

A new genus of the Compositae from North Africa

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The new, monotypic North African genus *Heliocauta* is formally published and its relationship to other genera of the *Anthemis* complex is discussed.

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On the basis of a detailed morphological and anatomical study it is possible to show that *Anacyclus*, like several other currently recognised genera of the *Anthemis* complex is a paraphyletic assemblage. The affinities of the curious mat-forming alpine species named by Litardière & Maire (1924) as *Anacyclus atlanticus* were brought into question in a revision of the genus (Humphries in prep.) as the capitulum, floret and cypselae differ in most respects from those of the type species and its close allies. In this species there are also several character states which are not shared by other genera of the *Anthemideae*. Thus, it is placed into a new genus, *Heliocauta*, described below, and the reasons for its separation from *Anacyclus* are discussed.

Heliocauta Humphries gen. nov. - Figs. 1, 2

Herbae perennes humiles; caudex brevis, praemorsus. Folia basalia, rosulata, triternatisecta, segmentis ultimis brevibus linearibus. Pedunculi simplices, monocephali ex axillis foliorum orti. Capitula hemisphaerica, parva (7-11 mm diametro) homogama, discoidea, flosculis hermaphroditis fertilibus; receptaculum conicum paleaceum. Anthodii phyllaria (involucri bractaeae seu squamae) triangularia vel oblongo-lanceolata, dorso viridia, margine scariosa fusco apice versus plusminusve erosa. Receptaculi phyllaria (paleae) oblongo-lineararia, carinata hyalina, scariosa apicibus obtusis serrulatis. Flosculi regulares hypocraeteriformes; minuti (2.5-3.2 mm longi) lobis limbi parvis patentibus triangularibus apicibus fere cucullatis. Antherae basi obtusae; filamenta infra antherum tumida. Stylus teres,

glaber, nectario conspicue lobato basi cinctus, ramis 2 brevibus divaricatis anguste oblongis apice paulo penicillatis. Cypselae anguste obtusae, leviter dorso-ventraliter compressae, costis lateralibus 2, costis intermediis utrinque 1-3 obscuris apice truncatae; pappus coroniformis, minutus.

Typus: *Heliocauta atlantica* (Litard. & Maire) Humphries. Nomen ex *ἡλιοκαυτεω* oritur, ob capitulorum aspectum adustum.

Perennial creeping herb; stems short, reduced to a praemorse caudex. Leaves in a basal rosette, tripinnatisect, with tiny, linear, ultimate lobes; primary lobes in 3-6 opposite or subopposite pairs; rachis flat or slightly canaliculate, narrowly triangular in outline, with a broad, hyaline, winged, sheathing base and 4-6 distinct veins. Peduncles simple, monocephalous, emerging from the leaf axils. Capitulum hemispherical, small (7-11 mm in diameter), homogamous, discoid with fertile, hermaphrodite florets; receptacle conical, paleaceous. Phyllaries in 3 rows, triangular to oblong-lanceolate, green on the dorsal surface, the margins scarios, brown at the apex. ± erose. Receptacular scales oblong-linear, carinate, hyaline scarios, the apex obtuse, serrulate. Florets regular, hypocraeteriform, minute (2.5-3.2 mm long), the lobes patent, triangular in shape, with a somewhat cucullate apex. Anthers obtuse at the base, the filaments distinctly enlarged at the collar. Style terete, slightly swollen at the base, set in a con-

spicuous lobed nectary; style branches short, about the same thickness or slightly thicker than the shaft, truncate-penicillate at the tips. *Cypselas* narrowly obconate, terete to slightly dorsally-ventrally compressed with 2 distinct, vascularized lateral ribs and 1-3 obscure dorsiventral ribs; truncate, dark-brown or grey-black due to a dense tannin layer in the testa; the scalariform, thickened epicarp is invested, here and there, with linear series of dark-brown resin cells; pappus a minute, erose corona. *Cotyledons* anteriorly-dorsally orientated.

***Heliocauta atlantica* (Litard. & Maire) Humphries**
comb. nov.

Basionym: *Anacyclus atlanticus* Litard. & Maire, Mem. Soc. Sci. Nat. Maroc 4 (1): 13 (1924).

