *Chaetanthera* is currently in progress.

Zusammenfassung:

Eine detaillierte und umfassende Untersuchung der Achänen von insgesamt 35 der 42 akzeptierten Arten der südamerikanischen Gattung *Chaetanthera* Ruiz & Pav. zeigt neue mikromorphologische Merkmale auf. Insbesondere die Achänenhaare liefern wichtige und für die Taxonomie verwertbare Merkmale. Drei grundlegende Achänenhaartypen können unterschieden werden: Zwillingshaare (in verschiedenen Formen), filiforme Haare und einzellige Papillen. Relativ häufig treten kahle Achänen auf; das Fehlen von Haaren ist artspezifisch, faßt jedoch, wie zu erwarten, keine größeren Gruppen zusammen. Innerhalb einer Art sind die auftretenden Haartypen einheitlich. Die Verteilung der Haartypen innerhalb der Gattung wird mit der von CABRERA (1937) vorgeschlagenen Unterteilung verglichen. Dabei ergibt sich folgendes Bild: Bei den in den Untergattungen *Proselia*, *Euchaetanthera*, *Tylloma* und *Glandulosa* zusammengefaßten Arten sind die Achänen nie kahl und weisen große Ähnlichkeit in den

Zwillingshaaren auf: Elliptisch oder lanzettförmig mit einer Länge von 90–120 μm . Die Arten der Untergattung *Oriastrum* tragen auf den Achänen kugel- oder kegel- bis deltaförmige Zwillingshaare mit einer Länge von 10–50 μm . Die Achänen der Arten der Untergattung *Carmelita* sind kahl oder besitzen kleine, kugelförmige Zwillingshaare mit einer Länge von 7–15 μm . Die Arten der Untergattung *Egania* haben überwiegend kahle Achänen mit Ausnahme von zwei Arten mit einzelligen Papillen auf den Achänen und zwei weiteren Arten mit filiformen, bis zu 450 μm langen Haaren (keine Zwillingshaare). Aus diesen Ergebnissen kann der Schluß gezogen werden, daß aufgrund der auf den Achänen gefundenen Haartypen eine deutlichere Gliederung der Gattung vorgenommen werden kann. Es ist jedoch notwendig, diese durch zusätzliche Merkmale zu stützen. Eine komplette Revision der Gattung *Chaetanthera* ist in Bearbeitung.

Introduction

Achene characters are often used to taxonomic advantage in many genera of the Compositae, (OBERPRIELER 1998, VINCENT 1996, ROMMEL 1979). Of particular interest is the ornamentation of the pericarp epidermal cells – that is the surface characters of the fruit bodies. It has been said that while using ultrastructure features can be useful in establishing concepts, they cannot be used as key characters (KING & ROBINSON, 1970). Nevertheless micro-morphological characters are often studied as generic markers in the Asteraceae. In some cases they are found to obscure generic relationships (Astereae, SUNDBERG, 1985), but equally so, micro-morphological characters can be both useful and consistent markers for generic delimitation (LANE 1985, SCOTT 1985).

1. Infra-generic taxonomy

The predominantly Chilean genus *Chaetanthera*, first described in 1794 by RUIZ and PAVÓN, now circumscribes approximately 40 species. The most recent revision by CABRERA (1937) divided the genus into seven subgenera. The defining generic character linking these species is said to be the possession of a winged membrane on the margins of the phyllaries, the outer series of which are foliaceous. The subgenera are distinguished by characters including capitulum size, ornamentation of the apices of the inner series of phyllaries, style arm dimensions, leaf shape, habit, life cycle and achene pubescence (after CABRERA, 1937). Table 1 below summarises the subgenera structure of *Chaetanthera* proposed by Cabrera and the species included in this study.

Since the 1937 revision was published five new taxa have been described: *Chaetanthera chiquianensis* Ferreyra, *C. boliviensis* J.Kost., *C. aymarae* Martic. & Quezada, *C. leptcephala* Cabrera, and *C. perpussilla* (Wedd.) Anderb. & Freire (the last solely distinguished from *Chaetanthera* by the presence of papillose hairs on the achenes). With the exception of *C. boliviensis*, these are broadly included in the subgenus “*Euchaetanthera*”. None of these were analysed here, and neither were examples of *C. australis* Cabrera, *C. brachylepis* Phil. or *C. flabellifolia* Cabrera.

2. Inter-generic taxonomy

Chaetanthera has two putative sister genera – *Pachylaena* D.Don (distinguished by having a plumose pappus) and *Brachyclados* Hook. & Arn. (distinguished by having non-foliaceous external phyllaries, pappus arrayed in 3–4 series and shrubby with \pm pedunculate capitulae). These two very small genera have not been revised since the 1830s. Examples of *Pachylaena atriplicifolia* Hook. & Arn., *Brachyclados lycioides* D.Don and *B. megalanthus* Speng. were observed with a view to their potential for outgroup comparison.

Table 1: Summary of the traditional infra-generic structure sensu CABRERA (1937) of *Chaetanthera* including only the taxa that were surveyed. (Author names after BRUMMITT & POWELL, 1992)

Subgenus	Species names	
<i>Glandulosa</i>	<i>C. glandulosa</i> Remy	
<i>Egania</i>	<i>C. acerosa</i> (Remy) Benth. & Hook. f.	<i>C. pulvinata</i> (Phil.) Hauman
	<i>C. apiculata</i> (Remy) F.Meigen	<i>C. revoluta</i> (Phil.) Cabrera
	<i>C. cochlearifolia</i> (A.Gray) B.L.Rob.	<i>C. sphaeroidalis</i> (Reiche) Hicken
	<i>C. dioica</i> (Remy) B.L.Rob.	<i>C. stuebelii</i> Hieron.
	<i>C. pentacaenoides</i> (Phil.)Hauman	
<i>Oriastrum</i>	<i>C. lycopodioides</i> (Remy) Cabrera	<i>C. planiseta</i> Cabrera
	<i>C. gnaphalioides</i> (Remy) I.M.Johnst.	<i>C. pusilla</i> (D.Don) Hook. & Arn.
	<i>C. minuta</i> (Phil.) Cabrera	
<i>Carmelita</i>	<i>C. villosa</i> D.Don	<i>C. spathulifolia</i> Cabrera
	<i>C. lanata</i> (Phil.) I.M.Johnst.	
<i>Tylloma</i>	<i>C. glabrata</i> (DC.) F.Meigen	<i>C. renifolia</i> (Remy) Cabrera
	<i>C. limbata</i> (D.Don) Less.	<i>C. splendens</i> (Remy) B.L.Rob.
<i>Proselia</i>	<i>C. elegans</i> Phil.	<i>C. serrata</i> Ruiz & Pav.
	<i>C. chilensis</i> (Willd.) DC.	<i>C. valdiviana</i> Phil.
<i>Euchaetanthera</i>	<i>C. ciliata</i> Ruiz & Pav.	<i>C. microphylla</i> (Cass.) Hook. & Arn.
	<i>C. euphrasioides</i> (DC.) F.Meigen	<i>C. moenchioides</i> Less.
	<i>C. flabellata</i> D.Don	<i>C. peruviana</i> A.Gray
	<i>C. incana</i> Poepp.	<i>C. tenella</i> Less.
	<i>C. linearis</i> Poepp.	

3. Achene hairs in the Compositae – morphology and importance

The description and publication concerning the hairs seen on the fruits of the Compositae has been accepted for many years. Although typified by HANAUSEK (1910), HESS (1938) wrote the seminal paper on the typical trichomes unique to the Compositae. They are named “Zwillingshaare” (twin hairs).

Achenes and often their hairs have frequently proven to be fundamentally useful indicators of generic and subgeneric relationships (*Felicia*, GRAU 1973; *Amellus*, ROMMEL 1979; *Grangea*, *Grauanthus* and *Dichrocephala*, FAYED 1979; *Gerbera*-complex, JEFFREY 1967, HANSEN 1989; *Anthemis* L., OBERPRIELER 1998), or even tribal distinctions (DITTRICH, 1985, 1996) in the Astereae. VELEZ (1981) demonstrated that some genera (of the American Asteraceae) have unique hairs, while in other cases several genera can share one hair type. One advantage of using achene characters, and in particular the hairs, is that they are considered to be independent of environment (Grau, pers. comm.). Therefore the variation expressed in these characters forms a source of reliable taxonomic indicators.

The presence or absence of achene hairs has been pivotal to the keying out of the seven subgenera of *Chaetanthera* in the past. CABRERA (1937) recognised two achene hair types - papillose and sericeous-villous, as well as glabrous achenes. HANSEN (1991) noted the presence of both hairy and glabrous achenes in the genus, the former carrying either of two hair types: inflated and tapering, or orbicular. The aim of this study was to establish on a firm basis the existing variation in the achenes and whether this variation might have taxonomic implications.

