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Taxonomic significance of trichomes in the genus *Acanthopsis* Harv. (Acanthaceae, tribe Acantheae)

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ABSTRACT
Hitherto characters derived mostly from macromorphology were used to distinguish among the members of *Acanthopsis* Harv., a taxonomically difficult group of plants endemic to arid parts of southern Africa. The taxonomic significance of leaf and bract indumentum in *Acanthopsis* was investigated using light, and scanning electron microscopy. Five non-glandular and three glandular trichome types were distinguished on the leaves and floral bracts. None of these trichome types are unique to the genus. Although the indumentum is variable in *Acanthopsis*, the density/dominance of specific trichome types was useful to distinguish among certain taxa, particularly on the abaxial surfaces of leaves and bracts. Each species of *Acanthopsis* has a characteristic trichome complement as far as dominant trichome types on both leaves and bracts are concerned. However, no obvious association between the type of trichomes and habitat (degree of aridity) or geographical distribution was evident.

KEY WORDS
Acanthopsis,
Blepharis,
anatomy,
ecology,
epidermis,
hairs,
indumentum,
trichomes.

RÉSUMÉ
Importance taxonomique des trichomes dans le genre Acanthopsis *Harv. (Acanthaceae, tribu Acantheae).*
Jusqu'à présent des caractères essentiellement macromorphologiques ont été pris en compte dans la subdivision de *Acanthopsis* Harv., un genre taxonomiquement difficile endémique des régions arides de l'Afrique australe. La signification taxonomique de l'indument des feuilles et des bractées d'*Acanthopsis* a été étudiée par microscopie photonique à balayage. Cinq types de poils non glanduleux et trois types glanduleux ont été distingués sur les feuilles et les bractées florales. Aucun d'entre eux n'est propre au genre. Malgré la variabilité de l'indument, le rapport densité/dominance de types de poils particuliers, notamment sur les faces abaxiales, s'est révélé utile pour séparer certains taxons. Chaque espèce d'*Acanthopsis* présente une combinaison de trichomes et une pubescence caractéristiques. Toutefois aucune corrélation simple n'a pu être mise en évidence entre les types de poils et l'habitat (degré d'aridité) ou la répartition géographique.

MOTS CLÉS
Acanthopsis,
Blepharis,
anatomie,
écologie,
épiderme,
poils,
indument,
trichomes.

INTRODUCTION

The taxonomic significance of trichomes in angiosperms has been widely recognised (Solereder 1908; Metcalfe & Chalk 1950, 1979; Carlquist 1961; Ellis 1979; Theobald *et al.* 1979; Winter & Van Wyk 1994; De Andrade Wagner *et al.* 2014). Carlquist (1961) was of the opinion that trichomes are perhaps the most important anatomical feature which could be used for taxonomic purposes as they are diverse, exist in a variety of taxa and are relatively easy to study. Metcalfe & Chalk (1950) have noted that length, size and density of trichomes are more variable as a result of environmental conditions than are the types of trichomes. Johnson (1975) similarly concluded that the type of trichome is usually more taxonomically significant than the indumentum, the latter which is more readily influenced by the environment.

In Acanthaceae the taxonomic and phylogenetic value of different features of trichomes (density, size, shape, surface texture, orientation) have been amply demonstrated (Obermeyer 1933; Metcalfe & Chalk 1950; Ahmad 1974, 1978; Kumar & Paliwal 1975; Singh & Jain 1975; Karlström 1978; Balkwill *et al.* 1988; Graham 1988; Immelman 1990; Manktelow 1996; Balkwill & Balkwill 1997; Darbyshire 2009; Bhatt *et al.* 2010; Patil & Patil 2011; Balkwill *et al.* 2017; Fisher 2017). However, even within a well-defined species there can be significant variation in the indumentum and trichome complement (Balkwill & Getliff Norris 1985; Balkwill & Balkwill 1997; Poriazis & Balkwill 2008; Darbyshire 2009; Darbyshire *et al.* 2010; Darbyshire *et al.* 2019). According to Ahmad (1978) the number of cells comprising the head in glandular trichomes is taxonomically significant. The latter noted that in Acanthaceae, glandular trichomes are more important at the suprageneric level (subfamily, tribe) while non-glandular trichomes are of diagnostic value at genus and species level. However, more recent studies indicate that variation in glandular trichomes is just as taxonomically significant as non-glandular trichomes at lower taxonomic ranks in Acanthaceae (Balkwill & Getliff Norris 1985; Darbyshire 2009; Fisher 2017; Darbyshire *et al.* 2019). For *Blepharis* Juss., Vollesen (2000) noted that the presence or absence of capitate (glandular) trichomes seems to be a more constant character on the calyx than in the floral leaves and bracts.

It has been suggested that the function of glandular and non-glandular trichomes in general may include the provision of defence against insects, large herbivores and pathogens, reduction of heat on the leaf surface or temperature regulation, increased reflection of UV light, reduction of physical abrasion, effecting the rate of transpiration, and maintaining the water balance in the leaves (Levin 1973; Johnson 1975; Ehleringer 1984; Immelman 1990; Wagner *et al.* 2004; Bhatt *et al.* 2010; De Andrade Wagner *et al.* 2014). The changes in inflorescence indumentum within *Isoglossa* Oerst. from non-glandular-ciliate in young inflorescences to glandular-viscid when fruiting are attributed to the protection of the fruit against predators (Poriazis & Balkwill 2008; Darbyshire *et al.* 2011). In members of some families such as Lamiaceae, glandular trichomes are the site of the production of essential oils and polysaccharides (Malechi & Giuliani 2006). According to Bhatt *et al.* (2010) the function of glandular trichomes in Acanthaceae has not yet been established, as the family is not reported to be aromatic. However, Manktelow (1996) noted that the glandular trichomes of *Phaulopsis* Willd. have a distinct smell, as do the glandular trichomes of *Petalidium* Nees and *Mimulopsis* Schweinf. (Darbyshire pers. comm.).

In past taxonomic works characters mostly derived from macromorphology were used to distinguish among the members of *Acanthopsis* (tribe Acantheae), a taxonomically difficult group of plants endemic to arid parts of southern Africa (Nees von Esenbeck 1847; Anderson 1864; Clarke 1901). Nees von Esenbeck (1847) mainly used habit and floral bract shape, Anderson (1864) considered the length of the corolla tube and calyx morphology to be important, while Clarke (1901) placed emphasis on habit, number of spines on the bracts, presence/absence of secondary spines on the bracts and bract indumentum. In a recent taxonomic revision of *Acanthopsis* (Steyn 2018; Steyn & Van Wyk 2015, 2016, 2017a, b), the characters used by Clarke (1901) were generally used, with additional characters including spike density, corolla size and colouration, pollen morphology, as well as geographical distribution patterns in the genus. The purpose of the present paper is to report on the taxonomic significance of leaf and floral bract indumentum in members of *Acanthopsis*. To try and relate structure and function, we also briefly discuss the possible ecological significance of the observed variation in the trichome complement.