Caudex 2-4 mm crassus, interdum stolonem emittens. *Folia* ambitu oblongo-lanceolata, 3-8 x 1-2.5 cm, plus minusve glabra ad villosa. *Pedunculi* decumbentes, 3.5-15 cm longi, apicem versus parce villosi sed sub capitulo dense pubescentes. *Capitula* 7-11 mm diametro. *Anthodii phyllaria* circa 2 mm longa. *Flosculi* primo pallide flavis demum brunnescentibus, tubo 2.5-3.2 mm longi, lobis 0.1-0.3 mm longi. *Antherae* 1-1.5 mm longae. *Cypselae* 1.5-2 mm longae, fere 1 mm latae.

Stems 2-4 mm thick, occasionally producing stolons. *Leaves* oblong-lanceolate in outline, 3-8 x 1-2.5 cm, ± glabrous to densely villous. *Peduncles* decumbent, 3.5-15 cm long, sparsely to densely pubescent below the capitulum. *Capitula* 7-11 mm in diameter. *Phyllaries* c. 2 mm long. *Floret tubes* 2.5-3.2 mm long, lobes 0.1-0.3 mm long. *Anthers* 1-1.5 mm long at anthesis. *Cypselas* 1.5-2 mm long and up to 1 mm wide.

var. *atlantica*

Anacyclus atlanticus var. *eu-atlanticus* Maire in Jahandiez & Maire, Cat. Pl. Maroc 3: 767 (1934).

A variety from the Atlas mountains occurring on granitic or porphyritic rocks between 2900 and 3600 m.

Specimens seen: Grand Atlas, Reraya: rocailles porphyriques terreuses au Tizi-n-Tagherat 3300-3600 m, 22.7.1922, Maire (MPU holotype, P, LD, S isotypes) - Great Atlas mountains, Refuge Neltner, Djebel Toubkal, 3200 m, Polunin 2155 (BM); same locality, granite gravel and scree nr. stream, Newbould 490 (BM); same locality, 9600 ft., pastureland on granite bedrock, 9.7.1966, Lambert 119 (BM); same locality, 22.7.1976, C. J. & A. R. Humphries 101 (BM); same

locality, 3506 m, 20.8.1951 Rauh 299 (M); same locality, 3600 m, 2.8.1951, Schoffer (M); same locality, 1933 Stodieck (M); Jbel Toubkal, nr. stream, 11,000 ft., 14.9.1955, Newbould 403 (BM) - Refuge d'Hangayevs 3000 m, Grand Atlas Central, 31.7.1938 in herb. Maire (MPU).

var. *dasyphylla* Humphries

Anacyclus atlanticus var. *vestitus* Humbert ex Jahandiez & Maire, Cat. Pl. Maroc 3: 768 (1934), nom. nud.

Varietas rara marocana in montibus Grand Atlas (in parte orientali) et Moyen Atlas inter 2800 et 3500 m supra mare crescens, a var. *atlantica* indumento foliorum pilis densis simplicibus distinguenda.

An extremely rare variety from the eastern High Atlas and the Middle Atlas mountains occurring between 2800 and 3500 metres, distinguished from the type variety by its dense indumentum of simple hairs on the leaves.

Specimens seen: Grand Atlas, Ari Ayachi, Humbert (AL holotype, RAB); same locality, Sindiert, 3600 m, Schmittfluren, 17.9.1953, Rauh 754 (M) - Middle Atlas, Chaîne du Bou Iblane, 2800-3200 m, Emberger & Maire (AL, RAB) - Mont Bou Nacer, 3000 m, Emberger (AL, RAB).

Distribution and habitat

H. atlantica is known exclusively from wet, cold montane pastures in the Middle and High Atlas mountains, where it has only been found in 4 locations (Fig. 2), all of which are over 2900 m.

Cytology

Twenty-two plants of var. *atlantica* collected during August 1976 (C. J. & A. R. Humphries 101) from Jbel Toubkal (High Atlas) were cultivated at the Chelsea Physic Garden. After pre-treatment overnight in a saturated solution of paradichlorobenzene root-tips were stained in Feulgen and squashed in 45% acetic acid. Fresh buds were squashed directly in aceto-orcein.

The chromosome number, reported here for the first time, was found to be $2n = 18$, the most common number for diploids in the Anthemideae. There are nine pairs of meta- and submetacentric chromosomes, two pairs of which have satellites on their shorter arms. Meiosis was normal with 9 pairs of bivalents at metaphase I.