Methods

Over 650 specimens of the genus *Chaetanthera* were received from the herbaria of GH, K, M, NY, P, W (abbreviated after HOLMGREN et al., 1990) and the private collections of Prof. J. Grau and Dr C. Ehrhart. Nearly 200 collections of 35 *Chaetanthera* species (covering all seven subgenera), 1 species of *Pachylaena*, and 2 of *Brachyclados* were sampled. Citations for typical material observed can be found in Appendix 1. Achenes from both ray and disc flowers were carefully extracted from the herbarium material and placed directly, without further treatment on carbon-coated stubs. These were then sputtered with platinum using a Bal-tec sputterer. Digital images were taken under a high vacuum using a LEO 483VP Scanning Electron Microscope (SEM) at both low and high magnifications.

Using these images the achenes were assessed for 51 characters covering 6 quantitative measures and 45 features including achene shape, achene surface, achene hair shape and construction, and 5 pappus characters.

Results

1. SEM observations and images

During this study three factors indirectly related to the research became apparent. These were the effect of collection age on sample quality, the consistency of achene surface structures relative to maturity and, perhaps most importantly, the SEM focus error.

1.1. Specimen age

The age of the herbarium specimens, with only few exceptions, did not contribute to, or detract from, the quality of achene hair preservation. One of the more distressing features of some specimens was the abundance of hyphal growth obscuring the characters of interest. The disintegration of some features has been attributed to environmental conditions at the time of collection. Only one taxon showed a tendency to have fused achenes – *C. villosa*.

1.2. Mature and immature or sterile achenes

The maturity of the achenes is a difficult parameter to quantify without precise glasshouse surveys. However, casual observation shows that the maturity and fecundity of the achenes particularly affects the size and shape of the achenes, but does not seem to alter the presence, or type, of hairs. As seen in one collection, an achene can increase in length by 30% and in width by 60% as it matures, while the changes in hair dimensions are negligible.

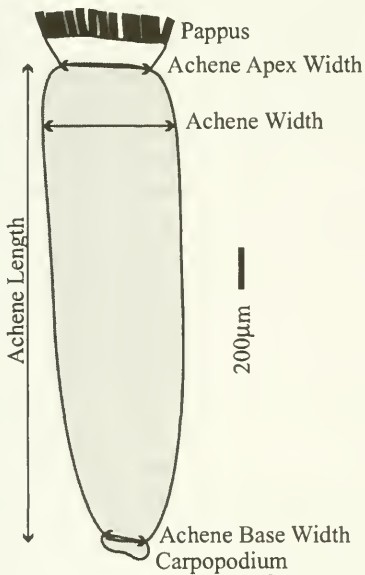
1.3. Focus error

Unusually for SEM observations, the total size of the material samples was sometimes quite large (> 4.00 mm). As a result, it was not always possible to have the complete object entirely in focus, affecting the apparent length of the object. The mean error for large achenes over 2.35 mm in length was calculated at 2.4% of the length. The greatest error was measured for the largest achenes, but rapidly tails off as the general size of the achene shrinks, and the error becomes almost negligible for achene lengths below 2.35 mm (0.4%).

2. Within the genus *Chaetanthera* – quantitative characters

Six quantitative characters were observed. These were achene length and width, achene apex width, achene base width, and achene hair length and width. The measurements of the various dimensions were taken using the guidelines shown in Plate 1 (Figs. 1–2). The Log₁₀ values of each character were plotted in rank order, with the graphs drawn to the same scale so that each character could be easily compared (see Graphs 1–4).

Fig. 1: Location from which the quantitative measurements on the whole achene were taken.



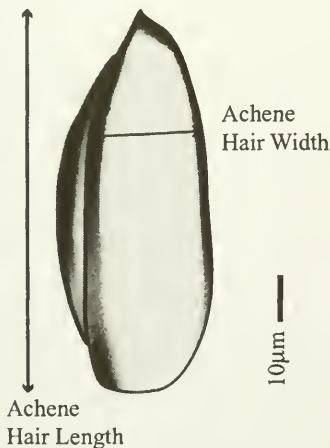
Achene Length: The length of the achene taken from the longest axis from the pappus insertion (apex) to (but not including) the carpodium (base).

Achene Width: taken from the widest point (perpendicular to the long axis) of the fruit.

Achene Apex Width: taken from below the pappus insertion.

Achene Base Width: taken from the where the carpodium and fruit meet. When no carpodium is present, the base width is taken from the homologous region.

Fig. 2: Location from which the quantitative measurements on the achene hairs were taken.

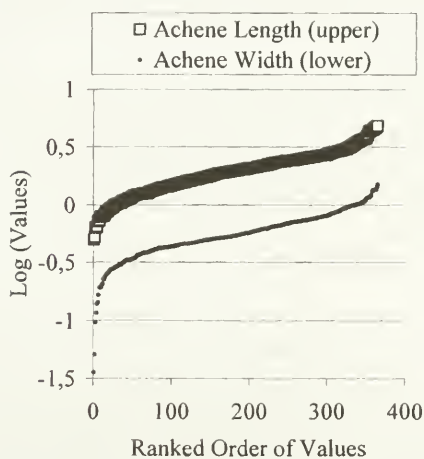


Achene Hair Length: the length is taken parallel to the central cell wall of the 'twin hairs', always from the point where the hair is inserted in the pericarp epidermis.

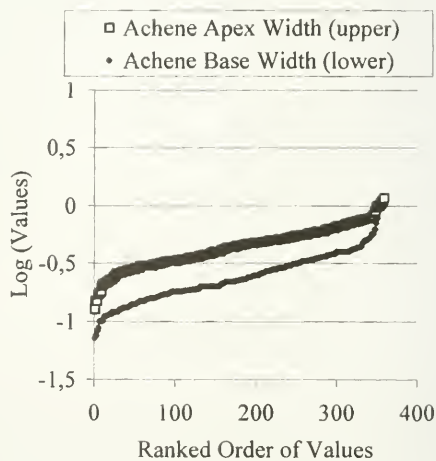
Achene Hair Width: taken from the widest point across the hair perpendicular to the long axis.

N.B. This figure is adapted from an image of a 'twin hair' of the species *C. linearis*.

2.1. Achene length and width: Achene length varies from 0.5 mm (*C. pusilla*) to 4.8 mm (*C. lanata*). The achene widths vary from 0.04 mm (*C. linearis*, immature) to 1.51 mm (*C. villosa*). Achene lengths and widths are continuously distributed in this sample (Graph 1).
 2.2. Achene apex and base widths: The apex widths vary from 0.13 mm (*C. linearis*) to 1.17 mm (*C. spathulata*). Achene base widths vary from 0.07 mm (*C. gnaphalioides*) to 0.79 mm (*C. villosa*). The measurements are continuously distributed in this sample (Graph 2).
 Although there are no discrete groupings, there is still a significant variation by over a factor of ten in achene length and width as well as achene apex and base widths across the data set. In all four cases the linear distribution (see Graphs 1–2) is approximately $y = 0.002x$, indicating that each quantitative character exhibits similar variation. Thus we deduce that all of these four characters (achene length and width, and achene apex and base width) are equally useful for analysing the data, even though they do not show clear evidence of clustering.

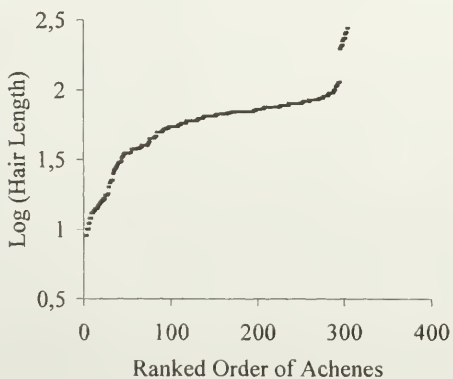


Graph 1: Ranked Order of Log (Achene Length) & Log (Achene Width)

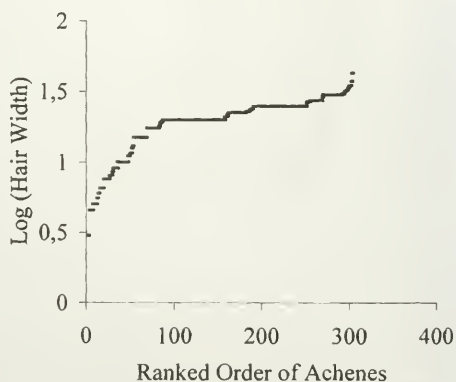


Graph 2: Ranked Order of Log (Achene Apex Width & Achene Base Width)

2.3. Achene hair length and width: When hairs are present on the achenes they can vary from 10 μm to over 450 μm in length. The hairs vary in width from 5 μm to 75 μm . Graphs 3 and 4 have comparatively less smooth, flatter curves, with much bigger tails, particularly at the lower end. They both vary in the same way, the flat part indicating that for about half the achenes, the size of achene hairs is not a good discriminator.



