



Notes on morphological characteristics and life history strategy of the genus *Acanthopsis* Harv. (Acanthaceae)

Authors

^{1,2}Hester M. Steyn 
^{1,2}Abraham E. van Wyk 

Affiliations

¹National Herbarium, South African National Biodiversity Institute, Private Bag X101, Pretoria 0001, South Africa.

²H.G.W.J. Schweickerdt Herbarium, Department of Plant and Soil Sciences, University of Pretoria, Pretoria 0002, South Africa.

Corresponding Author

Dr Hester M. Steyn; e-mail: h.steyn@sanbi.org.za

Dates

Submitted: 28 April 2023
 Accepted: 19 January 2024
 Published: 21 May 2024

How to cite this article:

Steyn, H.M. & Van Wyk, A.E., 2024, 'Notes on morphological characteristics and life history of the genus *Acanthopsis* Harv. (Acanthaceae)', *Bothalia* 54, a7. <http://dx.doi.org/10.38201/btha.abc.v54.7>

Copyright: © 2024. The Authors.
 Licensee: SANBI. This work is licensed under the Creative Commons Attribution 4.0 International License

Background: Morphological characteristics and life history strategies are vital in the success of plants to inhabit specific areas. Until recently the genus *Acanthopsis* was taxonomically poorly understood, and a recent revision rectified this aspect. The group comprises 20 species, all confined to arid parts of South Africa and Namibia. Much regarding the life history and ecology of the genus was still unknown.

Objectives: Members of the genus *Acanthopsis* adapted to harsh environmental conditions have evolved an array of functional traits to enhance their chances of survival. The present contribution focuses on a select few of these traits, with discussion centred around them.

Methods: This paper gives an overview of some casual and anecdotal observations made on the morphological characteristics and life history strategy during the taxonomic study.

Results: Significant adaptations include a perennial subshrub habit, spinous inflorescences/infructescences, and flowers exhibiting the classical syndrome for insect pollination, likely by insects possessing elongated proboscises. Additionally, the seeds are myxospermous and undergo dispersal solely when there is an ample supply of water for germination. Noteworthy is the prompt germination of seeds, occurring within 24 h.

Conclusion: Certain observations may potentially serve as catalysts for further, more in-depth investigations into the ecological significance of specific morphological traits and how the species might respond to anticipated future changes in temperature and precipitation.

Keywords: habit, functional traits, inflorescences, life form, morphology, myxospermy, pollen, pollination, seed dispersal.

Introduction

The success of plants to inhabit specific areas lies in the combination of plant functional traits, life history strategy and the success of dealing with competition, disturbance and environmental stress. The life history strategy of a plant can be defined as the patterns and timing of events (related to survival and reproduction) in a plant's life, including germination, flowering, fruiting and dispersal. According to Adler et al. (2014) there are strong relationships between plant functional traits (e.g., life form, plant height, leaf size and seed dispersal mode) and plant life histories. The life form classification of Raunkiaer (1934) is probably one of the best known classification systems for categorising plants and is based on the position of the plant's renewal (perennating) buds during seasons with adverse conditions. Plants have evolved three major strategies depending on the degree of disturbance and stress,

and can be labelled as competitors, stress-tolerators or ruderals (Grime 1977).

Acanthopsis Harv. (Acanthaceae) is a distinct and easily recognisable genus closely related to the genus *Blepharis* Juss. Both genera can be described as stress-tolerant plants (growing in habitats with high environmental stress and low disturbance) (Grime 1977; Bornhofen et al. 2011). The genus *Acanthopsis* is endemic to southern Africa (Namibia, Northern & Western Cape, South Africa) and most species are found in exposed habitats in full sun in rocky, sandy soils in areas that receive less than 200 mm of rainfall per year. The Succulent Karoo Biome is particularly rich in *Acanthopsis* diversity, with 21 of the 23 taxa occurring here. This biome is associated with the presence of low winter rainfall and extreme summer aridity (along the coast and west-facing Great Escarpment, the rainfall is supplemented by coastal fog) (Steyn et al. 2019).

The biogeography and conservation status of members of *Acanthopsis*, as well as the taxonomic importance of the indumentum, were dealt with by Steyn et al. (2019) and Steyn and Van Wyk (2021) respectively. The aim of this paper is to give an overview of some noteworthy, albeit often casual or anecdotal, observations made on the morphological characteristics and life history strategy during the taxonomic study that may help explain the biology of the genus in relation to the prevailing habitat conditions. Additionally, it is anticipated that certain observations may serve as catalysts for subsequent, more in-depth investigations into the ecological significance of specific morphological traits.

Research materials and methods

Materials

Taxonomic decisions were based on a detailed comparative morphological study of \pm 400 herbarium specimens from various herbaria worldwide. This study was conducted at the National Herbarium (PRE) of the South African National Biodiversity Institute (SANBI), South Africa. Relevant herbarium specimens held at BOL, K, KMG, M, NBC, NMB, P, PRE, PRU, SAM (in NBC), WIND and Z together with high resolution images of herbarium specimens on JSTOR (2018) and from the herbaria of B-W, BM, GZU, S and TCD were studied (abbreviations of herbaria follow Holmgren et al. 1990; Thiers 2023).

Fieldwork was done 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.

Methods

All measurements were taken from herbarium specimens, or in the case of floral parts, mostly from additional pressed material collected by the authors. Leaf and floral samples were taken from herbarium specimens and studied under a stereomicroscope (Zeiss Discovery V8) or 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. Digital images to illustrate the general morphology were obtained with a Zeiss Discovery V8 stereomicroscope and a Zeiss Axio light microscope.

Terminology follows Beentje (2016). Descriptors used to indicate abundance and frequency follow Schmid (1982).

Permitting

Relevant collecting permits were obtained before the collection of herbarium specimens.

Results

Life form and habit

The genus *Acanthopsis* comprises different life forms according to the classification of Raunkiaer (1934). Most of the species are considered chamaephytes, with *A. disperma* Nees and the annual form of *A. hoffmannseggiana* (Nees) C.B. Clarke as therophytes. The perennial rosette form of *A. hoffmannseggiana* may be classified as a hemicryptophyte.

Within *Acanthopsis*, the shrublet (dwarf shrub) group is one of the most readily recognisable entities in a genus otherwise characterised by acaulescent herbs or compact subshrubs. There is a gradual increase in woodiness, branching and internode length from annual/perennial herbs to subshrubs and shrublets. The shrublet group can be distinguished in usually being virgate, up to 25–40(–60) cm tall, with well-developed branches and clearly visible internodes; the latter are usually up to 10–20(–25) mm long. Shrubby species usually have scattered leaves (well-spaced) along woody stems (Figure 1C & D). The shrublet group includes the following species: *A. dregeana* H.M. Steyn, *A. erosa* H.M. Steyn, *A. horrida* (Nees) Nees and *A. spathularis* (Nees) Schinz.