Taxonomic remarks

This interesting taxon was originally described by Litardière & Maire (1924) from material col-

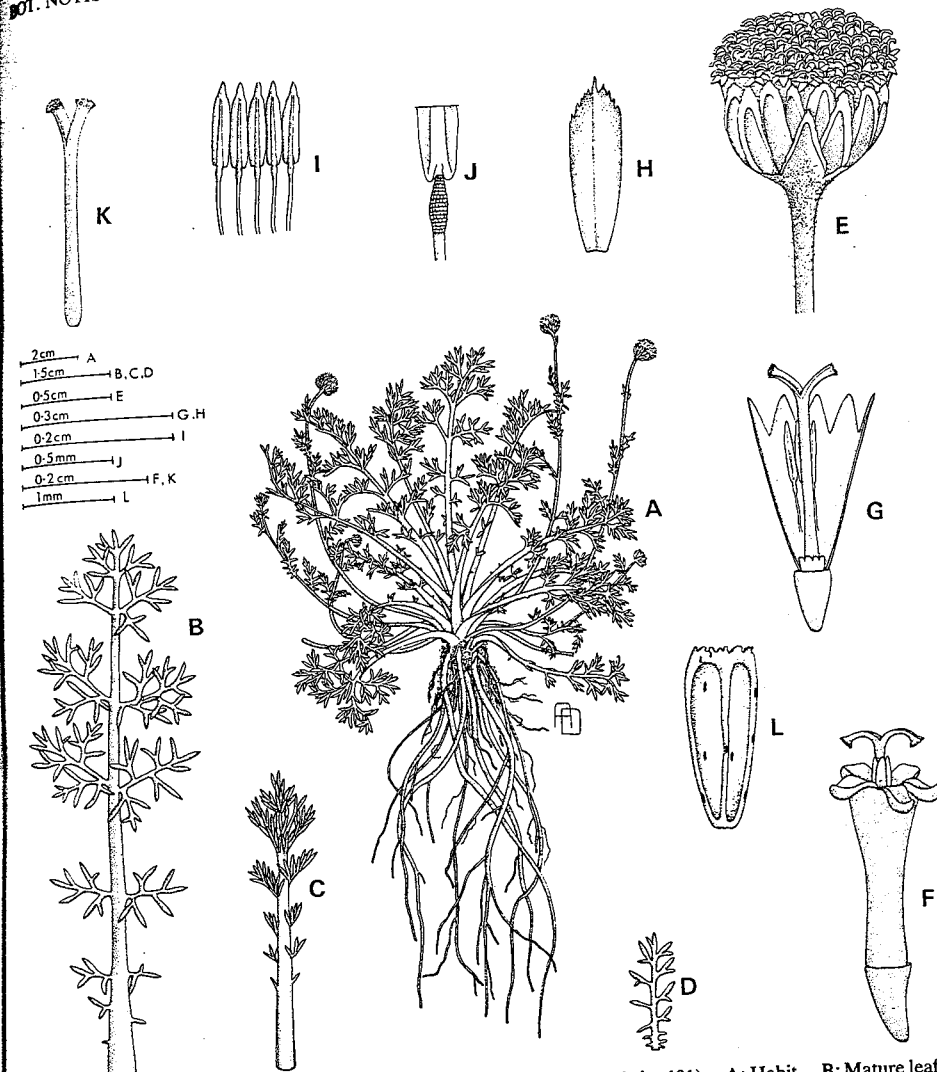


Fig. 1. *Heliocauta atlantica*. Based on live material (C. J. & A. R. Humphries 101). - A: Habit. - B: Mature leaf. - C: Young leaf. - D: Stem bract. - E: Flowering capitulum. - F: Floret at anthesis. - G: Dissected floret at anthesis. - H: Receptacular scale. - I: Anthers. - J: Filament collar and anther base. - K: Stigma. - L: Mature cypsel, anterior view.

lected in the High Atlas mountains: "In ditonion Ourika jugo Tachdir (Maire 1921, nondum florens, Maire and Litardière, 1922) et in valle amnis Ouelga (Litardière, 1923); in ditonion

Reraya valle amnis Ouenkrim (Litardière, 1923)."