MATERIAL AND METHODS

This study was conducted at the National Herbarium (PRE) of the South African National Biodiversity Institute (SANBI), South Africa. Taxonomic decisions were based on a detailed study of ± 400 herbarium specimens from various herbaria worldwide. Relevant herbarium specimens held at BOL, K, KMG, M, NBG, NMB, P, PRE, PRU, SAM (in NBG), WIND and Z, together with high resolution images of herbarium specimens on JSTOR (2017) and from the herbaria of B-W, BM, GZU, S and TCD were studied (acronyms of herbaria follow Thiers 2017).

Fieldwork was conducted over a period of three growing seasons to assess the variation of live plants in nature, and to collect spirit material, herbarium specimens, DNA samples and photographic images.

Leaf samples were taken from herbarium specimens and studied under a stereomicroscope (Zeiss Discovery V8) or compound (light) microscope (Zeiss Axio). For scanning electron microscope (SEM) work, a high resolution field emission SEM (Zeiss) housed in the Laboratory for Microscopy and Microanalysis, University of Pretoria and a desktop SEM (Phenom Pure+), in the National Herbarium, SANBI, were used.

TABLE 1. — Taxa of *Acanthopsis* Harv. and specimens studied with SEM.

Taxa	Specimens examined
A. adamanticola H.M.Steyn	*Germishuizen 10074*; *Smook 11204*
A. carduifolia (L.f.) Schinz	*Koekemoer 4620*; *Scholtz s.n.*; *Steyn 2106*
A. disperma Nees	*Koekemoer 4183*, *4187*, *4392*; *Steyn 1686*, *1845*, *1852*
A. dispermoides H.M.Steyn	*Steyn 1912*
A. dregeana H.M.Steyn subsp. *dregeana*	*Steyn 1822*
A. dregeana H.M.Steyn subsp. *longispina* H.M.Steyn	*Steyn 2141*
A. erosa H.M.Steyn	*Steyn 1874*
A. glabra (Nees) H.M.Steyn	*Koekemoer 3996*; *Steyn 1893*
A. glandulopalmata H.M.Steyn	*Steyn 1889*, *1990*, *2125*
A. glauca (Nees) Schinz	*Steyn 1888*, *2146*
A. hoffmannseggiana (Nees) C.B.Clarke (typical form)	*Steyn 758*, *1895*, *1900*, *1907*, *1915*, *2148*
A. hoffmannseggiana (Nees) C.B.Clarke (Pofadder form)	*Steyn 1908*, *2156*
A. horrida (Nees) Nees	*Steyn 1768*, *2121*
A. insueta H.M.Steyn	*Steyn 1805*
A. ludoviciana H.M.Steyn	*Koekemoer 4370*; *Steyn 1815*; *Von Staden 9138*
A. nitida H.M.Steyn	*Steyn 1884*, *2138*
A. pagodiformis H.M.Steyn	*Steyn 2147*
A. scullyi (S.Moore) Oberm.	*Steyn 2134*, *2139*
A. spathularis (Nees) Schinz	*Steyn 2135*, *2136*
A. tetragona H.M.Steyn subsp. *pedunculata* H.M.Steyn	*Steyn 2144*
A. tetragona H.M.Steyn subsp. *tetragona*	*Steyn 1848*
A. tuba H.M.Steyn	*Oliver et al. 181*, *800*; *Von Staden 9139*
A. villosa H.M.Steyn	*Koekemoer 4398*

Specimens on which different trichome types were observed using a stereo microscope and SEM (see Table 1 for a list of taxa with author names, and voucher specimens), were selected for further study with the light microscope (see Table 2). Leaf epidermal peels and transverse leaf sections were made to study the epidermal structures.

For epidermal peels, portions of leaf blades cut from herbarium specimens, were rehydrated in distilled water at 50°C, placed in glass tubes and covered with undiluted "Jik" household bleach (3.5% m/v sodium hypochlorite) for 24 to 48 hours. After the mesophyll was removed from the epidermis, the epidermal peels were washed in distilled water and stained with 1% safranin in 50% ethanol for 30 minutes. The stained material was dehydrated in an ethanol series and mounted in entellan (Product 7961, Merck KGaA, Darmstadt, Germany), as described by Mashau *et al.* (2013).

For transverse leaf sections, portions of leaf blades were cut from herbarium specimens and rehydrated in distilled water at 50°C. Freehand sections were made, placed in 50% ethanol and stained with 1% safranin in 50% ethanol for 5 minutes. Stained material was rinsed in 90% ethanol, counterstained with fast green FCF for 1 minute, rinsed twice with 100% ethanol, followed by 50:50 ethanol and xylol mixture and 100% xylol (1-2 minutes in each solution). Finally, the sections were mounted in entellan.

The indumentum of the calyces and bracteoles was not included in the systematic part of the study as initial observations did not show obvious differences between taxa, hence the present paper focuses on the trichome types observed on leaves and floral bracts only. The presence or absence, orientation and density of the different trichome types were recorded (Tables 3 and 4).

General terminology follows Beentje (2016). Descriptors used to indicate abundance and frequency of trichomes and glands follow Schmid (1982). A combination of the terminology of Solereder (1908), Metcalfe & Chalk (1950, 1979) and Fahn (1982) was used to describe the different trichome types.

TABLE 2. — Taxa of *Acanthopsis* Harv. and specimens selected for anatomical study with the light microscope.

Taxa	Specimens examined
A. carduifolia	*Koekemoer 4620*
A. disperma	*Steyn 1852*
A. dispermoides	*Steyn 1912*
A. glabra	*Steyn 1893*
A. glauca	*Steyn 2143*
A. hoffmannseggiana (typical form)	*Steyn 1895*, *1915*, *2148*
A. hoffmannseggiana (Pofadder form)	*Steyn 1908*, *2158*
A. horrida	*Steyn 2121*
A. ludoviciana	*Steyn 1815*
A. scullyi	*Steyn 2134*
A. tuba	*Oliver et al. 181*
A. villosa	*Koekemoer 4398*

RESULTS

The epidermal trichomes in *Acanthopsis* comprise an assortment of both glandular and non-glandular types. The basal cell of all these trichome types is more or less embedded among surrounding epidermal cells, with the structure often somewhat raised above the general level of the epidermis. Five non-glandular and three glandular trichome types (Fig. 1) were distinguished on the leaves and floral bracts. Non-glandular and glandular trichomes occur on both leaves and floral bracts of all taxa. The abaxial and adaxial leaf surfaces within a species generally have the same type of trichomes, with the adaxial surface usually less pubescent. The adaxial

surface of the floral bracts of almost all taxa of *Acanthopsis* presented the same type(s) of trichomes across the genus, while the trichome types of the abaxial surface show variation (especially in density and length of glandular trichomes) and this was found to be taxonomically significant. Although both adaxial and abaxial surfaces were studied, the results mainly concentrate on the abaxial surfaces as these were taxonomically more significant.