Subshrubs are much more compact plants, up to 25(–30) cm tall, with gnarled stems and reduced (usually not visible) internodes, usually < 5(–8) mm long, with



Figure 1. Different habits found in *Acanthopsis*. A, acaulescent herb; B, compact subshrub; C, shrublet (cushion-shaped); D, shrublet (virgate). Photographs: A, B, the authors; C, D: M. Koekemoer.

fascicled leaves (Figure 1B). Compact subshrubs are the most common in the genus and include *A. adamanticola* H.M.Steyn, *A. carduiifolia* (L.f.) Schinz, *A. dispermoides* H.M.Steyn, *A. glabra* (Nees) H.M.Steyn, *A. glandulopalmata* H.M.Steyn, *A. glauca* (E.Mey. ex Nees) Schinz, *A. hoffmannseggiana*, *A. insueta* H.M.Steyn, *A. ludoviciana* H.M.Steyn, *A. nitida* H.M.Steyn, *A. pagodiformis* H.M.Steyn, *A. scullyi* (S.Moore) Oberm., *A. tetragona* H.M.Steyn, *A. tuba* H.M.Steyn and *A. villosa* H.M.Steyn.

Acaulescent/rosulate herbs, with leaves in a basal rosette, are almost restricted to the annual or short-lived perennial species of *A. disperma* and *A. hoffmannseggiana*, while young plants of *A. dispermoides*, *A. glabra*, *A. pagodiformis* and *A. scullyi* could appear acaulescent (Figure 1A).

Certain species have pioneer or weedy tendencies, and they thrive under conditions of disturbance and

degradation often caused by overgrazing (e.g., *Acanthopsis carduiifolia*, *A. disperma*, *A. hoffmannseggiana* and *A. scullyi*). However, these species have never been observed to become invasive.

Inflorescences, flowers and flowering time

All species of *Acanthopsis* have bracteate spikes (Figure 2), which are solitary (terminal) in subshrub and shrublet species or in clumps at the base of the leaves in the rosulate species. The spikes range from lax where the inflorescence axis among the bracts is nearly always exposed with successive bract laminas only slightly overlapping, to dense, where the inflorescence axis among bracts is never exposed with the bract laminas deeply overlapping. The floral bracts are stiff, apically 3–7-lobed, with each lobe ending in a simple or compound spine.

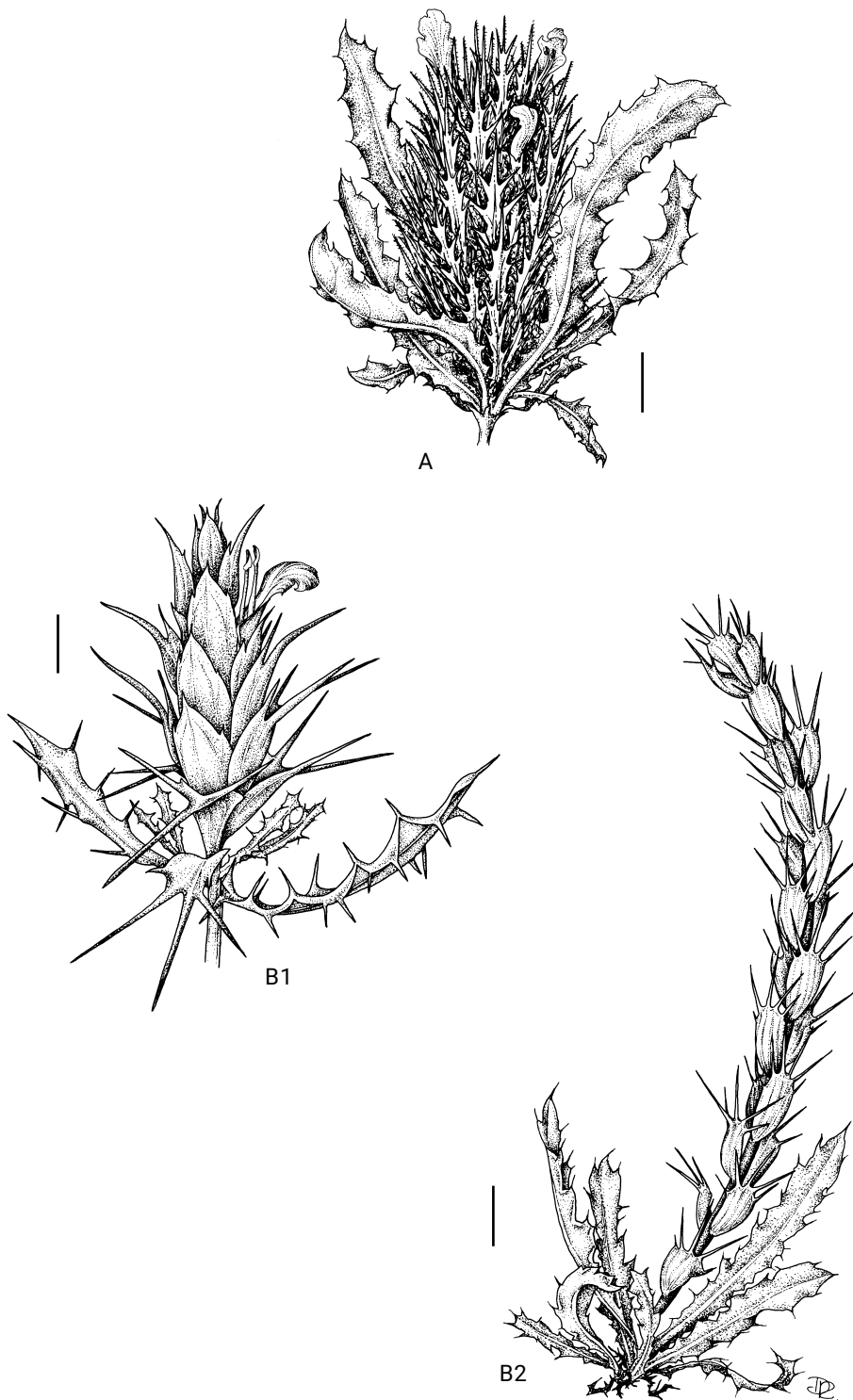


Figure 2. Types of inflorescences found in *Acanthopsis* based on the density of individual flowers and their bracts. A, dense (> 60% bract overlap); B, lax (B1, 30–60% bract overlap; B2, < 30% bract overlap). Scale bar: 10 mm. Artist: Daleen Roodt.