Graph 3: Ranked Order of Log (Achene Hair Length)



Graph 4: Ranked Order of Log (Achene Hair Width)

However, the dramatic tails on the graphs indicate that for large and small extremes hair size, particularly length, becomes an increasingly valuable discriminator. Plotting a linear regression on these curves would not be useful, as it would only apply to about half the sample.

Quantitative characters like these that indicate some clustering, together with those which show less clear patterns of segregation, can be combined to be more informative. We have plotted the Log_{10} values of achene lengths and achene hair lengths against each other (Graph 5). A third qualitative character, achene hair shape, is also represented on the plot. Glabrous achenes are included for illustrative purposes. The various hair types (see qualitative characters) are represented by different symbols. We can see that the 4 hair types have broad hair length distributions. Three obvious bands of hair lengths are seen which correlate with the following hair shapes; filiform, globular and obovate-lanceolate. The glabrous achenes show a similar broad distribution along the x-axis.

Graph 5 indicates that for nearly the same wide range of achene lengths it is possible to have hairs or no hairs. When present the length of these hairs is really tightly associated with their shape. Thus globular hairs are always, in this data set, much shorter in length than any of the obovate-lanceolate hairs. These are in turn always shorter than the filiform hairs. Graph 5 clearly demonstrates that achene hair length and shape are, to some extent, correlated. Furthermore, the hair shape allows the data set to be divided into discrete clusters that were not apparent from the hair length distribution alone.

3. Within the genus *Chaetanthera* – qualitative characters

Qualitative characters of the achenes included shape, cross-section, apical morphology, and surface ornamentation and, for the achene hairs, types, orientation and features. Achene shape varied from pyriform, turbinate, fusiform to oblong, and in cross-section from compressed, terete, semi-terete or triangular. The angles in cross-section can be rounded and shallow, or prominent and sharply angular. The pericarp epidermal cells were classed as parenchymatous, subisodiametric, papillate, striate, centrally depressed or having no surface sculpture.

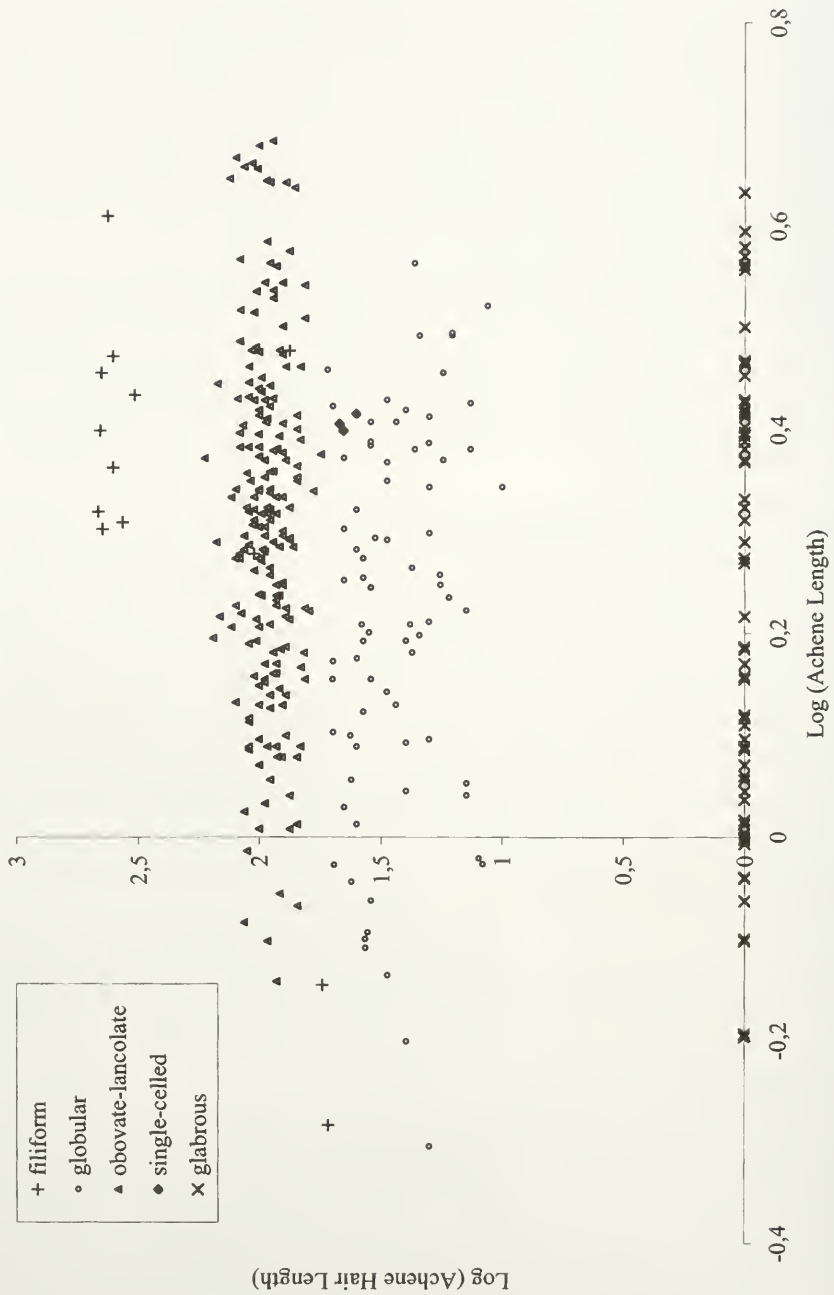
The achene hairs when present were 1-, or 2-celled (parallel or stacked) and displayed a range of shapes (after STEARN, 1995) lanceolate or elliptic, to very small globular, conical or ampulliform hairs, long filiform hairs (RAMAYYA, 1962), or papillae (METCALFE & CHALK, 1979). The tips varied from obtuse or acute and mucronate or apiculate, sometimes shortly bifurcated, rarely depressed. They were variously found to be erect to appressed, and either deflated or inflated (symmetrically or asymmetrically) about the horizontal axis. They covered the achenes sparsely to densely.

Achene hairs were recorded in 30 different species. Within these, three basic hair types were identified: “Zwillingshaare”, filiform hairs and single-celled papillae. The variation is outlined below and the species placements are given in Table 3. The achene hairs were found to be mostly consistent in both shape and size within species (i.e. between collections).

3.1. “Zwillingshaare”

3.1.1. Obovate elliptic to lanceolate or rarely naviculate

These hairs are large, varying in length from (80)–90–120–(130) μm . This hair type is associated with a relatively featureless epidermal surface. The 17 species with these sorts of hairs (*C. chilensis*, *C. ciliata*, *C. elegans*, *C. glabrata*, *C. glandulosa*, *C. incana*, *C. lanata*, *C. limbata*, *C. linearis*, *C. microphylla*, *C. moenchioides*, *C. peruviana*, *C. renifolia*, *C. serrata*, *C. splendens*, *C. tenella*, and *C. valdiviana*) generally have hairs on both the disc and ray achenes, and are very rarely nearly glabrous. This is the most common hair type in *Chaetanthera* and it shows so much variation that it is seldom possible to distinguish collections of species without practice. The extremes of variation in this group of hairs are illustrated with images that can be seen in Plate 2 (Figs. 3–10).



Graph 5: Log (Achene Length) against Log (Achene Hair Length), with different achene hair types denoted according to symbols in key.

3.1.2. Spherical (to rarely conical)

Seven species fall into this category. The hairs are smaller but consistently spherical, vary in length from 8–50 μm , and can be subdivided into 3 sections. In *C. planiseta* and *C. pusilla* (section 3.1.2.a.) the hairs are found on both disc and ray achenes and, while often deflated to some extent, have a distinctly thickened cell wall. The length of these hairs varies from 35–50 μm (Plate 3, Fig. 15). Section 3.1.2.b. includes three taxa (*C. euphrasioides*, *C. flabellata* and *C. lycopodioides*). The hairs have an indistinct dividing cell wall, in some cases tending towards conical rather than spherical in outline, and in one species the ray achenes are often glabrous. The hair length measures between 20–40 μm (Plate 3, Figs. 11–14). Lastly *C. lanata* and *C. spathulifolia*, distinguished as section 3.1.2.c., possess spherical hairs that vary from 7–15 μm and are sparsely distributed over the surface. They are however frequently poorly preserved. In these cases the achenes can appear to be glabrous (Plate 3, Fig. 16).