KEY TO THE DIFFERENT TRICHOME TYPES ON LEAVES AND FLORAL BRACTS OF *ACANTHOPSIS* HARV.:

1a. Trichomes non-glandular 2
1b. Trichomes glandular 5

2a[1]. Trichomes relatively thin-walled with a broad lumen (> ⅓ of cell diameter); uni- or multicellular; surface ornamented 3
2b. Trichomes thick-walled with a narrow lumen (< ¼ of cell diameter); uni- or multicellular; surface smooth or with helical pattern 4

3a[2]. Trichomes unicellular ..... Type A
3b. Trichomes multi-cellular; nodes often slightly swollen ..... Type B

4a[2]. Trichomes unicellular ..... Type C
4b. Trichomes multi-cellular; nodes distinctly swollen ..... Type D

5a[1]. Trichomes sessile or subsessile to short (usually < 200 µm long); stalk, if present, 1- or 2(3)-celled 6
5b. Trichomes long (nearly always > 250 µm); stalk 3-celled ..... Type G

6a[5]. Trichomes sessile or subsessile; stalk, if present, 1-celled ..... Type E
6b. Trichomes short; stalk 2 (or 3)-celled ..... Type F

DESCRIPTION OF TRICHOME TYPES

Non-glandular trichomes

Non-glandular trichomes are usually straight, of various lengths, consisting of 1-3 uniseriate cells, thin- or thick-walled stalks, with or without wall ornamentation.

Type A. Non-glandular, unicellular, lanceolate with relatively thin walls and a broad lumen; surface distinctly ornamented (Fig. 1A1, A2). In Type A1 the trichomes could be erect or appressed or any combination thereof, while in Type A2 the trichomes are anvil-shaped (asymmetrically T-shaped), appressed to the leaf surface and usually very densely packed, giving the leaves a glaucous appearance. Note that these two subtypes are only distinguished in leaves.

Type B. Non-glandular, multicellular with relatively thin walls and a broad lumen; surface distinctly ornamented (Fig. 1B).

Type C. Non-glandular, unicellular with thick walls and a narrow lumen, the latter being enlarged towards the base; surface usually smooth (Fig. 1C).

Type D. Non-glandular, multicellular with thick walls and a narrow lumen, the latter being enlarged towards the base; nodes distinctly swollen; surface often with helical pattern (Fig. 1D).

Glandular trichomes

Glandular trichomes are of various lengths, consisting of 1-3 uniseriate, thin-walled stalks, with or without wall ornamentation.

Type E. Glandular, uni- or multicellular; sessile or subsessile; stalk, if present, 1-celled, surface usually smooth; head globose (Fig. 1E).

Type F. Glandular, multicellular; stalk 2 (or 3)-celled, surface smooth or ornamented; head globose (Fig. 1F).

Type G. Glandular, multicellular; stalk 3-celled; surface usually smooth; head globose (usually viscid, the latter which manifests as the plant surfaces being sticky to the touch in fresh material, or with adherent sand grains and/or small bits of debris in herbarium specimens) (Fig. 1G).

DISTRIBUTION AND TAXONOMIC SIGNIFICANCE OF TRICHOME TYPES

Trichome Type A is common on both leaves and bracts, while Type B is predominantly found on leaves and Types C and D mostly on bracts. Sessile or subsessile glandular trichomes (Type E) are present on the bracts (and leaves) of nearly all members of *Acanthopsis*. Types F and G are found on both leaves and bracts but are more frequently found on bracts.

The most common non-glandular trichome types found on the leaves of *Acanthopsis* are A1 and B (Table 3; Figs 2B, C, F; 4A, D; 5G, H) with the presence and abundance of Type A2 trichomes (Fig. 4B, C) being taxonomic significant. A group of species that can be distinguished from the rest based on the presence of Type A2 trichomes on the leaves include *A. adamanticola*, *A. dregeana*, *A. glauca*, *A. insueta*, *A. ludoviciana* and *A. spathularis*. Unicellular, unornamented trichomes with thick walls and a narrow lumen (Type C) (Fig. 5F) are restricted to the leaves of *A. scullyi* and *A. villosa*. The abundance of long, non-glandular trichomes (Type D; Figs 2E; 3E) on the leaves