The flowers consist of a 4-partite calyx and tubular corolla. The corolla of *Acanthopsis* is zygomorphic, 1-lipped and 5-lobed, with the outer lobes much reduced (except in *A. tuba*) and the lip much longer than the tube (except in *A. tuba*) (Figure 3). The corollas of *Acanthopsis* have ascending cochlear aestivation (abaxial corolla lobe is always wholly overlapping the lateral lobes) (Scotland et al. 1994). The corolla sizes generally vary between 23–25 × 9–11 mm, with the longest corollas found in *A. glandulopalmata*, *A. scullyi*, *A. tetragona* subsp. *pedunculata* and *A. tuba*. *Acanthopsis tuba*

has the longest flowers in the genus (45–50 mm long), which is probably an adaptation to a specific pollinator. Corollas are usually lilac to purple with darker veins (e.g., *A. disperma*, *A. horrida* and *A. dregeana*) or whitish/cream with purple veins (annual form of *A. hoffmannseggiana* as well as *A. scullyi*). The corolla throat varies from white or cream to lemon-yellow (Figure 4). The reduced outer corolla lobes are usually the same colour as the corolla throat, except for *A. horrida*, *A. tuba* and *A. villosa*, where the outer lobes are the same colour as the corolla limb, namely lilac to purple.



Figure 3. Corolla, androecium and gynoecium of *Acanthopsis* flowers. A, corolla, *A. tuba* (Von Staden 9139); B, corolla, *A. horrida* (Koekemoer 4370, PRE); C, androecium, *A. horrida* (Koekemoer 4370, PRE); D, gynoecium and one lateral sepal of calyx; note the tuft of glandular hairs at base of style, *A. scullyi* (Steyn 1911, PRE). Scale bar: A, B = 10 mm, C, D = 1 mm. Artist: Daleen Roodt.

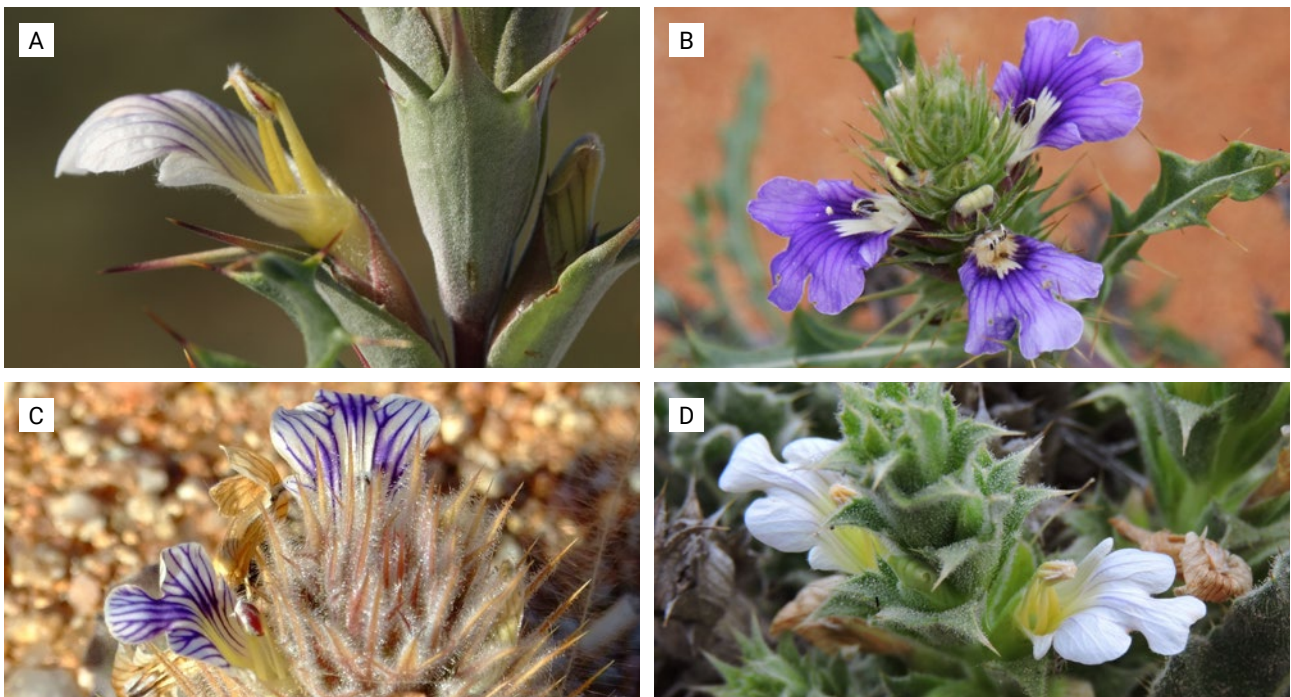


Figure 4. Corolla of *Acanthopsis* flowers showing colour variation. A, *A. glauca*; B, *A. horrida*; C, *A. hoffmannseggiana*; D, *A. scullyi*. Photographs: A, B, M. Koekemoer; C, D, the authors.