Because *Heliocauta atlantica* resembles the two perennial varieties of *Anacyclus pyrethrum*

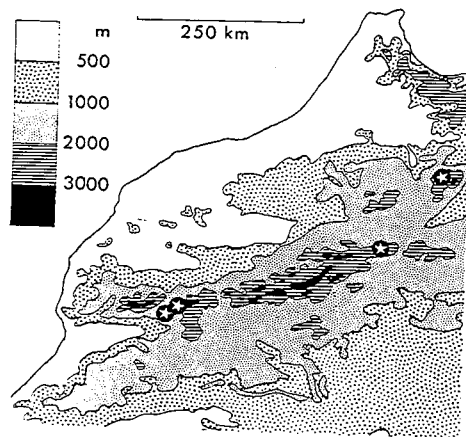


Fig. 2. Known range of *Heliocauta atlantica*.

(Humphries in prep.) in gross morphology Maire placed it in the same genus with the comment, "Affinis *A. pyrethro* L. et *A. depresso* Ball, a quibus valde differt caudice brevi praemorso radices fasciculatas edenti (nec in radicem crassam palarem abeunti, capitulis minoribus homogamis, florescentia valde serotina etc. Sectioni Pyrethrariae DC etsi eligulatus. ob perennitatem, flosculos regulares, tubum compressum et vegetationis modum adscribendus." This is clearly a classification mainly based on an overall resemblance in convergent characters, i.e. similar adaptations to the alpine environment in which both species occur. A more detailed examination shows that the two species are very different from each other.

Mature individuals of *A. pyrethrum* are characterised by the presence of a solitary, woody rootstock which can be up to four or five years old. The premorse stem of *H. atlantica*, on the other hand, produces at least three fasciculate roots (Fig. 1A). Transverse sections show that these roots rarely survive for longer than two years. Instead perenniality is achieved by the development of stolons, capable of reaching lengths of up to 12 cm. Transverse sections of the protracted stem show that it can survive for two or three years. Both species produce an annual rosette of leaves which emerges from the centre of the perennating stocks. The flowering shoots in

A. pyrethrum, homologous to the lateral branches of cauline corymbose cymes in other genera of the Anthemideae (Humphries in prep.), emerge during the month of February to form a rosette of procumbent shoots which flower at the tips from March until June. The decumbent flowering shoots of *H. atlantica* do not form flat rosettes but develop from the axils of the leaves and flower from August until October or November.

The flowers and fruits of *H. atlantica* differ in many respects from those of *Anacyclus*. The receptacular scales of the former are extremely narrow, delicate, carinate and chartaceous with an acuminate, brown-tipped apex and somewhat erose at maturity. By comparison the scales of *Anacyclus* are tough, mucronate and barely keeled but distinctly herbaceous at the base and centre, particularly in those from the outer parts of the capitulum. The heads of *Heliocauta* are homogamous consisting only of disc florets with regular corolla lobes. Homogamous heads are found in annual species of *Anacyclus* (*A. monanthos* and *A. valentinus*) but these frequently have zygomorphic corollas with two of the apical lobes longer than the other three. The cypselas of *Heliocauta* are also very different from anything to be found in *Anacyclus*, especially by the thin pericarp, the small ribs and the overall size (Figs. 1 L, 3). The epicarp consists of colourless, horizontally thickened cells and is invested with tanniferous sphaecelae which appear to be 4-7-celled resin glands (Fig. 1 L). The pappus is a tiny, marginal, toothed corona. In a transverse section of the pericarp a one-celled, scalariform epicarp (Fig. 3 C), a narrow 1-2-celled mesocarp and 3-5 sclerenchymatous ribs are shown. The deep brown colour is brought about by a very thick tanniferous substance in the inner layers of the testa (Fig. 3 B).

The cypselas of *Anacyclus*, as in so many other genera of the Anthemideae, provide the unambiguous diagnostic features of the genus (Humphries in prep.). They are flattened in an anterior-dorsal plane with 2 lateral wings. The pericarp consists of a basal layer of sclerenchyma, some 2-3 cells thick covered by a 1-2-celled layer of parenchyma. The wings contain radially elongated parenchymatous tissue surrounding 2 laterally placed vascular bundles. The epicarp is covered with slime cells in linear series, as in *Heliocauta*, but they contain colourless mucilage. The pappus

varies in different species from a marginal rim to an anterior appendage.