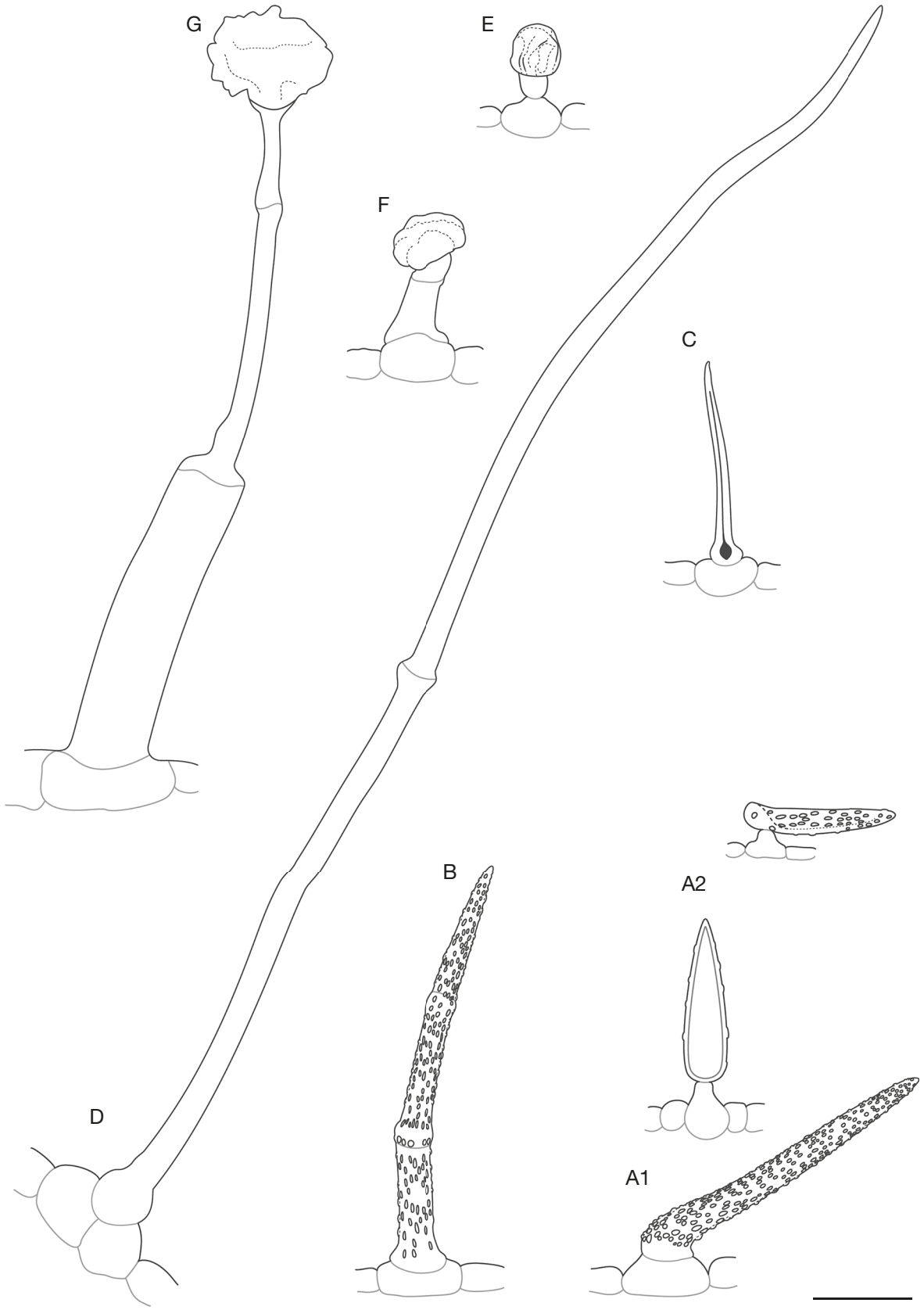

Fig. 1. — Trichome types (**A1**-**G**; illustrations labelled accordingly) found in *Acanthopsis*; as seen in surface view, unless indicated otherwise. **A1 (bottom)**, non-glandular, unicellular trichome, *A. glandulopalmata*, leaf (*Steyn 2125*); **A1 (top)**, optical section, *A. horrida*, leaf (*Steyn 2121*); **A2**, non-glandular, unicellular trichome, *A. dregeana* subsp. *longispina*, leaf (*Steyn 2141*); **B**, non-glandular, multicellular trichome, *A. hoffmannseggiana* Pofadder form, leaf (*Steyn 1908*); **C**, optical section, non-glandular, unicellular trichome, *A. disperma*, bract (*Steyn 1845*); **D**, non-glandular, multicellular trichome, *A. villosa*, leaf (*Koekemoer 4398*); **E**, glandular, uni- or multicellular trichome with or without 1-celled stalk, *A. glandulopalmata*, leaf (*Steyn 2125*); **F**, glandular, multicellular trichome with 2 (or 3)-celled stalk, *A. glandulopalmata*, leaf (*Steyn 2125*); **G**, glandular, multicellular trichome with 3-celled stalk and viscid head, *A. hoffmannseggiana* typical form, bract (*Steyn 1915*). Scale bar: 50 µm. Artist: Elizma Fouché.

TABLE 3. — The presence and relative frequency of trichome types on leaves (abaxial surface) in *Acanthopsis* Harv. (*, surface often smooth). For illustrations and definitions of trichome types see Fig. 1 and text. Indicators of frequency refer to any one specimen within the specific taxon. ×, rare to occasional; ××, frequent to common; ×××, abundant.

	Non-glandular trichome types					Glandular trichome types			Dominant
Taxa	**A1**	**A2**	**B**	**C**	**D**	**E**	**F**	**G**	**trichome types**
A. adamanticola	–	×××	–	–	–	×	–	–	A2
A. carduifolia	××	–	×	–	×	××	×	–	A1, E
A. disperma	××	–	××	–	×	×	×	–	A1, B
A. dispermoides	××	–	×	–	–	×	–	–	A1
A. dregeana subsp. *dregeana*	–	×××	–	–	–	×	–	–	A2
A. dregeana subsp. *longispina*	–	×××	–	–	–	×	–	–	A2
A. erosa	×××	–	–	–	–	×	–	–	A1
A. glabra	××	–	××	–	×	×	×	–	A1, B
A. glandulopalmata	××	–	×	–	–	××	×	–	A1, E
A. glauca	–	××	×	–	–	×	×	–	A2
A. hoffmannseggiana (typical form)	××*	–	×	–	–	×	××	×	A1, F
A. hoffmannseggiana (Pofadder form)	×	–	××	–	×	×	××	–	B, F
A. horrida	××	–	×	–	–	×	××	–	A1, F
A. insueta	–	×××	–	–	–	×	–	–	A2
A. ludoviciana	–	×××	×	–	–	×	–	–	A2
A. nitida	××	–	–	–	–	××	×	–	A1, E
A. pagodiformis	××	–	–	–	–	×	××	–	A1, F
A. scullyi	–	–	×	×	××	×	××	–	D, F
A. spathularis	–	×××	–	–	–	×	–	–	A2
A. tetragona subsp. *tetragona*	××	–	×	–	–	×	××	–	A1, F
A. tetragona subsp. *pedunculata*	××	–	–	–	–	×	×	–	A1
A. tuba	××	–	–	–	–	××	–	–	A1, E
A. villosa	–	–	–	××	××	×	××	–	C, D, F

TABLE 4. — The presence and relative frequency of trichome types on floral bracts (abaxial surface) in *Acanthopsis* Harv.. For illustrations and definitions of trichome types see Fig. 1 and text. Indicators of frequency refer to any one specimen within the specific taxon. ×, rare to occasional; ××, frequent to common; ×××, abundant.

	Non-glandular trichome types				Glandular trichome types			Dominant
Taxa	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**trichome types**
A. adamanticola	××	–	××	×	×	×	–	A, C
A. carduifolia	××	–	–	×	×	×	–	A
A. disperma	××	–	××	××	×	×	–	A, C, D
A. dispermoides	×	–	××	–	×	×	–	C
A. dregeana subsp. *dregeana*	××	–	××	×	×	××	×	A, C, F
A. dregeana subsp. *longispina*	××	–	××	×	×	××	×	A, C, F
A. erosa	×××	×	×	–	×	×	–	A
A. glabra	××	–	××	×	×	–	–	A, C
A. glandulopalmata	××	×	×	–	–	××	–	A, F
A. glauca	××	–	×	–	×	×	–	A
A. hoffmannseggiana (typical form)	×	–	××	×	×	××	××	C, F, G
A. hoffmannseggiana (Pofadder form)	×	–	××	××	×	××	–	C, D, F
A. horrida	×	–	×	××	×	××	–	D, F
A. insueta	××	–	×	×	×	–	–	A
A. ludoviciana	×	–	××	×	×	××	–	C, F
A. nitida	×	–	–	–	×	××	–	F
A. pagodiformis	×	–	××	×	×	××	×	C, F
A. scullyi	×	–	××	××	×	×	–	C, D
A. spathularis	××	–	×	×	×	–	–	A
A. tetragona subsp. *tetragona*	××	–	××	–	×	××	×	A, C ,F
A. tetragona subsp. *pedunculata*	×	–	××	–	×	××	–	C, F
A. tuba	×	–	××	××	×	×	–	C, D
A. villosa	×	–	×	××	×	×	–	D

can be used to distinguish *A. scullyi* and *A. villosa* from the other species. These trichomes are usually supported by a basal cellular pedestal that probably provides mechanical support and the thickened basal cell may add extra support (Bhatt *et al.* 2010). The sessile or sub-sessile glandular trichomes (Type E) are present in all members of *Acanthopsis*, with short-stalked glandular trichomes (Type F; Fig. 2D) frequent to common on the leaves of *A. hoffmannseggiana* (both forms), *A. horrida*, *A. pagodiformis*, *A. scullyi*, *A. tetragona* subsp. *tetragona* and *A. villosa.* Long-stalked (usually viscid) trichomes (Type G)