3.1.3. Ampulliform to nearly deltoid

Only two species belong to this group - *C. gnaphalioides* and *C. minuta*. These hairs can be found with an occasional recurved, rostrate apical tip and may or may not appear to be collapsed. The hairs vary in length from 7–20 μm . These images can be seen in Plate 3, Figs. 17–18.

3.2. Filiform hairs

Only two species (*C. apiculata* and *C. acerosa*) possessed these hairs. The long, filamentous, sericeous-villous hairs are constructed of two vertically stacked cells; one short basal cell, and the second, elongated apical cell. They have an approximate length of 450 μm . Some collections of the two species can be completely glabrous. No correlation to disc and ray distribution was observed. Filiform hairs confined to a sparse ring near the pappus insertion were only rarely recorded (two samples, not *C. apiculata* and *C. acerosa*). Their cell construction remains unclear, but it seems most likely that they are an artefact of the pappus morphology rather than an achene epidermal character. Plate 4, Fig. 23. illustrates the filiform hairs.

3.3. Single-celled papillae

Single-celled papillae were only found in a couple of species (*C. pulvinata* and *C. revoluta*), the oblate flattened hairs densely covering the achenes, and with a mean length between 25–45 μm . These images can be seen in Plate 4, Figs. 21–22.

3.4. Glabrous achenes within the genus *Chaetanthera*

Twelve *Chaetanthera* species had glabrous achenes. Half of these were consistently glabrous both within and between capitula of the same and different collections. These were *C. cochlearifolia*, *C. dioica*, *C. pentacaenoides*, *C. pulvinata*, *C. sphaeroidalis*, and *C. stuebelii*. These achenes had the most interesting epidermal surfaces; for example the image shown on Plate 4, Fig. 19. Further, these taxa are arranged in the same sub-genus “*Egania*”. In six taxa (*C. acerosa*, *C. apiculata*, *C. lanata*, *C. minuta*, *C. revoluta*, and *C. villosa*) combinations of both glabrous and pubescent achenes in collections of the same species were observed. These did not follow any set pattern, nor do the species concerned come from the same group of taxa. The epidermal surfaces in these cases were relatively featureless (Plate 4, Fig. 20.). The varying combinations of glabrous and pubescent achenes within and between collections of the same taxa are presented in Table 2.

Table 2: Table summarising combinations of glabrous (-) and pubescent (+) achenes in collections of the same species.

Taxa	Ray floret	Disc floret
3 (<i>C. acerosa</i> , <i>C. lanata</i> , <i>C. minuta</i>)	-	-
	+	+
2 (<i>C. villosa</i> , <i>C. revoluta</i>)	Not observed	-
	Not observed	+ (rare)
1 (<i>C. apiculata</i>)	+	+
	-	-
	-	+ (rare)

4. Between the genera – *Pachylaena* and *Brachyclados*

Pachylaena and *Brachyclados* were also studied. *Pachylaena atriplicifolia* was represented by 2 collections. The first had only glabrous achenes, while the second possessed small (20–35 µm L.) lozenge-shaped achene hairs – again, twin-celled (see Table 3, section 3.1.4.). They were however, sparsely distributed, and rather poorly preserved.

Brachyclados lycioides material possessed both long (120–175–(200) µm in length) oblate-lanceolate “Zwillingshaare” (section 3.1.5.), and shorter (25–45 µm in length) globular hairs (Table 3, section 3.1.2.a.) *B. megalanthus* only had the former hair type, but marginally smaller in length (80–130 µm). The results are pictured in Plate 4, Figs. 24–26.

5. Summary of results

The information in Table 3 presents a summarised view of the achene hair types, which species carry these hair types, and to which subgenus these species are traditionally ascribed. The section numbers given in Table 3 correspond mostly to the section numbers in the text.

Table 3: Summary table showing achene hair type and the species (and subgenera) which carry these types. (*indicates which species are illustrated in this paper)

Hair Type		Taxon Names - Subgenus [Species]
3.1. “Zwillingshaare”	1.	<i>Proselia</i> [<i>C. chilensis</i> *, <i>C. elegans</i> , <i>C. serrata</i> , <i>C. valdiviana</i>] <i>Euchaetanthera</i> [<i>C. ciliata</i> *, <i>C. incana</i> *, <i>C. linearis</i> , <i>C. microphylla</i> *, <i>C. moenchioides</i> *, <i>C. peruviana</i> , <i>C. tenella</i>] <i>Tylloma</i> [<i>C. glabrata</i> , <i>C. limbata</i> *, <i>C. renifolia</i> *, <i>C. splendens</i>] <i>Glandulosa</i> [<i>C. glandulosa</i> *] <i>Carmelita</i> [<i>C. lanata</i> (?)]
		2.
	b <i>Oriastrum</i> [<i>C. lycopodioides</i> *] <i>Euchaetanthera</i> [<i>C. euphrasioides</i> *, <i>C. flabellata</i> *]	
	c <i>Carmelita</i> [<i>C. lanata</i> , <i>C. spathulifolia</i> *]	
	3.	<i>Oriastrum</i> [<i>C. gnaphalioides</i> *, <i>C. minuta</i> *]
4.	<i>Pachylaena atriplicifolia</i> *	
5.	<i>Brachyclados megalanthus</i> *, <i>B. lycioides</i> *	
3.2. Filiform		<i>Egania</i> [<i>C. acerosa</i> *, <i>C. apiculata</i>]
3.3. Papillose		<i>Egania</i> [<i>C. pulvinata</i> *, <i>C. revoluta</i> *]
3.4. Glabrous		<i>Egania</i> [<i>C. acerosa</i> *, <i>C. apiculata</i> , <i>C. cochlearifolia</i> , <i>C. dioica</i> , <i>C. pentacaenoides</i> , <i>C. pulvinata</i> , <i>C. revoluta</i> , <i>C. sphaeroidalis</i> *, <i>C. stuebelii</i>] <i>Carmelita</i> [<i>C. lanata</i> , <i>C. villosa</i>] <i>Oriastrum</i> [<i>C. minuta</i>] <i>P. atriplicifolia</i>

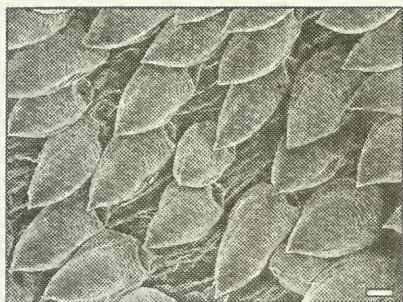


Fig. 3: bar 20µm

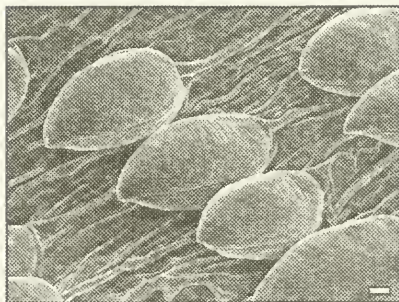


Fig. 4: bar 10µm

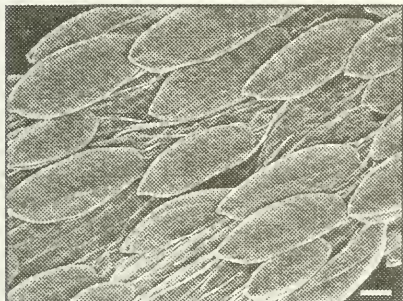


Fig. 5: bar 20µm

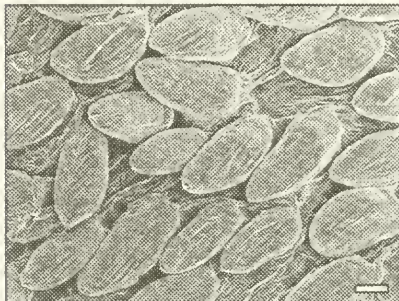


Fig. 6: bar 30µm



Fig. 7: bar 10µm

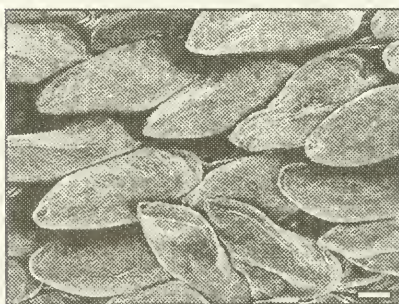


Fig. 8: bar 20µm



Fig. 9: bar 20µm

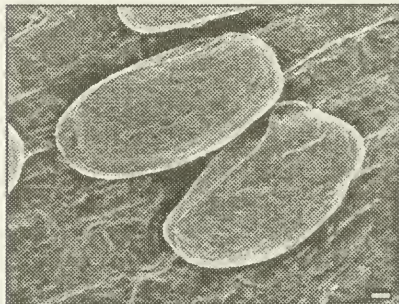


Fig. 10: bar 10µm

Plate 2: 3: *C. moenchioides* Less., Pirion 492 (GH); 4: *C. ciliata* Ruiz & Pav., Rosas 1890 (M); 5: *C. microphylla* (Cass.) Hook. & Arn., Wagenknecht 18489 (GH); 6: *C. chilensis* (Willd.) DC., Elliott 292 (K); 7: *C. glandulosa* Remy, Rosas 1592 (M); 8: *C. limbata* (D. Don) Less., Morrison 16740 (GH); 9: *C. incana* Poepp., Jiles 5001 (M); 10: *C. renifolia* (Remy) Cabrera, Seibold 2850 (W).