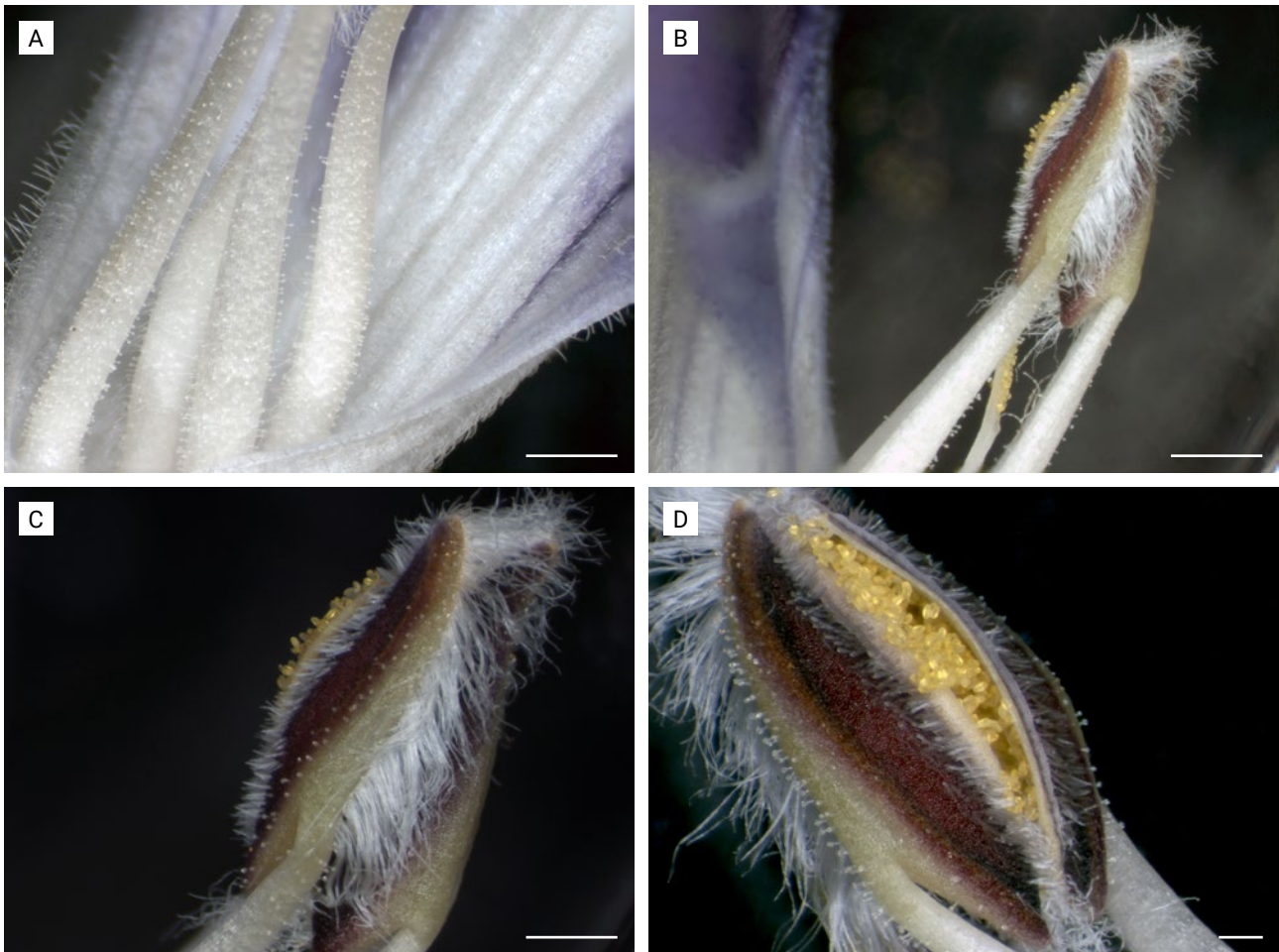


Figure 5. Androecium of *Acanthopsis disperma* flowers. A, stout filaments; B, anthers and style; C and D, anthers, showing long hairs and pollen grains exposed on the side facing the corolla lip. Scale bar: A = 0.8 mm, B = 0.7 mm, C = 0.5 mm, D = 0.2 mm.

The androecium comprises four fertile stamens of equal length and shape, without staminodes. The filaments are stout and the anthers densely bearded along the lateral edge (Figures 3 & 5), connivent (held together by hairs), monothechal, sub-basifixed and non-versatile. In *Acanthopsis* the filaments are without an appendage at the tip – this is present in *Blepharis*. The anthers are introrse, but expose the bright yellow pollen through an opening between the two anterior anthers on the side facing the corolla lip (Figure 5). In *Acanthopsis* the style is filiform with an unlobed stigma (one lobe is highly reduced). In *Blepharis* there are two elliptic or rounded patches of very short glandular hairs on the same side at the base of the style, while in *Acanthopsis*, the base of the style is covered with a ring or a patch of glandular hairs (Figure 3D). The taxonomic and functional significance of these glandular hairs, as well as the hairs on the anthers, needs further investigation.

Most species flower during spring and early summer with the exception of *A. disperma* and *A. hoffmannseggiana*, which often flower during autumn. The difference in flowering time is probably the result of late summer rain in the transition areas between summer and winter rainfall where these species are found.

Pollen and pollination

Acanthaceae, a classical eurypalynous family, is noted for its wide variety of pollen types. This fact was first highlighted by Radlkofer (1883), and the variation in the morphology of pollen grains is of considerable diagnostic value (e.g., Lindau 1893, 1895; Bremekamp 1944, 1965; Raj 1961; Munday 1980; Immelman 1987; Balkwill & Getliffe Norris 1988; Graham 1988; Furness 1990, 1991, 1995, 1996; Scotland & Vollesen 2000; Perveen & Qaiser 2010; House & Balkwill 2016). Most species of *Acanthopsis* have beige to orange-brown anthers with the exception of *A. adamanticola*, *A. disperma*, *A. erosa*, *A. hoffmannseggiana*, *A. horrida*, *A. spathularis* and *A. tuba*, which have dark brown to purple-black anthers. In *Acanthopsis* pollen is shed as monads. Grains are isopolar, prolate to perprolate (Polar axis/Equatorial diameter = 1.45–2.17), 3-colpate, with a triangular outline in polar view and an elliptical outline (somewhat angular in *A. tuba*) in equatorial view (Figure 6). The exine sculpturing of the mesocolpi is essentially microreticulate to foveolate with some variation adjacent to colpi (Figure 6). A distinct elevated ridge surrounds colpi with the surface adjacent to the ridge, usually verrucate (rugulate in *A. tuba*).