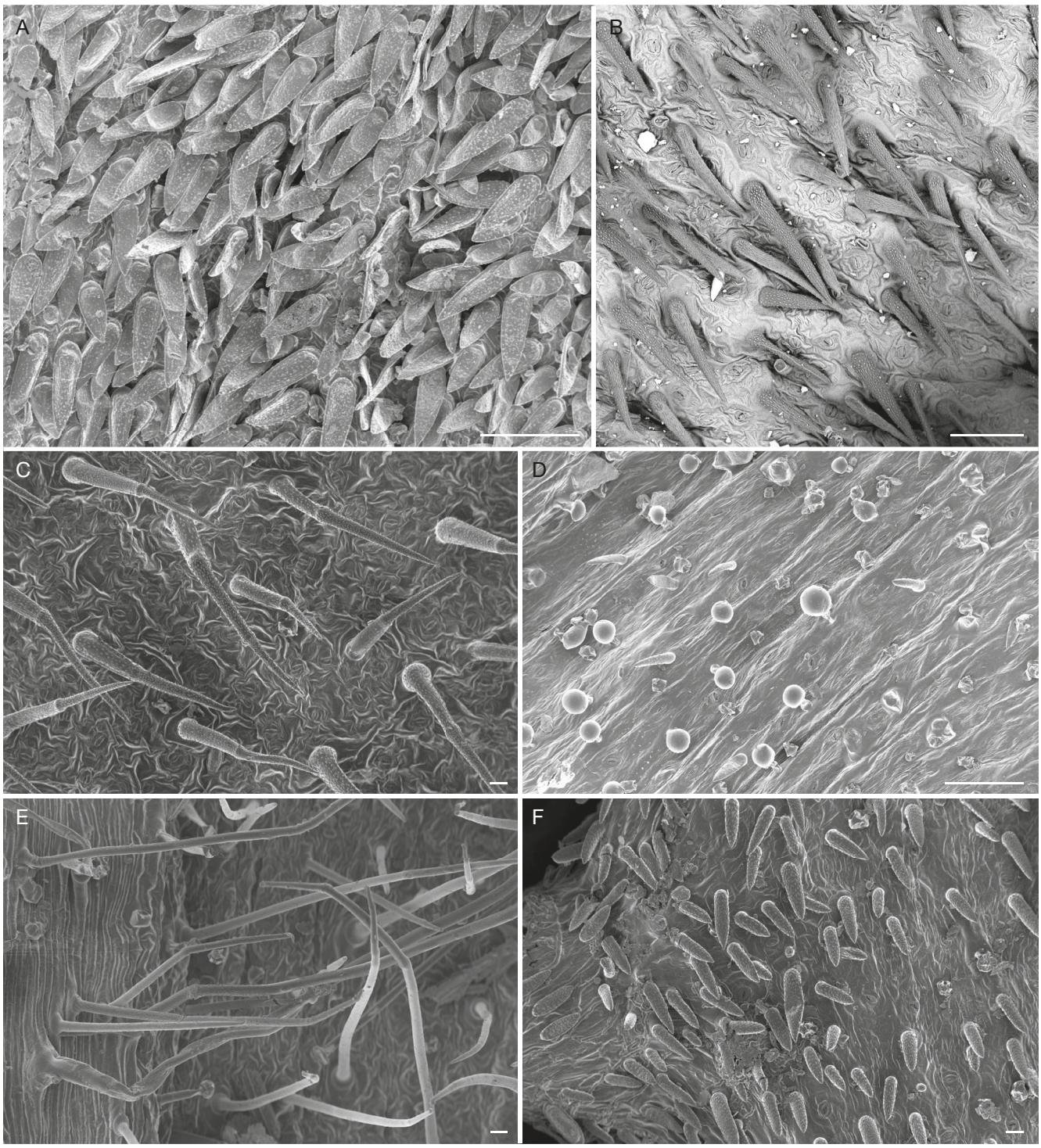

FIG. 2. — SEM images of leaf indumentum and predominant trichome types of various taxa of *Acanthopsis*: **A**, *A. dregeana* subsp. *longispina*, Type A2 (*Steyn 2141*); **B**, *A. hoffmannseggiana* typical form, Type A1 (*Steyn 758*); **C**, *A. disperma*, Type B (*Steyn 1845*); **D**, *A. horrida*, Type F (*Steyn 2121*); **E**, *A. villosa*, Type D (*Koekemoer 4398*); **F**, *A. nitida*, Type A1 (*Steyn 1884*). Scale bars: A, B, D, 100 µm; C, E, F, 20 µm.

are restricted to *A. hoffmannseggiana* (typical form) (Fig. 5B). In *Acanthopsis* the degree of leaf pubescence varies from villose (usually comprising Type D trichomes as in *A. scullyi* and *A. villosa*), densely pubescent (comprising Types G and A1 as in *A. hoffmannseggiana*) to seemingly glabrous (comprising Types A1 and E as in *A. nitida*). Members of *Acanthopsis* with reduced indumentum on the leaves are rare (*A. nitida* and *A. tuba*). The differences in trichome types of leaves among taxa are summarized in Table 3.

As opposed to the leaves, non-glandular, unicellular trichomes with thick walls and a narrow lumen (Type C; Fig. 3D; Fig. 5A, D) are commonly found on floral bracts