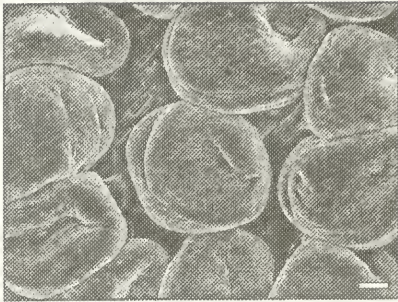


Fig. 11: bar 10µm

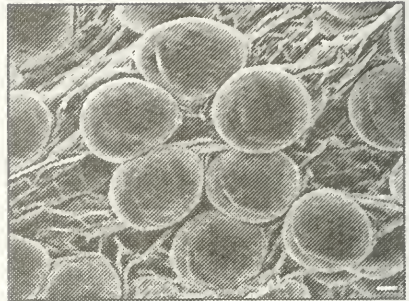


Fig. 12: bar 10µm

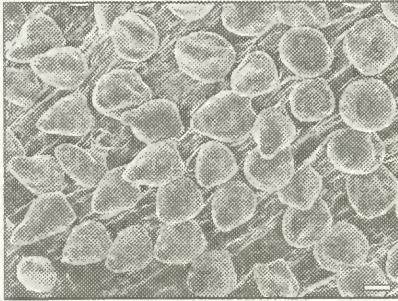


Fig. 13: bar 20µm

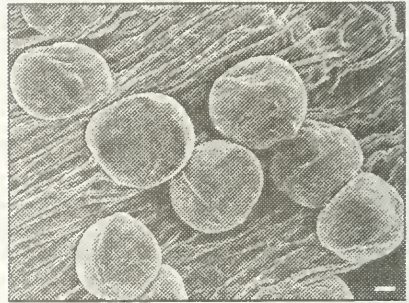


Fig. 14: bar 10µm

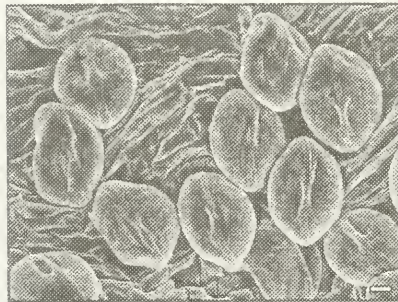


Fig. 15: bar 10µm

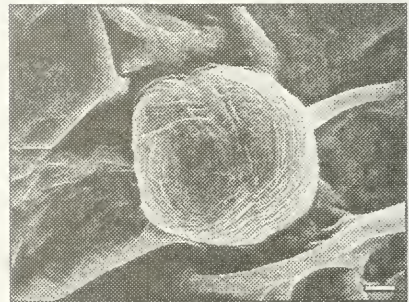


Fig. 16: bar 3µm

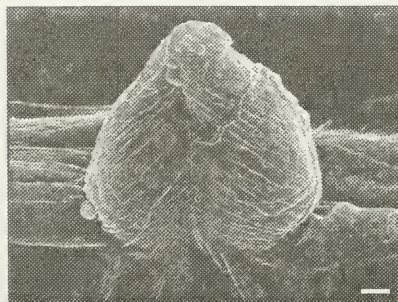


Fig. 17: bar 2µm



Fig. 18: bar 10µm

Plate 3: 11: *C. euphrasioides* (DC.) F.Meigen, *Morrison 17071* (GH); 12: *C. flabellata* D.Don, *Philippi s.n.* (W); 13: *C. flabellata* D.Don, *Grau 2440* (M); 14: *C. lycopodioides* (Remy) Cabrera, *Werdermann 632* (M); 15: *C. pusilla* (D.Don) Hook. & Arn., *Hastings 432* (NY); 16: *C. spathulifolia* Cabrera, *Kiesling, Ulibarri & Krapovikao 7467* (NY); 17: *C. gnaphalioides* (Remy) I.M.Johnst., *Wagenknecht 18590* (GH); 18: *C. minuta* (Phil.) Cabrera, *Castellanos 71644* (W).

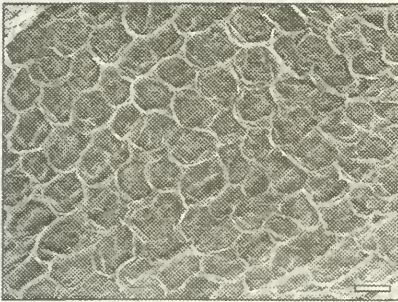


Fig. 19: bar 10 µm

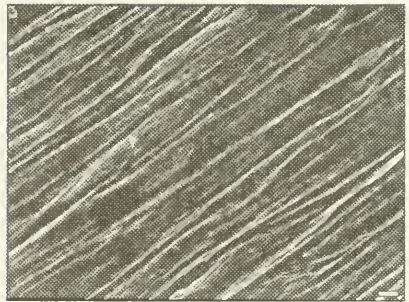


Fig. 20: bar 10 µm



Fig. 21: bar 10 µm



Fig. 22: bar 10 µm

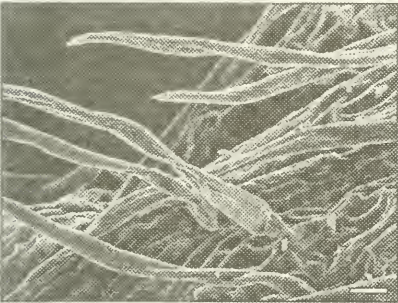


Fig. 23: bar 20 µm

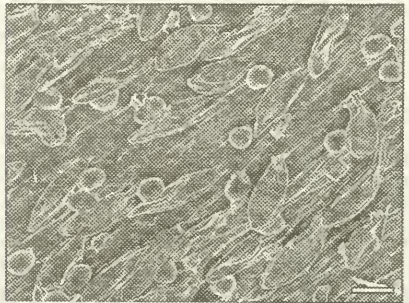


Fig. 24: bar 100 µm

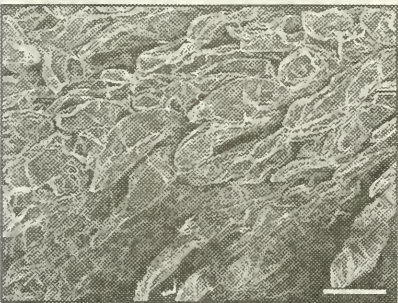


Fig. 25: bar 100 µm

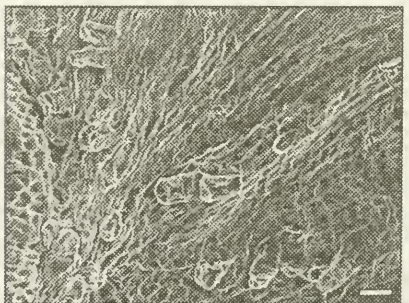


Fig. 26: bar 30 µm

Plate 4: 19: *C. sphaeroidalis* (Reiche) Hicken, *Werdermann* 253 (K); 20: *C. acerosa* (Remy) Benth. & Hook., *Werdermann* 627 (M); 21: *C. pulvinata* (Phil.) Hauman, *Vervoorst* 3239 (W); 22: *C. revoluta* (Phil.) Cabrera, *Werdermann* 1020 (M); 23: *C. acerosa* (Remy) Benth. & Hook., *Ehrhart & Grau* 95/818 (M); 24: *Brachyclados lycioides* D. Don, *Jiles* 4870 (M); 25: *Brachyclados megalanthus* Speg., *King & Heinz* 9390 (M); 26: *Pachylaena atriplicifolia* Hook. & Arn., *Schajovsky s.n.* (M).