Relationship to other genera

The representatives of the *Anthemis* and *Achillea* complexes in the Northern Hemisphere form a group of 11 related genera (Table 1). Although each possesses many differential features the individual taxa can be delimited on a few diagnostic character states of unique status, as these help to define monophyletic groups, an essential requirement for natural classifications (Hennig 1966). The most important features of this kind are obtained from the morphology of the cypselas and the capitulum. Other possibly useful character states are found in the type of embryo-sac development (Harling 1950, 1951) and in the distribution of secondary metabolites (Greger 1975, 1977, Harborne et al. 1970). A summary of useful morphological features of genera in the *Anthemis* complex together with *Achillea*, *Heliocauta* and *Sclerorhachis* is given in Table 1.

A detailed examination of the fruits in the genera of the *Anthemis* complex reveals a number of parallel morphological trends which tend to obscure actual relationships. Such features include the anteriorly-dorsally compressed cypselas of *Anthemis* section *Cota* which have 7-22 ribs and a similar number of vascular bundles in the pericarp (Wagenitz 1968, Kynčlova 1970, Reitbrecht 1974); the weakly monosymmetric shape, the barely visible ribs and the thin pericarp of the cypselas in *Chamomilla*; and the thick tanniferous layers of the testa in the dark coloured cypselas of *Matricaria*. The presence of myxogenic cells on the pericarp represent a plesiomorphic condition as they are common to all of the main generic complexes in the Anthemideae. However, the resin-filled glands of the type found in *Heliocauta* have only been observed elsewhere in *Sclerorhachis*.

Heliocauta can immediately be distinguished together with *Anacyclus*, *Leucocyclus* and *Achillea*, from the remainder of the complex on the basis of slightly or completely anteriorly compressed cypselas with 2 distinct lateral ribs or wings containing only 2 vascular bundles in the pericarp wall. The remaining genera have more or less terete, angled, monomorphic, laterally compressed or even occasionally anteriorly-dorsally compressed cypselas but with at least 3, usually

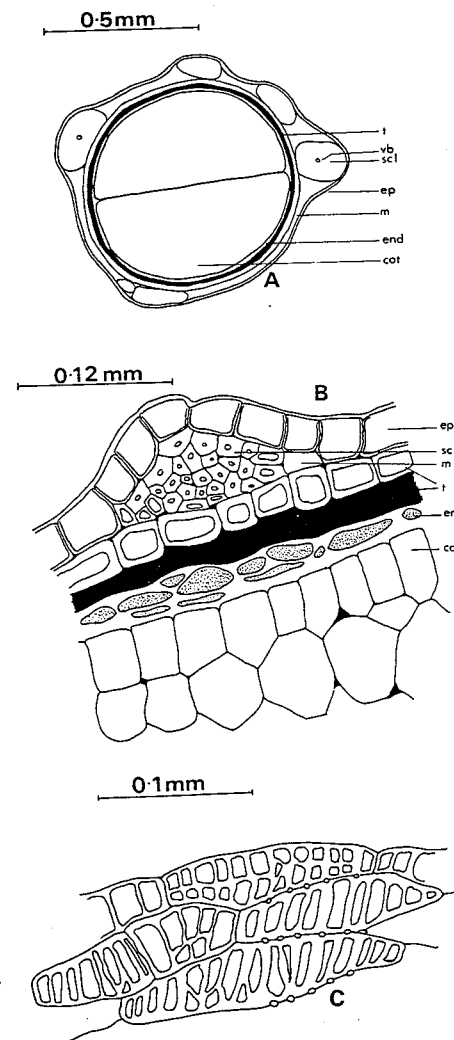


Fig. 3. Cypselas anatomy of *Heliocauta atlantica*. -A: T.s. across the median region. -B: T.s. in the region of a rib. -C: Surface view of the epicarp to show scalariform thickening of the cell walls. -cot cotyledon, end endosperm, ep epicarp, m mesocarp, scl sclerenchyma, t testa, vb vascular bundle.