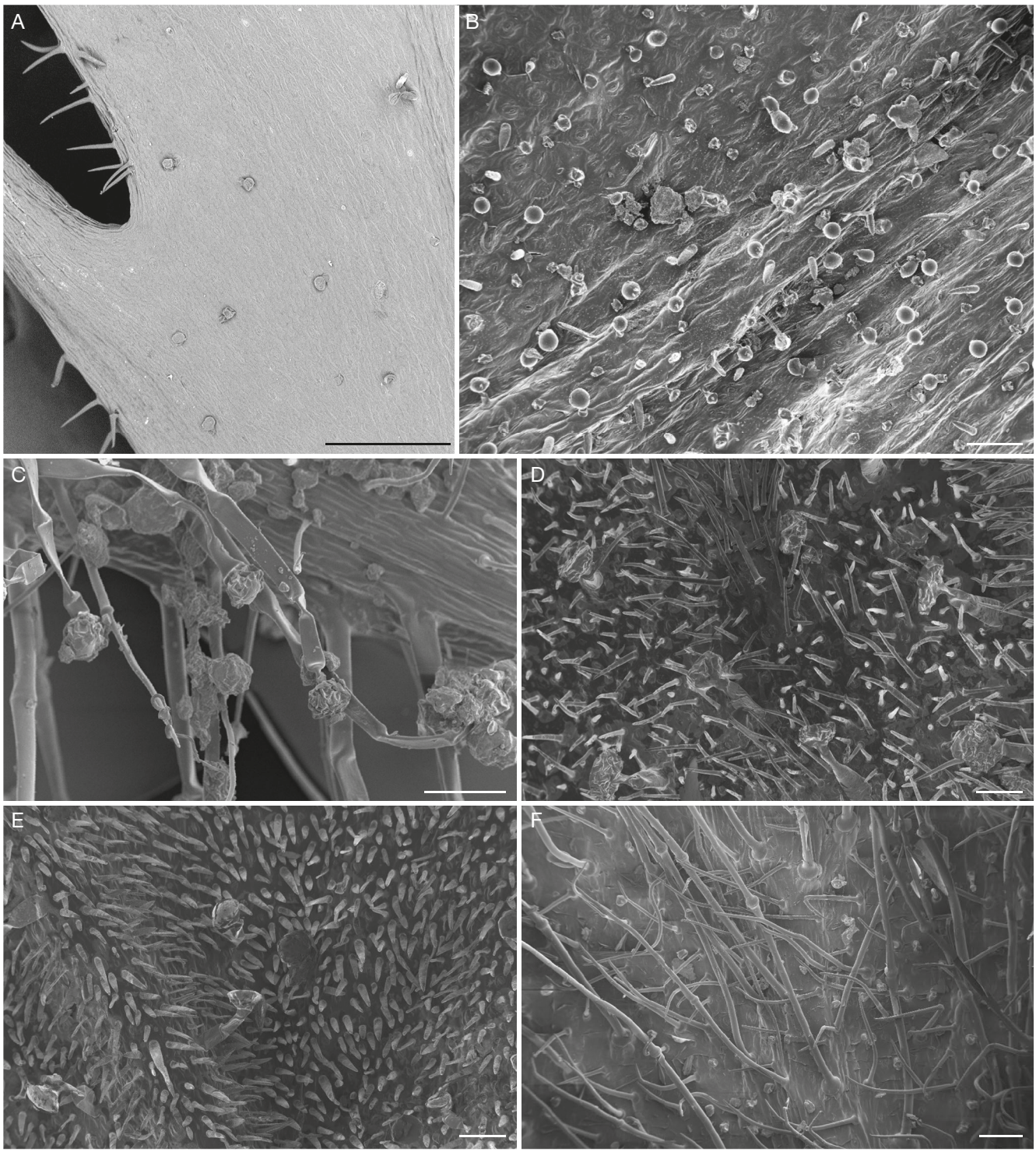

Fig. 3. — SEM images of bract indumentum (abaxial surface) and predominant trichome types of different taxa of *Acanthopsis*: **A**, *A. disperma*, Type E on blade, Type C on margin (*Koekemoer 4187*); **B**, *A. horrida*, Type F (*Steyn 2121*); **C**, *A. hoffmannseggiana* typical form, Type G (*Steyn 1895*); **D**, *A. pagodiformis*, Type C (*Steyn 2147*); **E**, *A. glandulopalmata*, Type A (*Steyn 2125*); **F**, *A. scullyi*, Type D (*Steyn 2139*). Scale bars: 100 µm.

while long, multicellular trichomes, often with a helical pattern on the surface (Type D; Fig. 3F), are less common. Type B trichomes were only recorded on the bracts of *A. erosa* and *A. glandulopalmata*. Both sessile or subsessile and short-stalked glandular trichomes (Fig. 5E) are present on the bracts in nearly all taxa of *Acanthopsis,* with long-stalked (usually viscid) trichomes (Type G) restricted to only a few taxa (*A. dregeana*, *A. hoffmannseggiana* (typical form), *A. pagodiformis* and *A. tetragona* subsp. *tetragona*) and usually conspicuous in *A. hoffmannseggiana* (typical form) (Fig. 3C; Fig. 5A, C). The dominance of Type D trichomes on the floral bracts of *A. disperma*, *A. hoffmannseggiana*

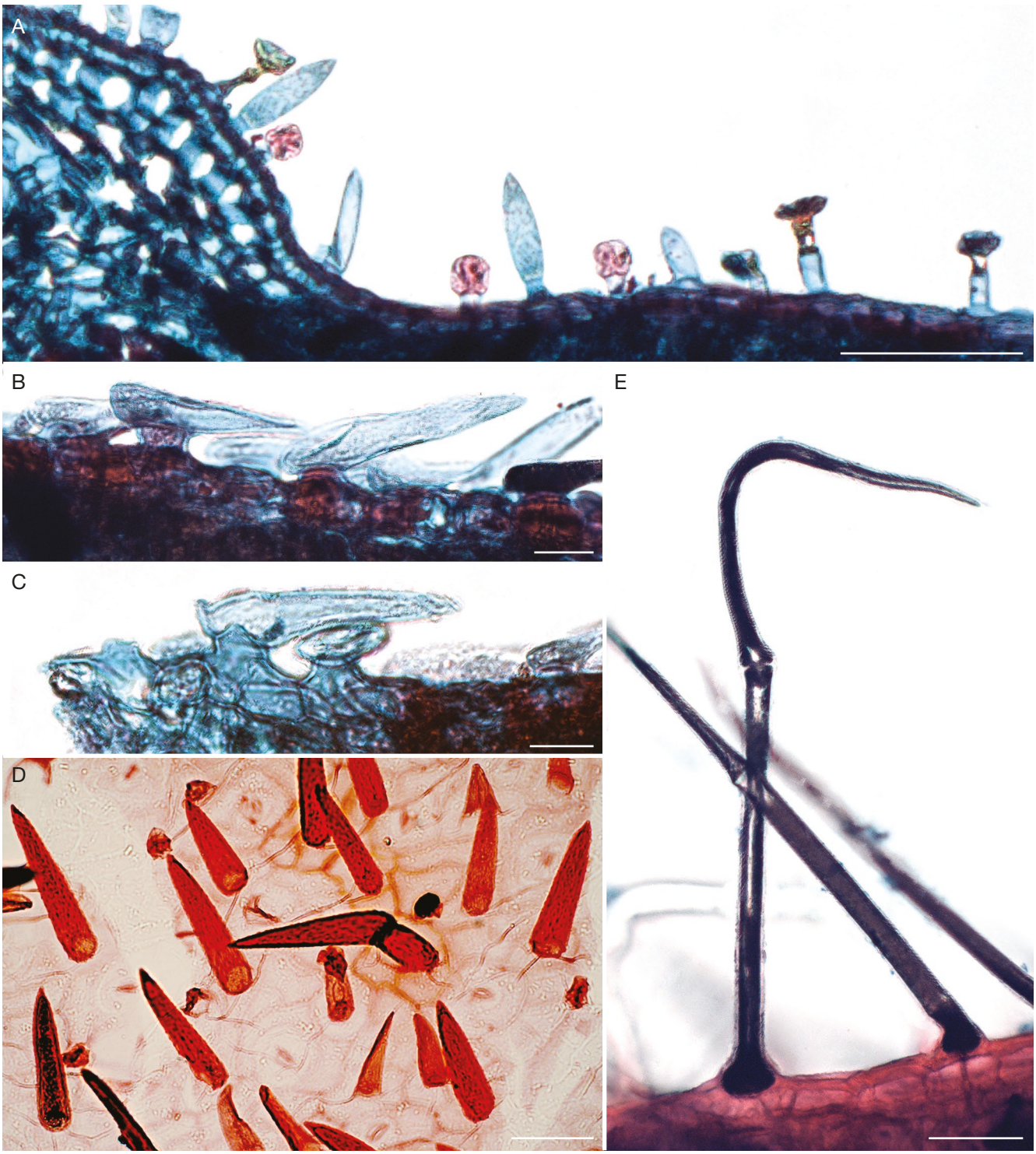

Fig. 4. — Light microscope images illustrating different trichome types on leaves (abaxial surface) of different taxa of *Acanthopsis*: **A**, *A. horrida*, Type A1, E, F (*Steyn 2121*); **B**, **C**, *A. glauca*, Type A2 (*Steyn 2143*); **D**, *A. dispermoides*, Type A1, B (*Steyn 1912*); **E**, *A. scullyi*, Type D (*Steyn 2134*). Scale bars: A, 100 µm; B, C, 20 µm; D, E, 50 µm.