Discussion

1. The taxonomic value of achene hairs above other characters

Historically achene hairs have been rather tentatively used in *Chaetanthera* classifications, even though often used to taxonomic advantage in other Compositae taxa. Now that modern technology has the wherewithal to reveal micro-characters, the true value of these achene variations can be utilised.

Many characters, both qualitative and quantitative were considered. The quantitative characters, such as achene length, did not show useful, discrete discontinuities. Given the large amount of variation they could, however, form a useful contribution to a multivariate analysis of a larger data set. Qualitative characters such as achene shape were found to be unreliable because of fecundity, maturity etc. The achene hairs appeared to be independent of these factors. The shape and size, especially length, was found to be statistically and visually a good discriminator for taxa in this genus. The absence of hairs, or the glabrous state, is not a reliable taxonomic indicator above the species level.

2. Achene hair diversity in the context of subgeneric divisions of *Chaetanthera*

The information regarding achene hair type distribution across the genus is summarised in Table 3. The table shows that clusters of species, traditionally placed in the same subgenera possess similar achene hairs. The patterns of hair type and subgenus fall into one of two categories:

- one hair type groups several subgenera, and
- individual subgenera group several hair types.

This is also illustrated in Plate 5. The hairs are schematically represented (to scale) and accompanied by transverse sections through the hairs, showing hair cell-wall variations, hair width ranges, and hair cell-number.

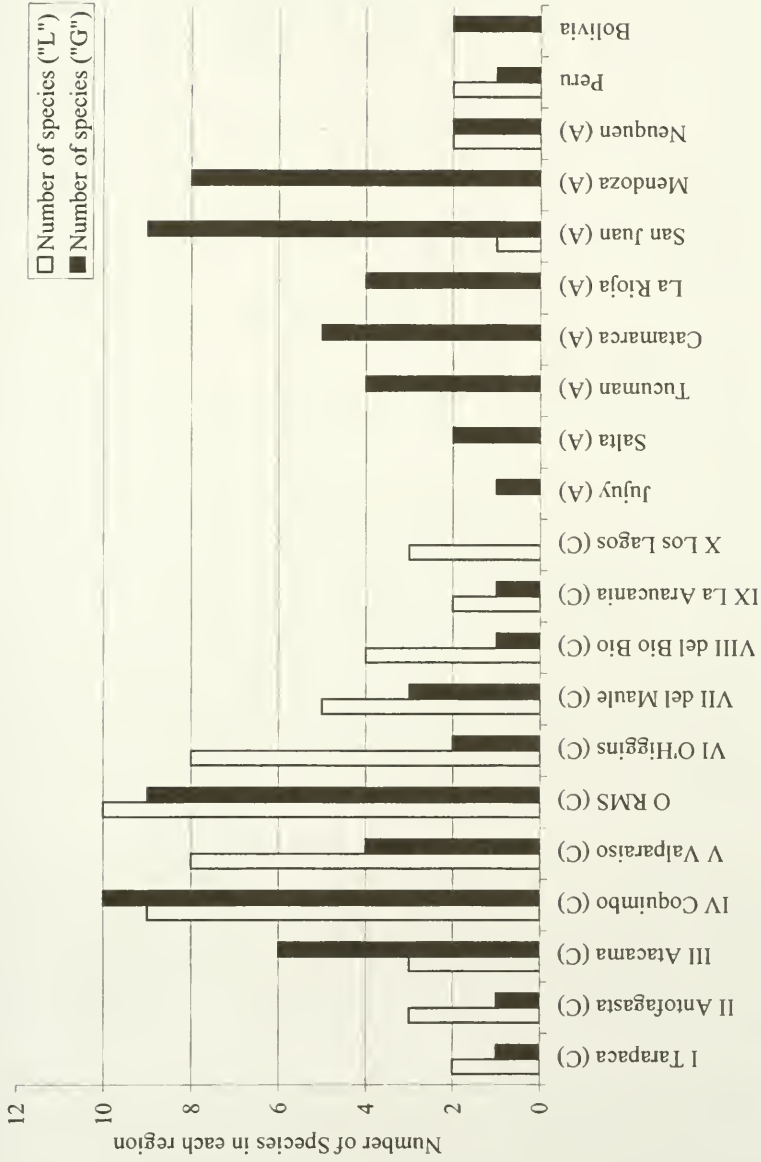
2.1. One hair type – several subgenera.

This grouping represents those species and even subgenera whose achene characters group them together within *Chaetanthera*. The taxa in the subgenera *Proselia*, *Euchaetanthera*, *Tylloma*, and *Glandulosa* are virtually inseparable on the basis of their achene features. With only two exceptions (*C. euphrasioides* and *C. flabellata*) the species traditionally placed within these four subgenera share the same type of achene hairs (elliptic or obovate to lanceolate “Zwillingshaare”) on both disc and ray achenes and, within a broader sense, have similar sized achenes. There is also little variation in the achene characters among the subgenera themselves. This lack of diversity itself is distinctive. They are quite separate from the remaining taxa in the study.

The taxa in these four subgenera, in particular within *Proselia* and *Euchaetanthera*, are very closely related and often express a wide range of morphological variation. This is reflected in the taxonomy where examples of taxa with several varieties are described (e.g. *C. chilensis*), as well as suites of species that are hard to distinguish from each other (e.g. *C. microphylla* and *C. linearis*).

2.2. One subgenus – several hair types.

The taxa in this grouping pose more of a challenge to interpretation, and in effect represent the taxa that are least well-collected and tricky to sample. Three subgenera fall into this group. The first two, *Egania* and *Oriastrum* show 2–3 hair types, each type found in only 2 or 3 species. The third, *Carmelita*, forms somewhat of an outlier as it, for the most part, exhibits only one hair type. However, there were a couple of oddities that require further investigation.



Regions of Chile (C) & Argentina (A), Peru & Bolivia

Graph 6: Distribution of *Chaetanthera* species with lanceolate ("L") and glabrous or globular ("G") achene hairs over South America

2.2.1. Nine species are traditionally grouped into the subgenus *Egania*. United mostly by the possession of interior phyllaries with coloured apical scales and having buds on the lower stem regions, these taxa represent the most under-collected species in the genus, and are consequently the most poorly sampled taxa in this study. Two hair types were revealed: long filamentous hairs and papillae. This was the only subgenus in which some species had consistently glabrous achenes. These hair types are not duplicated elsewhere in the genus *Chaetanthera*.

Five of the species had consistently glabrous surfaces on both disc and ray achenes. This is not a very exciting taxonomic feature, and certainly not a good discriminator considering the propensity of glabrous achenes to appear in amongst otherwise pubescent achene collections. As an aspect of variation this is, however, worth mentioning. The reversal or reduction to the glabrous state is frequent within species of the tribe Mutisieae s.str. (HANSEN, 1991).

C. apiculata and *C. acerosa* were glabrous or had achenes with long filamentous hairs. The distribution of hairy and glabrous achenes in these two species appears to be largely a feature of population variation. A variety of *C. acerosa* (*C. acerosa* var. *dasycarpa* Cabrera) is described as having long sericeous-villous hairs on the achenes, as opposed to the glabrous achenes of var. *typica*. These two varieties are reputed to co-exist in mixed populations. This is a good example where a detailed population survey could determine whether this is really population variation or a true taxonomic difference. The repeated occurrence of filiform hairs on the fruits of the Compositae is documented. These are considered to be plesiomorphic in the Nassauviinae at least (HANSEN, 1989).

Uniquely in this study, achenes from collections identified as *C. revoluta* and *C. pulvinata* were densely clothed in single-celled deflated papillae. Glabrous achenes were seen in collections of *C. pulvinata*.

2.2.2. The subgenus *Oriastrum* includes 5 species (after CABRERA, 1937). Three sorts of “Zwillingshaare” were identified in this group, and are not found in any other taxa of *Chaetanthera*. *C. pusilla* and *C. planiseta* had nearly identical achenes and hairs. The species are morphologically close, separated from each other by phyllary apex colour, and the pappus bristle form. The small spreading floccose species of *C. minuta* and *C. gnaphalioides* share distinct achene hairs. There is a slightly different third hair shape in the collections that may indicate an hitherto undescribed taxon. Only *C. minuta* has both glabrous and pubescent achenes. *C. lycopodioides* is grouped here with 2 taxa normally included in *Euchaetanthera* – *C. flabellata*, and *C. euphrasioides*. All three species share achene hairs on both disc and ray achenes that are strictly spherical to softly conical (on same achene). The achene is also often a distinct pyriform shape. Currently there is little else to support the grouping of these three taxa.