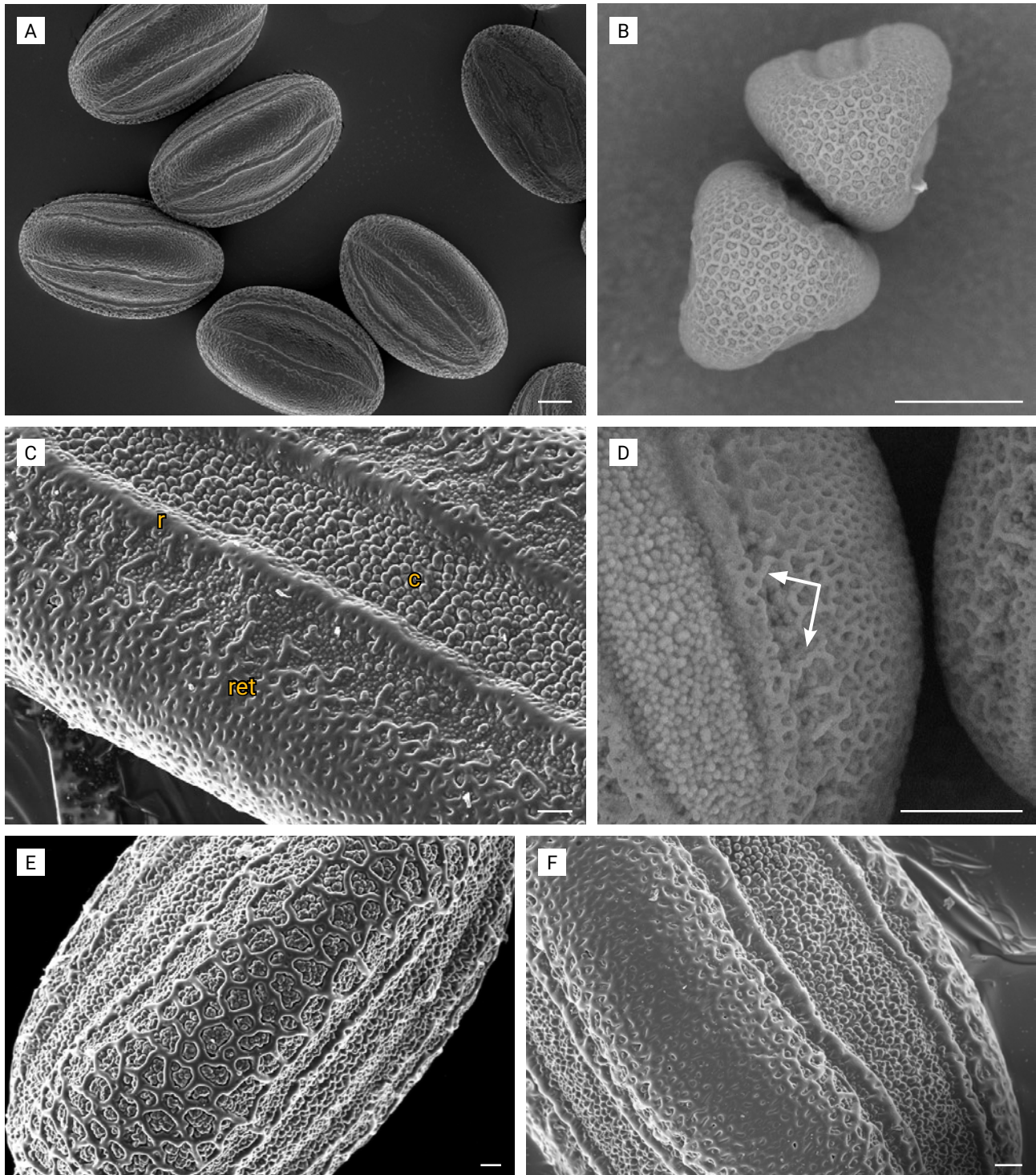


Figure 6. SEM images of pollen grains (unacetolised) of *Acanthopsis*. A, *A. glauca*, equatorial view (Steyn 1888, PRE); B, *A. hoffmannsegiana* typical form, polar view (Steyn 1900, PRE); C, *A. spathularis*, showing reticulum (ret), colpus (c) and ridge (r) (Steyn 2135, PRE); D, *A. adamanticola*, showing muri (see arrows) connecting the ridge and reticulum (Smook 11204, PRE); E, *A. carduifolia*, surface sculpturing of mesocolpium reticulate (Koekemoer 4260, PRE); F, *A. tetragona* subsp. *tetragona*, surface sculpturing of mesocolpium microreticulate to foveolate (Steyn 1848, PRE). Scale bar: A = 10 μm , B = 20 μm , C = 2 μm , D = 8 μm , E, F = 2 μm .

Muri connecting the ridge with the reticulum can be absent or present (Figure 6).

Furness (1996) studied pollen of the so-called 'group with long-exserted stamens and bone-like filaments' within *Acantheae*, which includes *Acanthopsis*, *Acanthus*, *Blepharis* and *Sclerochiton*. She stated that pollen

morphology was taxonomically significant at genus, as well as species level, and five pollen types, with ten subtypes, were described (Furness 1996). Four species of *Acanthopsis* were included in the above-mentioned study, and it was concluded that pollen of *Acanthopsis* is dissimilar to that found in the other genera, being relatively large compared to the closely related *Acanthus*



Figure 7. The flowers of *A. horrida* showing the stigma deflected towards the corolla lip. Photograph: M. Koekemoer.

and *Blepharis*. Furness (1996) distinguished *Acanthopsis hoffmannseggiana* from *A. carduifolia*, *A. disperma* and *A. spathularis* (misapplied name = *A. horrida*) based on its pollen type. However, during the current study, it was found that the presence/absence of muri joining the ridge of tectum to the reticulum, used by Furness (1996) to distinguish between pollen types, is variable among samples within the above-mentioned species and *A. disperma* and *A. hoffmannseggiana* display both pollen types.

From images taken in the field of plants in flower, it is clear that the style is shortly exerted at the top of the anthers (at a stage without any obvious pollen grains presented by the anthers or the protruding style), and it was suspected that the flowers are protogynous. However, preliminary observations from a cultivated specimen of *A. disperma* indicated that there is no temporal separation of pollen maturation and stigmatic receptivity within a flower. Although the style lengthens until it is exerted from the anther 'tube' and the stigma deflects towards the corolla lip (Figure 7), it does not seem to function as a 'pollen presenter' (Ladd & Donaldson 1993).

Hardly any information is available on the pollinators of *Acanthopsis*, but the dark purple veins on the corolla probably serve as nectar guides to insect pollinators.

Flowers of certain species of *Blepharis* are known to be visited and pollinated by bees, wasps and pollen wasps (Gess & Gess 2010, 2014) (Figure 8). The flowers of *Acanthopsis* have no noticeable scent during the day, but nectar was observed in fresh flowers as a droplet at the base of the corolla tube. Fruit flies (Tephritidae) and ants (*Crematogaster* species) were often observed on *Acanthopsis* flowers (before and after anthesis) (Figure 8), and bee flies were observed visiting populations of *A. tuba* plants (P. van Wyk, pers. comm. 2017; F. Grenier, pers. comm. 2018).

Fruit and seed

The fruit in *Acanthopsis* is a bilocular capsule enveloped in a persistent zygomorphic calyx. All members of *Acanthopsis* have ovate, flattened, glabrous, 2-seeded capsules with ovate, flattened seeds covered with long white hygroscopic hairs. As the availability of capsules and seeds was limited (especially in some taxa, e.g., *A. spathularis* and *A. tuba*), the full taxonomic potential of these characters, particularly as a source of diagnostic characters for species, could not be established. However, in general, the capsules are 6–8 × 3–4 mm and the seeds 4 × 3 mm. The capsules of *A. carduifolia*, *A. nitida* and *A. scullyi* tend to be slightly bigger (8–9 × 3–4 mm) than the rest of the taxa. *Acanthopsis tetragona* subsp.



Figure 8. Insects observed on *Acanthopsis* flowers. A, fruit fly on *A. hoffmannseggiana*; B, fruit fly and ant on *A. nitida*; C, long-proboscid bee fly probing a flower of *A. tuba*. Photograph: A, B, the authors; C, F. Grenier.

pedunculata has relatively large seeds (6×5 mm) compared to the other taxa [for more information, see Steyn (2018)].

Despite water being a limiting factor in arid areas, hydrochory (here defined as dispersal by rain or dew) plays an important part in this environment (Van Rheede van Oudtshoorn & Van Rooyen 1999). *Acanthopsis* and *Blepharis* are antitelechoric genera where seed dispersal does not take place immediately after the fruit has ripened, but the mature capsules are retained unopened on the plant until the conditions are favourable (sufficient water for germination is present) (Gutterman 1994; Vollesen 2000). In *Acanthopsis* the dry capsule remains covered (protected) by the hydrochastic bract and four sepals, and only upon wetting does the bract diverge (open up) and the upper and lower sepals separate to expose the apex of the capsule (Figure 9). Gutterman et al. (1967) reported that upon wetting, capsules of *Blepharis persica* (Burm.f.) Kuntze [= *B. ciliaris* (L.) B.L.Burtt] explode, and seeds are dispersed dry. The seeds of *Acanthopsis* were very rarely observed to be forcefully expelled from the mature but relatively young

capsule (but see next paragraph) upon wetting or even after scarification of the apex, as observed in *Blepharis* by Gutterman et al. (1967). Even when moistened, the apex of the *Acanthopsis* capsule (apical 'lock' according to Gutterman et al. 1967) usually had to be damaged before the capsule opened up slightly, and the seeds were exposed but usually not ejected.