(Pofadder form), *A. horrida*, *A. scullyi*, *A. tuba* and *A. villosa* gives these inflorescences a villose appearance (Fig. 3F). The abundance of glandular trichomes on the floral bracts of the typical form of *A. hoffmannseggiana* (Types E, F and G) (viscid) results in these inflorescences often being covered with sand. The differences in trichome types of bracts among taxa are summarized in Table 4.

As indicated above and in Tables 3 and 4, each species of *Acanthopsis* has a characteristic trichome complement as far as dominant trichome types on both leaves and bracts are concerned. When combined with morphological characters, trichomes are a useful aid in the identification of infrageneric taxa. A guide to species/subspecies based on trichome types and macromophology is supplied below.

Simplified key (for full variation see Tables 3 and 4) to the species of *Acanthopsis* Harv. based on a combination of trichome and morphological characters.

Note: for distinction between semi-dense and dense inflorescences, see Steyn & Van Wyk (2017b).

1a. Leaves with dense indumentum of appressed, anvil-shaped (asymmetrically T-shaped) trichomes (Type A2) giving plants a glaucous appearance 2
1b. Leaves with indumentum of varied trichomes but not dense, appressed, anvil-shaped trichomes (Type A2); rarely glaucous (*A. erosa*), but then due to Type A1 trichomes 8

2a[1]. Plants erect, virgate shrublets (> 25 cm tall) with well-developed branches and distinct internodes; leaves scattered (well-spaced) along woody stem 3
2b. Plants cushion-shaped subshrubs (usually < 20 cm tall) with gnarled stems and reduced internodes; leaves tufted or in basal rosette 5

3a[2]. Floral bracts with central primary spine distinctly spathulate ..... *A. spathularis* (Nees) Schinz
3b. Floral bracts with central primary spine not spathulate 4

4a[3]. Leaf base attenuate; inflorescences clearly pedunculate; basal floral bracts with spines up to 15 mm long ..... *A. dregeana* H.M.Steyn subsp. *dregeana* (also see *A. erosa*)
4b. Leaf base usually auriculate; inflorescences subsessile; basal floral bracts with spines 20-25(-30) mm long ..... *A. dregeana* H.M.Steyn subsp. *longispina* H.M.Steyn

5a[2]. Leaves with non-glandular, ornamented, multi-cellular trichomes (Type B) 6
5b. Leaves without non-glandular, ornamented, multi-cellular trichomes (Type B) 7

6a[5]. Leaf base not decurrent with spines 5-8 mm long; inflorescences pedunculate, semi-dense, 8-10 mm in diameter ..... *Acanthopsis glauca* (Nees) Schinz
6b. Leaf base decurrent with spines 4-6 mm long; inflorescences sessile, dense, 12-14 mm in diameter..... ..... *A. ludoviciana* H.M.Steyn

7a[5]. Leaves with spines on margins 2(-3) mm long; inflorescences dense ..... *A. adamanticola* H.M.Steyn
7b. Leaves with spines on margins 4-7(-8) mm long; inflorescences semi-dense ..... *A. insueta* H.M.Steyn

8a[1]. Leaves villose due to dominance of long, non-glandular, multi-cellular trichomes with nodes distinctly swollen (Type D) 9
8b. Leaves variously hairy, but not villose 10

9a[8]. Inflorescences semi-dense, 80-120(-150) mm long ..... *A. scullyi* (S.Moore) Oberm.
9b. Inflorescences dense, 25-50(-70) mm long ..... *A. villosa* H.M.Steyn

10a[8]. Plants erect, virgate shrublets (> 25 cm tall) with well-developed branches and distinct internodes; leaves scattered (well-spaced) along woody stem 11
10b. Plants cushion-shaped subshrubs (usually < 20 cm tall) with gnarled stems and reduced internodes; leaves tufted or in basal rosette 12

11a[10]. Leaves and bracts with indumentum almost exclusively composed of non-glandular, ornamented, erect or spreading unicellular trichomes (Type A1); inflorescences semi-dense ..... *A. erosa* H.M.Steyn
11b. Bracts with indumentum mainly composed of long, non-glandular, multicellular trichomes (Type D) and glandular, multicellular trichomes with short stalks (Type F); inflorescences dense... *A. horrida* (Nees) Nees

12a[10]. Floral bracts with glandular, multicellular trichomes with 3-celled stalk and viscid head (Type G) 13
12b. Floral bracts without glandular, multicellular trichomes with 3-celled stalk and viscid head (Type G) 15

13a[12]. Trichomes glandular, multicellular with 3-celled stalk and viscid head (Type G) dominant on floral bracts, and present on leaves ..... *A. hoffmannseggiana* (Nees) C.B.Clarke (typical form)
13b. Trichomes glandular, multicellular with 3-celled stalk and viscid head (Type G) present (not dominant) on floral bracts, but absent on leaves 14

14a[13]. Leaf base not decurrent; inflorescences dense, 12-14 cm in diameter; floral bracts ending in 5 primary spines ..... *A. pagodiformis* H.M.Steyn
14b. Leaf base decurrent; inflorescences semi-dense, 14-16(-20) cm in diameter; floral bracts ending in 3 primary spines ..... *A. tetragona* H.M.Steyn subsp. *tetragona*

15a[12]. Leaves shiny, glabrous or almost so 16
15b. Leaves not shiny or glabrous; variously hairy 17

16a[15]. Leaf base decurrent; floral bracts with non-glandular uni- and multicellular trichomes (Types C and D) frequent to common; inflorescences dense, (8-)10-13 mm in diameter ..... *A. tuba* H.M.Steyn
16b. Leaf base not decurrent, floral bracts without non-glandular uni- and multicellular trichomes (Types C and D); inflorescences semi-dense, 12-16 mm in diameter ..... *A. nitida* H.M.Steyn

17a[15]. Leaves and bracts with long, non-glandular, multi-cellular trichomes (Type D) 18
17b. Leaves and bracts without long, non-glandular, multi-cellular trichomes (Type D) 21

18a[17]. Spines on leaf base 3-5 mm long; floral bracts without short, non-glandular, unicellular trichomes (Type C) ..... *A. carduifolia* (L.f.) Schinz
18b. Spines on leaf base absent or 1-3 mm long; floral bracts with short, non-glandular, unicellular trichomes (Type C) frequent to common 19

19a[18]. Leaves distinctly petiolate, margins dentate-spinose with spines 1-3 mm long; spines on leaf base absent; inflorescences dense, 13-15 mm in diameter ..... *A. disperma* Nees
19b. Leaves sessile, margins coarsely dentate-spinose with spines 1-4(-7) mm long; spines on leaf base 1-3 mm long; inflorescences dense or semi-dense, 7-12 mm in diameter 20