2.2.3. The three taxa in the subgenus *Carmelita* are generally very distinct, on account of the individual nature of the leaves and phyllary morphology. *C. lanata* and *C. spathulifolia* have very similar but sparse hairs, all occurring in some state of deterioration. *C. lanata* however also had examples of completely glabrous achenes, like those of *C. villosa*, and, very rarely, large hairs, as seen in the taxa belonging to *Tylloma*. These collections of *C. lanata* are currently under more intensive review. They have not been illustrated in Plate 5 because of the puzzling nature of the result.

From this brief discussion regarding the distribution of the achene hairs across the genus *Chaetanthera* the taxonomic significance of the achene hairs can be seen to vary in different subgenera. The variation in these achene characters raises the question “Is the rank of subgenus the correct rank for the separation of these groups of species?” The informative potential of the geographical distribution of the hair types is considered next.

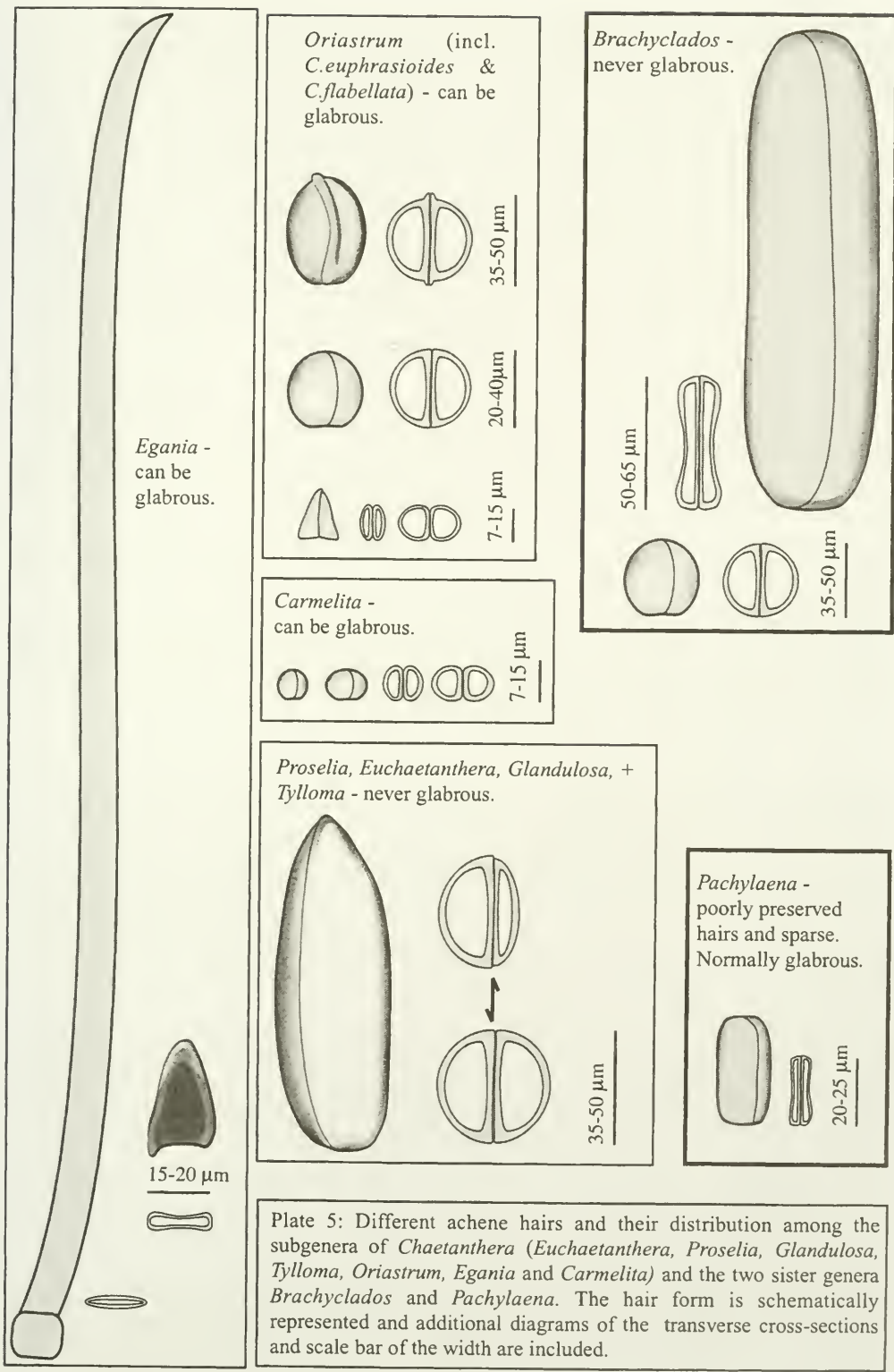


Plate 5: Different achene hairs and their distribution among the subgenera of *Chaetanthera* (*Euchaetanthera*, *Proselia*, *Glandulosa*, *Tylloma*, *Oriastrum*, *Egania* and *Carmelita*) and the two sister genera *Brachyclados* and *Pachylaena*. The hair form is schematically represented and additional diagrams of the transverse cross-sections and scale bar of the width are included.

3. Achene hairs and their geographical distribution

The species in *Chaetanthera* can be arbitrarily divided into two large groups based on their achene hair type. The species numbers in both groups also include those described taxa interpreted as belonging to the group from a morphological point of view, although no achenes were seen. The distribution of each taxon was collected using primarily the herbarium collection information, but supplemented by literature citations too.

The first group comprises all 22 species, in the subgenera *Proselia*, *Euchaetanthera*, *Tylloma*, and *Glandulosa*, possessing the obovate-lanceolate hair type on both achenes. It is identified by the epithet “L” (this is effectively Table 3, section 3.1.1.). The second group “G” contains 21 species mostly from subgenera *Carmelita*, *Egania* and *Oriastrum* (Table 3, sections 3.1.2., 3.1.3., 3.2., 3.3., and 3.4.). It includes all taxa described as being glabrous or having globular (or filiform or papillose) hairs. A histogram showing the geographical distribution over South America of numbers of species in each group (“L”) and (“G”) is plotted in Graph 6.).

This shows us the hotspots of species diversity in each group; “L” is centred in Chilean Región Metropolitana de Santiago (RMS), and “G” is centred over the high Andean border between RMS (Chile), and the neighbouring regions of San Juan and Mendoza in Argentina. Furthermore, the “L” group is confined (with the exception of 2 records in San Juan and Neuquen, Argentina) to the west of the Andean mountain range with 2 species exclusive to Peru. The “G” group is confined to the Andes, but spread both to the east and west of the main mountain chain, with over 70% of the species in this group found in both Chile and Argentina. Thus we see two different patterns of distribution for the two artificial species groupings based solely on achene hair type.

If we consider the altitude information as well, as a general rule the “L” species are distributed at altitudes ranging from sea level to just over 2000 m. The “G” species are usually to be found above this altitude (2000 m) up to 5000 m.

The summary of distribution, altitude and geography is in Table 4.

Table 4: Summary of information supporting the 2 groups of achene hairs.

Source	“L” (= <i>Proselia</i> , <i>Euchaetanthera</i> , <i>Tylloma</i> , <i>Glandulosa</i>)	“G” (= <i>Egania</i> , <i>Oriastrum</i> and <i>Carmelita</i>)
Distribution	Chile & Peru. Concentrated in RMS (Chile).	Chile, Argentina, Bolivia & Peru. Concentrated over RMS (Chile) & San Juan & Mendoza (Argentina).
Geography & Altitude	Coastal lowlands & mountains; lower Andean regions. Mostly 0–2000 m.	High Andean regions. Mostly 2000–5000 m.

It seems that several sources of information (achene characters, and distribution) point towards a split within the genus *Chaetanthera* that is not really reflected by the assignment of the rank “subgenus”. Nevertheless it is well recognised that a single character – here strongly weighted towards achene hairs – is not sufficient to bind or separate ranks in a taxonomic hierarchy. Correlating suites of morphological characters drawn from other sources should support the achene characters. Further correlating character progressions are currently under investigation. These include parallel progressions seen in the two groups in capitulum size and floret ratios, life cycles, and habit, among others.

4. Achene hair diversity between the genera

The significance of the results from *Pachylaena* and *Brachyclados* cannot be extensively interpreted. *Pachylaena* achenes show preliminary similarities to the achenes and hairs seen on species included in the *Chaetanthera* subgenus *Tylloma*, but much smaller. The two *Brachyclados* species both had “Zwillingshaare” (Table 3, section 3.1.5.) of a similar nature

to the obovate-lanceolate achene hairs but distinctly longer. However, *B. lycioides* also had a second hair type – the spherical “Zwillingshaare” (Table 3, section 3.1.2.b). The presence of two hair types on the same achenes, which in *Chaetanthera* are so clearly segregated, is interesting.