Gutterman et al. (1967) and Van Rheede van Oudtshoorn and Van Rooyen (1999) argued that the rate and degree of separation of the sepals vary with their age, implying that the studied infructescences of *Acanthopsis* were possibly not weathered (old) enough for the capsules to explode and eject the seeds as mentioned above. During an irrigation experiment in autumn 2020, infructescences of different species of *Acanthopsis* collected in 2015 were indeed seen to eject their seeds after wetting (receiving a mist spray for approximately 10 minutes), thus supporting the hypothesis that age of fruit and ejection of seeds are linked.

The hygroscopic hairs covering the seeds of *Acanthopsis* species are mucilaginous. They immediately start

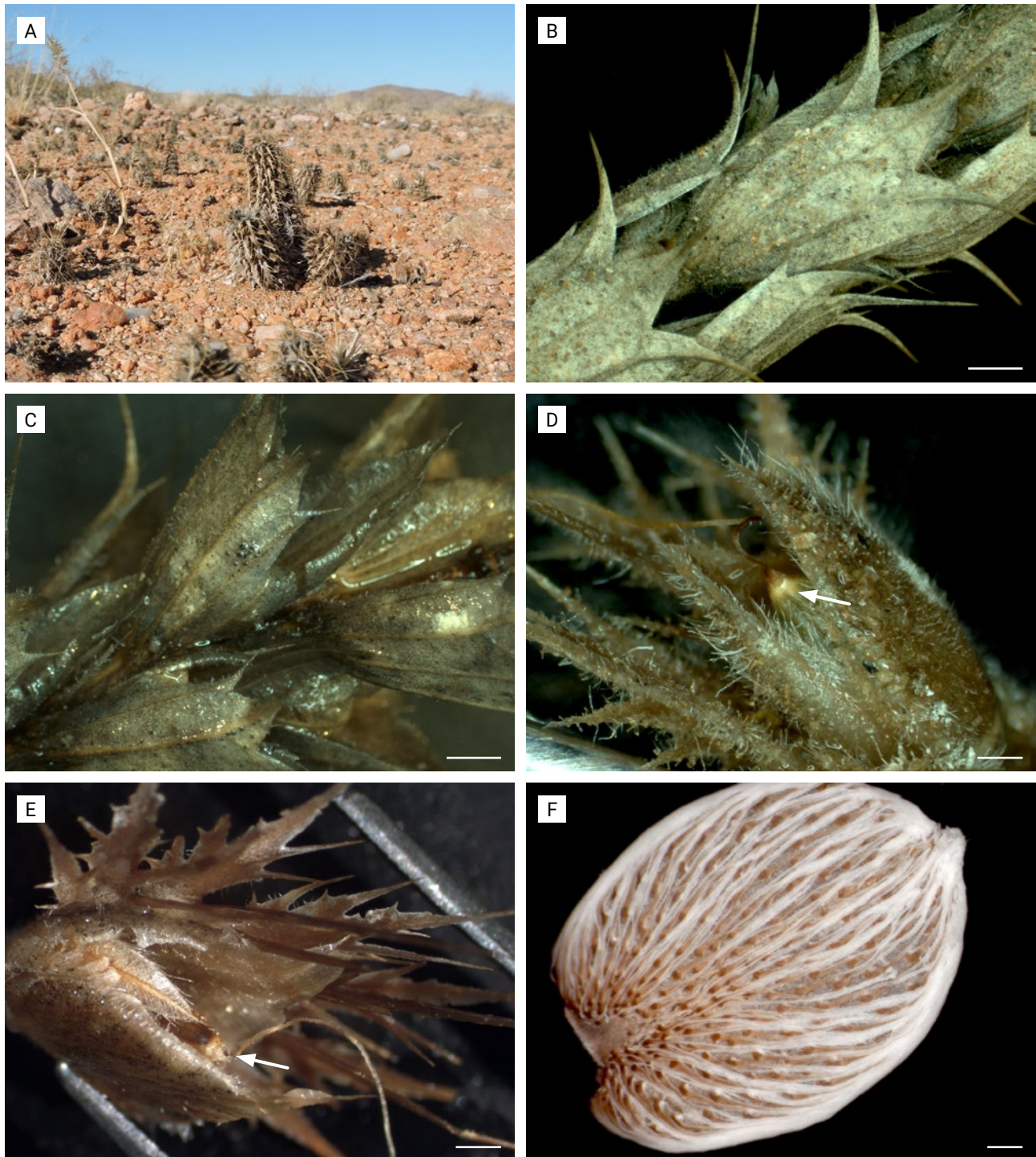


Figure 9. Mature *Acanthopsis* infructescence morphology. A, persistent dry infructescences of *A. hoffmannseggiana* typical form; B, dry infructescence, *A. scullyi* (Steyn 1911, PRE); C, wet infructescence, *A. scullyi* (Steyn 1911, PRE); D and E, opened sepals exposing the apical tip of the capsule (wet state), *A. hoffmannseggiana* typical form (Steyn 2148, PRE); F, appressed hygroscopic hairs on seed (dried state), *A. horrida* (Steyn 1814b, PRE). Scale bar: B, C = 2 mm, D, E = 1 mm, F = 0.5 mm.

to unfold when the seed is moistened, and it almost doubles in size as the helical thickenings relax (partly uncoil) (Figure 10). Gutterman et al. (1967) observed in *Blepharis ciliaris* that non-lignified reticulate secondary wall thickenings are found at the base of the hygroscopic hairs and annular or spiral thickenings at the tips. According to Gutterman et al. (1967, 1973), the primary wall of cells at the tip of the hygroscopic hairs

hydrates rapidly and becomes mucilaginous. Gutterman et al. (1973) and Van Rheede van Oudtshoorn and Van Rooyen (1999) stated that a thick deposit covering the hairs and seed surface of *Blepharis* hydrates rapidly upon wetting and the spiral and annular secondary wall thickenings spread out in the mucilage. Seeds of *Acanthopsis* start to germinate within 24 hours after wetting (Figure 10F).