20a[19]. Leaves with short, glandular, multicellular trichomes (Type F) rare to occasional; inflorescence semi-dense, 70-140 mm long, 7-9 mm in diameter ..... *A. glabra* (Nees) H.M.Steyn
20b. Leaves with short, glandular, multicellular trichomes (Type F) frequent to common; inflorescence dense, 50-80 mm long, 9-12 mm in diameter ..... *A. hoffmannseggiana* (Nees) C.B.Clarke (Pofadder form)

21a[17]. Leaf base decurrent; inflorescences semi-dense with floral bracts ending in 3 primary spines ..... *A. tetragona* H.M.Steyn subsp. *pedunculata* H.M.Steyn
21b. Leaf base not decurrent; inflorescences semi-dense or dense with floral bracts ending in 5 primary spines 22

22a[21]. Leaves dentate-spinose, spines on margins 1-3 mm long, 1 mm long at base; inflorescences 10-12 mm in diameter; floral bracts with short, glandular, multicellular trichomes (Type F) rare to occasional ..... *A. dispermoides* H.M.Steyn
22b. Leaves coarsely dentate-spinose, spines 3-6 mm on margins, 3-5 mm long at base; inflorescences 8-10 mm in diameter; floral bracts with short, glandular, multicellular trichomes (Type F) frequent to common ..... *A. glandulopalmata* H.M.Steyn

DISCUSSION

Glandular trichomes, mostly with short stalks (see Types E and F), generally occur throughout Acanthaceae (Metcalfe & Chalk 1950, 1979). Long-stalked glandular trichomes (see Type G) were reported in *Petalidium* Nees, *Dyschoriste* Nees, *Mimulopsis* Schweinf. and *Phaulopsis* Willd. (all in tribe Ruellieae), *Brachystephanus* Nees, *Justicia* L. and *Isoglossa* Oerst. (all in tribe Justicieae), and *Crossandra* Salisb. (tribe Acantheae) (Ahmad 1978; Karlström 1978; Vos & Edwards 1992; Manktelow 1996; Champluvier & Darbyshire 2009; Balkwill *et al.* 2017; Fisher 2017). Immelman (1990) and Munday (1980) reported straight and anvil-shaped, heavily ornamented, non-glandular trichomes (see Types A and B) in *Justicia s.s*. and *Monechma* Hochst. (synonym of *Justicia*). This type is also present in *Barleria* L. (tribe Barlerieae) (Balkwill & Balkwill 1997; Darbyshire 2010) and *Blepharis* Juss. (tribe Acantheae) (Vollesen 2000). Short unicellular or bicellular, thin-walled trichomes as well as long, uniseriate trichomes have been reported in the tribe Acantheae (including *Acanthopsis*) (Solereder 1908; Metcalfe & Chalk 1950, 1979; Ahmad 1978; Karlström 1978; Vos & Edwards 1992). No detailed studies on the indumentum of the two genera most closely related to *Acanthopsis*, namely *Blepharis* and *Acanthus* L., are available. However, none of the trichome types identified in *Acanthopsis* are unique in the family.

Although the indumentum in any particular taxon may display variation, this variation usually relates to the degree of pubescence and not the absence/presence of a particular type of trichome. The variation is usually within definable limits and the absence/presence and density/dominance of specific trichome types are useful to distinguish among certain taxa especially when combined with morphological features. There are some species-specific trichome complements that enable easy identification of some taxa or groups of taxa of *Acanthopsis* (e.g. *A. nitida*, *A. hoffmannseggiana* [typical form], *A. scullyi*, *A. tuba* and *A. villosa*), but other taxa are more difficult to distinguish from one another without the use of several characters in combination.

This corresponds with the findings of other workers regarding the importance of trichome type as a character of taxonomical significance in Acanthaceae both on its own and in combination with other characters (Balkwill & Getliff Norris 1985; Balkwill *et al.* 1988; Immelman 1990; Manktelow 1996; Balkwill & Balkwill 1997; Darbyshire 2009, 2010; Bhatt *et al.* 2010; Balkwill *et al.* 2017; Fisher 2017; Darbyshire *et al.* 2019).

The respective physiological or physical role of the indumentum, if any, remains speculative. The indumentum as a whole and especially the ornamented trichome surfaces of Types A1, A2 and B, may be involved in keeping leaves free of dust by promoting self-cleaning during rainfall as

Fig. 5. — Light microscope images illustrating different trichome types on leaves and bracts (abaxial surface) of different taxa of *Acanthopsis*: **A**. Bract, *A. hoffmannseggiana* typical form, Type C, G (*Steyn 2148*); **B**, Leaf, *A. hoffmannseggiana* typical form, Type G (*Steyn 2148*); **C**, Bract, *A. hoffmannseggiana* typical form, Type G (*Steyn 2148*); **D**, Bract, *A. hoffmannseggiana* typical form, Type C (*Steyn 2148*); **E**, Bract, *A. hoffmannseggiana* typical form, Type E (*Steyn 2148*); **F**, Leaf, *A. scullyi*, Type C (*Steyn 2134*); **G**, Leaf, *A. hoffmannseggiana* typical form, Type B (*Steyn 2148*); **H**, Leaf, *A. disperma* Type B (*Steyn 1852*). Scale bars: A, 100 µm; B, C, F, H, 50 µm; D, E, G, 20 µm.

described by Nosonovsky & Bormashenko (2009). Immelman (1990) suggested that the bent shape and heavier ornamentation of trichomes found in the acanthaceous genus *Justicia* (resembling Types A1, A2 and B; see Fig. 1) may add to the effectiveness of these trichomes as potential light shields. The predominance of relatively short pubescence in

members of *Acanthopsis*, often consisting of bent trichomes with heavy ornamentation, is probably an adaptation to their preferred habitat of exposed positions with relatively high radiation. The densely packed trichomes (Type A2; see Fig. 2A) could play a role in water absorption, since fog occurs frequently in the semi-desert habitats of these species (e.g., *A. adamanticola*, *A. glauca* and *A. ludoviciana*). *Acanthopsis hoffmannseggiana* (typical form) plants show regular occurrence of a sand cover due to active fixing of sand to the plants' surface (psammophory) as a result of the dominance of viscid glandular trichomes. This could be an adaptation to protect the plants against large herbivores, insects (Levin 1973; Poriazis & Balkwill 2008), or physical destruction by sandblasting in their arid, windy environment (Jürgens 1996).

The indumentum of *Acanthopsis* species is largely diagnostic as far as dominant trichome types on both leaves and floral bracts are concerned. The absence/presence as well as the dominant trichome types in *Acanthopsis* are valuable characters to distinguish certain taxa, especially in non-flowering material. However, indumentum is best used in combination with other morphological characters, including growth form and inflorescence morphology to successfully identify members of *Acanthopsis* to species and subspecies level. No clear-cut association between the type of trichomes and indumentum, and the habitat (degree of aridity) or geographical distribution was noted and the functional significance of both non-glandular and glandular trichomes needs further investigation.

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