The achene hair information from these two genera *Pachylaena* and *Brachyclados* indicates that they are indeed outliers to *Chaetanthera*, and do not form part of this carpologically diverse genus as it stands.

KARIS et al. (1992) sampled collections of six *Chaetanthera* species in their phylogenetic analysis of the Cichorioideae. They found that *Chaetanthera* formed part of a monophyletic cluster with, among others, *Gerbera*, *Mutisia* and *Trichocline*. Unfortunately they did not consider *Pachylaena* or *Brachyclados*. BREMER (1994) postulated that *Pachylaena* could have its sister group within a paraphyletic *Chaetanthera*. Were *Chaetanthera* to be monophyletic, then this could be resolved with a cladistic analysis of *Chaetanthera* and *Pachylaena* with *Brachyclados* as an outgroup.

Other studies (GRAU, 1980; BREMER, 1994), conducted at the generic level, cite *Chaetanthera* results that are often based on material pertaining only to taxa belonging to the “L” group. In the light of the achene hair results, these studies have limited usefulness for a discussion of generic limits of *Chaetanthera*.

Conclusion

Many studies indicate that where divergent achene hair types are found, they are frequently indicative of natural generic boundaries. The question then remains: do the divergent achene hair types found in this study represent a fundamental split in the “genus” *Chaetanthera* different to that hitherto reflected in the current classification?

Several points can be highlighted:

- There is more variation among the achenes of the genus *Chaetanthera*, in particular regarding the achene hairs, than hitherto described. The variation in the achene hairs shows a dramatic division of the species found in the genus *Chaetanthera* Ruiz & Pav.
- Although achene hair length is closely correlated to shape, achene hair type was found to be a clear descriptor of species clusters above the specific level, at the subgeneric level. The absence of achene hairs (the glabrous state) is not, as a rule, a taxonomically useful feature at the sub-generic level.
- 4 subgenera *Proselia*, *Euchaetanthera*, *Tylloma*, and *Glandulosa* form one group with the same achene hair type (obovate-lanceolate “Zwillingshaare”). 3 subgenera, *Oriastrum*, *Egania* and *Carmelita*, express 6 different achene hair types and include the majority of glabrous achenes. Geographical distribution data and altitude information show correlating trends with species groupings based on achene hair characters.
- The two genera *Brachyclados* and *Pachylaena* were shown to be distinct from all groupings within the genus *Chaetanthera* based on achene hairs.

This study implies that achene diversity could be representative of significant divisions within the genus *Chaetanthera* as it stands. In particular the separation of the subgenera *Proselia*, *Euchaetanthera*, *Tylloma*, and *Glandulosa* (as one group) from *Oriastrum*, *Egania* and *Carmelita* seems a possibility. The achene characters of the outlying genera *Pachylaena* and *Brachyclados* while interesting, do not help clarify these divisions. The variation we have found has highlighted those areas of the genus which urgently need reviewing. The search for more characters to resolve the question of the generic limits of *Chaetanthera* continues and a full revision is currently in progress.

Grateful thanks are extended to Prof. J. Grau, the Curators and Directors of the herbaria who generously loaned the material used in this research and to Dr R. Davies.

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Appendix

The collections cited here represent specimens (limited to a maximum of two) that had typical achene hairs for the species. The collections that contributed to the wider understanding of this project are not cited. The collections in bold are photographically illustrated in this paper.

Taxonomic Name	Typical Collections Surveyed
<i>C. acerosa</i> (Remy) Benth. & Hook.	<i>Buchtien 84</i> (M); <i>Johnston 5925</i> (GH)
<i>C. apiculata</i> (Remy) F. Meigen	<i>Ehrhart & Grau 95/818</i> (M); <i>Werdermann 627</i> (M)
<i>C. chilensis</i> (Willd.) DC.	<i>Elliott 292</i> (K); <i>Grau 2495</i> (JG)
<i>C. ciliata</i> Ruiz & Pav.	<i>Grau 2400</i> (M); <i>Rosas 1890</i> (M)
<i>C. cochlearifolia</i> (A. Gray) B. L. Rob.	<i>MacBride & Featherstone 845</i> (GH)
<i>C. dioica</i> (Remy) B. L. Rob.	<i>Sleumer 1875</i> (W)
<i>C. elegans</i> Phil.	<i>Rosas 1875</i> (M); <i>Werdermann 1256</i> (M)
<i>C. euphrasioides</i> (DC.) F. Meigen	<i>Morrison 17071</i> (GH); <i>Philippi s.n.</i> (W)
<i>C. flabellata</i> D. Don	<i>Grau 2440</i> (M); <i>Philippi s.n.</i> (W)
<i>C. glabrata</i> (DC.) F. Meigen	<i>Rosas 1076</i> (M); <i>K. & W. Rechinger 63504</i> (M)
<i>C. glandulosa</i> Remy	<i>Rosas 1592</i> (M); <i>Morrison & Wagenknecht 17104</i> (K)
<i>C. gnaphalioides</i> (Remy) I. M. Johnst.	<i>Jiles 4158</i> (M); <i>Wagenknecht 18590</i> (GH)
<i>C. incana</i> Poepp.	<i>Jiles 5001</i> (M); <i>K. & W. Rechinger 63743</i> (W)
<i>C. lanata</i> (Phil.) I. M. Johnst.	<i>Werdermann 934</i> (M); <i>Jiles 2487</i> (M)
<i>C. limbata</i> (D. Don) Less.	<i>Rosas 1226</i> (M); <i>Morrison 16740</i> (GH)
<i>C. linearis</i> Poepp.	<i>K. & W. Rechinger 63321</i> (M); <i>Werderman 890</i> (M)
<i>C. lycopodioides</i> (Remy) Cabrera	<i>Morrison 17300</i> (K); <i>Werdermann 632</i> (M).
<i>C. microphylla</i> (Cass.) Hook. & Arn.	<i>Grau 2542</i> (M); <i>Wagenknecht 18489</i> (GH)
<i>C. minuta</i> (Phil.) Cabrera	<i>Castellanos 71644</i> (W); <i>Johnston 6094</i> (GH)
<i>C. moenchioides</i> Less.	<i>Grau 2360</i> (JG); <i>Pirion 492</i> (GH)
<i>C. pentacaenoides</i> (Phil.) Hauman	<i>Sparre 1572</i> (K)
<i>C. peruviana</i> A. Gray	<i>Weberbauer 6876</i> (GH)
<i>C. planiseta</i> Cabrera	<i>Germain #1246</i> (W); <i>Hastings 432</i> (NY)
<i>C. pulvinata</i> (Phil.) Hauman	<i>Sleumer 374</i> (W); <i>Vervoorst 3239</i> (W)
<i>C. pusilla</i> (D. Don) Hook. & Arn.	<i>Grau 3293</i> (M); <i>Seibold 2990</i> (W)
<i>C. renifolia</i> (Remy) Cabrera	<i>C. Grandjot s.n.</i> (M); <i>Seibold 2850</i> (W)
<i>C. revoluta</i> (Phil.) Cabrera	<i>Werdermann 1020</i> (M)
<i>C. serrata</i> Ruiz & Pav.	<i>Grau s.n.</i> (M); <i>Pennell 12836</i> (GH)
<i>C. spathulifolia</i> Cabrera	<i>Kiesling, Ulibarri & Krapovickao 7467</i> (K); <i>Malme 2940</i> (GH)
<i>C. sphaeroidalis</i> (Reiche) Hicken	<i>Castellanos 71647</i> (W); <i>Werdermann 253</i> (M)
<i>C. splendens</i> (Remy) B. L. Rob.	<i>Jiles 4816</i> (M)
<i>C. stuebelii</i> Hieron.	<i>Venturi 9266</i> (GH)
<i>C. tenella</i> Less.	<i>Grau 2407</i> (M); <i>Werdermann 815</i> (GH)
<i>C. valdiviana</i> Phil.	<i>Philippi 359a</i> (P)
<i>C. villosa</i> D. Don	<i>Holler Mayer 415</i> (W); <i>Schajovskoy s.n.</i> (M)
<i>Brachyclados lycioides</i> Hook. & Arn.	<i>Jiles 4870</i> (M); <i>Schajovskoy 150</i> (M).
<i>Brachyclados megalanthus</i> Speg.	<i>King & Heinz 9390</i> (M)
<i>Pachylaena atriplicifolia</i> Hook. & Arn.	<i>Schajovskoy 321</i> (M); <i>Schajovskoy s.n.</i> (M)

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