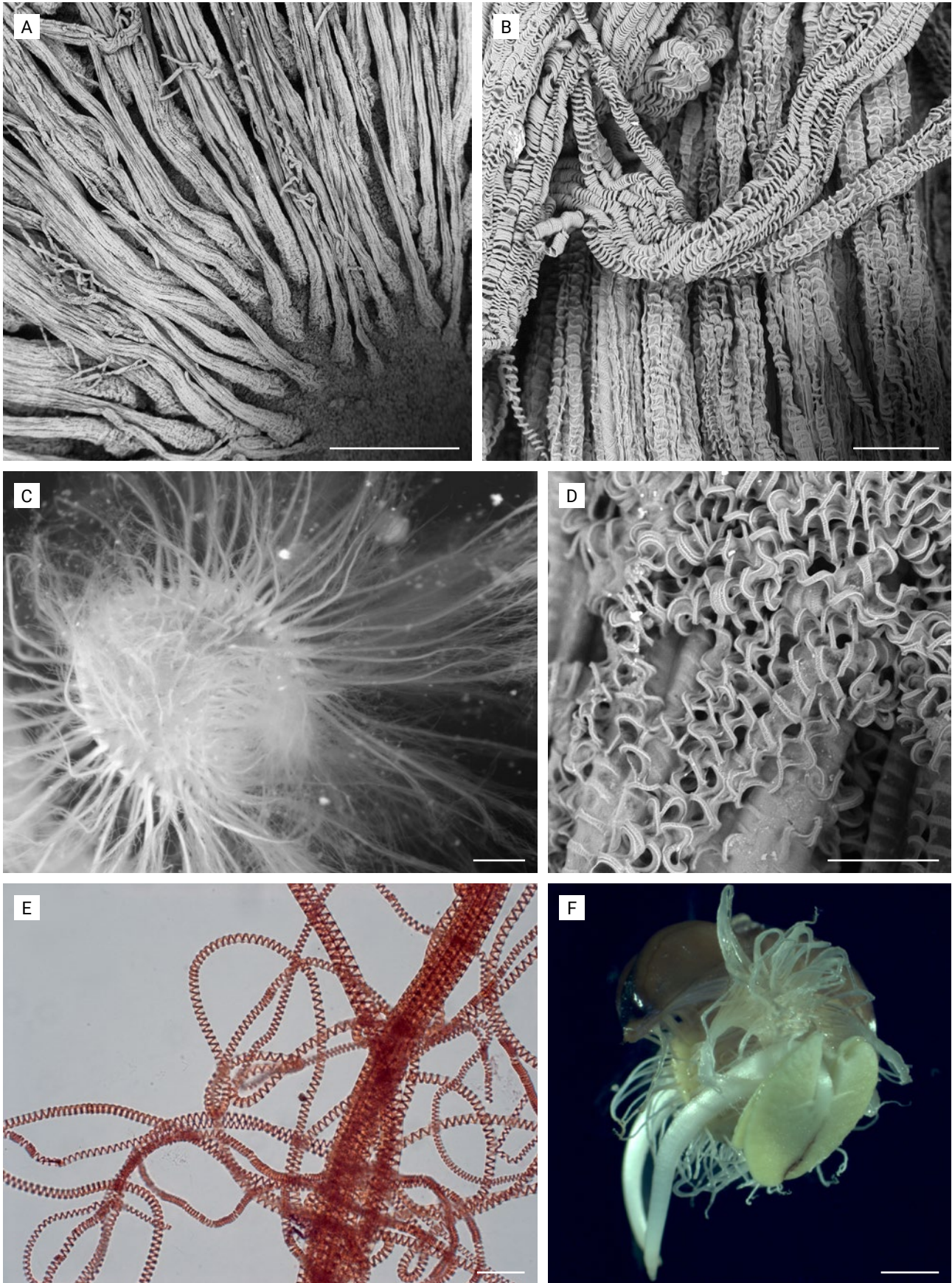


Figure 10. SEM and stereomicroscope images of *Acanthopsis* seeds, showing appressed hygroscopic hairs when dry and uncoiled mucilaginous hairs upon wetting. A and B, appressed hairs of seed (dried state), *A. dregeana* subsp. *longispina* (Steyn 2141, PRE); C, seed with uncoiled hairs upon wetting, *A. disperma* (Steyn 1845, PRE); D, uncoiled hair showing helical thickening of walls, *A. disperma* (Steyn 1845, PRE); E, uncoiled hairs stained with safranin, *A. disperma* (Steyn 1845, PRE); F, seedling, *A. hoffmannseggiana* typical form (Steyn 2148, PRE). Scale bar: A = 300 μm , B = 80 μm , C = 1 mm, D = 30 μm , E. 50 μm , F = 2 mm.

Discussion

The predominance of compact subshrubs in *Acanthopsis* might be explained by the generally arid and exposed habitats where this genus is found. In *A. horrida*, dense cushion-shaped shrublets, up to 600 mm high, are formed when growing among rocks on mountain slopes, but when growing in deep sandy soils of the coastal plains, the habit tends more towards an open virgate shrublet of more or less the same height than the dense cushion-shaped plants. More compact, low-growing and extensively branched plants are usually found in exposed conditions. According to Balkwill (1993), the specific growth form of plants in *Barleria* L. is often strongly correlated with the habitat in which they grow. This also appears to be the case in *Acanthopsis*.

Members of *Acanthopsis* are best adapted to warmer, drier climates (Succulent and Nama-Karoo biomes) and, therefore, virtually absent from relatively colder, wetter areas (Fynbos Biome). Some species, notably *Acanthopsis disperma* and *A. hoffmannseggiana* (both usually annuals), have a wide ecological amplitude and are capable of adapting to diverse edaphic and abiotic factors. The rest of the species (perennials) have restricted ranges, with at least eight known from only one or two subpopulations each, and are likely to have a more restricted ecological amplitude. The preponderance of perennials in *Acanthopsis* seemingly contradicts the general tendency for annuals to be favoured in hot and dry regions of the world (Poppenwimer et al. 2023). The latter authors, however, have refined this observation by showing that the prevalence of annual species is driven more by temperature and precipitation in the driest quarter, rather than by yearly means. Poppenwimer et al. (2023) also argued that future climate change may favour annuals, but impact negatively on ecosystem services provided by perennials, raising some conservation concerns considering the several perennial species with restricted ranges in *Acanthopsis*.

Floral bracts usually protect the developing flowers of a plant by forming a physical shield around it. In *Acanthopsis*, the floral bracts ending in rigid spines not only protect the flowers, but also the fruit and seed and most probably mechanically deter herbivory, notably of mammalian browsers like antelope. Spines as a defensive strategy may extend beyond larger browsers like antelope, as research indicates that spines also serve as an effective defence against browsing/herbivory by small mammals such as rodents (Cooper & Ginnett 1998). In the case of *Acanthopsis*, the safeguarding of fruit through spines would likely be advantageous, particularly given the prolonged period during which dry but still indehiscent fruits are retained in old infructescences. However, it was observed that the dried, persistent bracts (including spines) soften considerably when moistened, and it is believed that species known to be browsed (e.g., *A. carduiifolia*

and *A. dregeana*), are being utilised in this way shortly after rains when the inflorescences are soft and more palatable. Whether coincidental consumption of the fruit in this manner holds any advantages for seed dispersal, requires further investigation.

Very little information is available on the reproductive biology of *Acanthopsis* but the similarity in corolla shape and colour among taxa may be indicative of them sharing a similar pollination biology. Pollen grains of *Acanthopsis* are sculptured (usually with a reticulate or microreticulate mesocolpium) and relatively large compared to those of *Acanthus* and *Blepharis*. Chaloner (1986) suggested that sculptured pollen grains would retain their electrostatic charge longer and, as a result, would be more adhesive to the stigma. Electrostatic charges may also play a role in the attachment of pollen grains to insect vectors (Thorp 1979; Vaknin et al. 2000). Ornamented grains (as found in nearly all species of *Acanthopsis*), therefore, have an advantage not only in its adhesion to the stigma, but also in attaching to the insect vector.