Table 1. Morphological features of *Heliocauta*, *Achillea* and related genera. The characters are as follows:

1 Habit: a annual, b biennial, c perennial	sclerocarp, c oval braced, d palisade, e multi-stranded, f 1-2-stranded
2 Perennial habit: a rhizomes, b stolons	12 Pericarpic resin ducts and glands: + present, - absent
3 Receptacular scales: + present, - absent	13 Pericarp lacunae: + present, - absent
4 Receptacular hairs: + present, - absent	14 Slime cells: - absent, a present, b sphacelate, c on ribs, d over whole surface
5 Cypselas: + heteromorphic, - homomorphic	15 Number of nuclei in embryo-sac
6 Cypselas symmetry: a terete/actinomorphic, b laterally compressed, c anteriorly/dorsally compressed, d zygomorphic	16 Corolla: - not basally enlarged, a basally saccate, b anteriorly-dorsally overlapping fruit, c dorsally overlapping fruit
7 Number of vascular bundles in the pericarp	17 Cotyledons: a anteriorly-dorsally orientated, b laterally orientated
8 Number of cypselas ribs	
9 Cypselas wings: + 2 wings, - absent	
10 Cypselas parenchyma: a absent, b spongy, c single-layered, d multi-layered	
11 Cypselas sclerenchyma: a absent, b hypodermic	

Genus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Leucocyclus</i>	c	a	+	-	-	c	2	±	+	c	e	-	-	c		b	
<i>Achillea</i>	c	a	+	-	-	c	2	2	-	b	f	-	-	c	2	-	b
<i>Sclerorhachis</i>	b		+	-	-	a b	4-5	0				+	-	c			
<i>Heliocauta</i>	c	b	+	-	-	c	2	3-5	-	b	f	+	-	-			a
<i>Anacyclus</i>	a c	(a)	+	-	-	c	2	0	+	b	e	-	-	d	1	(c)	a
<i>Cladanthus</i>	a		+	+	-	b		0	-	a	e	-	-	-	1		b
<i>Anthemis</i> sect.																	
<i>Anthemis</i>	a-c	a	+	-	-	a	10	8-10	-	c d	e	-	-	(a)	4	-	a b
<i>Anthemis</i> sect.																	
<i>Cota</i>	a-c	a	+	-	-	a c	22	22	-	d	c	-	-	-	4	-	b
<i>Anthemis</i> sect.																	
<i>Ammanthus</i>	a		(+)	-	-	a		0-10	-			-	-	-			
<i>Chamaemelum</i>	a c	(a)	+	-	-	b	5	0	-	d	b d	-	-	-	1		b
<i>Chamomilla</i>	a		-	-	-	b	4-5	3	-	b	f	(+)	-	d	1		b
<i>Matricaria</i>	a c	(a)	-	-	-	b d	3	4-5	-	d	f	-	(+)	(a)	4	-	a b
<i>Otospermum</i>	a		-	-	+	a	5	5-6	-	d	e	-	-	-			

5-10, or even up to 22 vascular bundles in the pericarp wall. *Anacyclus* and *Leucocyclus* together form a monophyletic assemblage characterized by large cypselas with lateral wings and thick, continuously thickened pericarp walls. Grierson (1975) considers *Leucocyclus* to be unique on account of its vermiform leaves, the narrow wings on the cypselas and the dorsiventrally compressed disc corollas divided into 2 overlapping lobes at the base, which clasp the upper part of the cypselas on the anterior and dorsal faces.

By comparison both *Heliocauta* and *Achillea* have relatively tiny cypselas with 2 distinct lateral ribs rather than wings, and extremely thin pericarp walls (cf. Briquet 1916, Reitbrecht 1974, for details of *Achillea*). The relationship between *Heliocauta* and *Achillea* was originally suggested by phytochemical data. Greger (1977) has shown that the flavonoid profile of *Heliocauta* represents a widespread plesiomorphous pattern

with compounds similar to those found in *Tanacetum*, *Artemisia*, *Anthemis* and *Achillea* although the exact profile is identical only to the one of *Achillea*. Morphologically, *H. atlantica* is closest to the montane species of the *Achillea barrelieri* (Ten.) Schultz Bip. - *A. oxyloba* (DC.) Schultz Bip. group of the European Alps, on the basis of the monocephalous heads, slender, brown-tipped receptacular scales, dark-brown margins on the phyllaries, cypselas size, pinnatisect leaves and its perennial habit.

Although *Achillea* is one of the largest genera in the Anthemideae and comprises a wide variation in many characters, *Heliocauta* cannot be included without a grave distortion of its coherent definition. Features of *Heliocauta* not found in any species of *Achillea* include the actual position of the vascular bundles in the ribs of the cypselas (basal rather than central), the horizontal wall thickenings of the cells in the pericarp, the variable strands of sclerenchyma

forming extra ribs and the small, erose coroniform pappus.

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