Floral traits of *Acanthopsis* show the classical syndrome for insect pollination (entomophily) (Faegri & Van der Pijl 1979; Proctor et al. 1996; Dellinger 2020). These features encompass zygomorphic flowers, characterised by a conspicuous lip that may function as a landing site, a slender corolla tube and well-defined nectar guides. The prevalent bluish hue of the corollas may serve as a visual attractant, complemented by the provision of both nectar and possibly pollen as rewards. However, the observation that the anthers do not release the pollen conspicuously, suggests that nectar is the main reward; and the presenting of pollen in the direction of the corolla lip, suggests that the pollen is most probably deposited on the dorsal side of the visiting insect. The conspicuous horizontal corolla lip found in most species, suggests a landing platform and therefore a hovering insect would probably not be a primary pollinator. That the nectar is concealed within a narrow corolla tube (± 1 mm wide), suggests a pollinator with a relatively long, thin proboscis. Although bees would be the implied pollinators of *Acanthopsis* based on the predominant colours (lilac to purple) of the corollas (Corbet et al. 1991; Menzel & Schmida 1993; Gess & Gess 2010, 2014), they would not be able to reach the nectar as the corolla tube is too long and narrow.

While casual observations have noted the presence of insects from various groups visiting the flowers, the narrow and often elongated corolla tubes, with nectar primarily concentrated at the tube's base, also suggest a potential adaptation for pollination by long-proboscid insects such as tangle-veined flies (Nemestrinidae) and bee flies (Bombyllidae). *Acanthopsis tuba* has a particularly pronounced corolla tube, (15–)25–35 mm long, and is sympatric with *Lapeirousia dolomitica* Dinter (Iridaceae), a small, long-tubed geophyte (Goldblatt & Manning 2015). The latter species has pale blue

to violet or lilac flowers and a perianth tube 25–35(–40) mm long and is visited (and probably pollinated) by a long-proboscid tangle-veined fly (Goldblatt 2000; Goldblatt & Manning 2015). A long-proboscid fly or bee fly could therefore also be the pollinator of *A. tuba* as the corolla lip of the latter species is more vertical than the rest of the species and would suggest a hovering insect as pollinator. Hitherto limited but noteworthy field observations have documented instances of bee flies visiting *Acanthopsis* flowers, as illustrated in Figure 8C (P. van Wyk, pers. comm. 2017; F. Grenier, pers. comm. 2018), but not yet any tangle-veined flies.

Rostás and Tautz (2010) mentioned that sticky blossoms and trichomes [as present in e.g., *A. glandulopalmata*, *A. hoffmannseggiana* (typical form) and *A. tetragona*] might be adaptations by the plant to prevent ants from robbing pollen, damaging anthers or pistils or scaring away potential pollinators (thereby preventing ant pollination). However, members of *Acanthopsis* include traits suggested to be characteristic of an ant pollination syndrome (Rostás & Tautz 2010): plants short and growing in dry, warm habitats with an abundance of foraging ants; flowers easily accessible, with little nectar and a few flowers blooming synchronously and few or relatively small pollen grains. The production of nectar, a lack of a pronounced odour, the darker purple veins on the corolla (nectar guides), and the size and sculpture of the pollen grains suggest diurnal insects (bees, ants, bee flies and fruit flies) as possible pollinators.

Plants often distribute their offspring during favourable conditions over time, to take the best advantage of unpredictable environments. The timing of seed germination is the earliest trait in plant life-history, and allows plants to regulate when and where they grow (Liu et al. 2017). The bilocular capsules of *Acanthopsis* remain covered by four sepals in the dry state, and only upon wetting do the bracts open up (diverge) and the sepals separate to expose the capsule. This antitelechoric behaviour ensures that mature capsules are retained unopened on the plant and that seeds are only dispersed when sufficient water for germination is present (Gutterman et al. 1967; Gutterman 1994; Van Rheede van Oudtshoorn & Van Rooyen 1999). Portioned dispersal ensures that even with sufficient rain, not all the seeds are dispersed with the first rainfall event of the season and a reserve for later dispersal is left (Gutterman et al. 1967; Gutterman 1994) as sepals of older fruit open in light rain, while younger ones tend to stay closed (Van Rheede van Oudtshoorn & Van Rooyen 1999). The observation that relatively young but dry fruit of *Acanthopsis* do not readily dehisce to release the seed, may also be indicative that the seeds themselves have a dormancy requirement. Seed dormancy is an important survival strategy of plants in their natural environments (Finch-Savage & Leubner-Metzger 2006).

The incidence and ecology of very fast germination (within 24 h) among flowering plants were reviewed by Parsons

(2012). In species with very fast germination all the seeds may germinate within a very short time following wetting, or only a small fraction may germinate, whereas the rest would remain as a long-lived soil seed bank (Parsons 2012). In Acanthaceae, Gutterman (1972) reported that the seed of *Blepharis ciliaris* (L.) B.L.Burt [as *B. persica* (Burm.f.) Kuntze] germinates within less than 50 minutes after wetting. Moreover, in studied species of *Blepharis* all seeds germinate at the same time (Gutterman 2002). Rapid germination is important for plant survival, especially in arid areas where rain is infrequent and where dispersed seeds are collected by ants (Gutterman 1994; Parsons 2012). A seed starts to germinate in favourable conditions, in the case of *Acanthopsis* in response to the availability of moisture. Germination is a physiologically complex process (e.g., Nonogaki et al. 2010; Rajjou et al. 2012), hence the rapid germination of *Acanthopsis* seed within 24 h after wetting is rather unusual and comprises a highly specialised adaptation, most probably to its arid environment. It remains to be established if in the case of *Acanthopsis*, all the released seeds germinate simultaneously, as in *Blepharis*.

In both *Acanthopsis* and *Blepharis*, the appressed, hygroscopic hairs on the seeds immediately start to unfold when the seeds are moistened and mucilage is produced. The mucilage binds the seed (and the future seedling) to the soil, a phenomenon known as myxospermy (Gutterman et al. 1967; Manktelow 1996; Van Rheede van Oudtshoorn & Van Rooyen 1999; Vollesen 2000), and possibly acts as a counterforce to the penetrating root (Gutterman et al. 1967, 1973). It may also help to prevent ants from collecting the seed, protect the seed from the abrasive powers of the wind during dry periods, and ensure that they germinate in the same favourable microclimate as the mother plant (Van Rheede van Oudtshoorn & Van Rooyen 1999). The mucilage could also be an initial source of moisture and nutrients for the young seedling (Gutterman et al. 1967; Gutterman et al. 1973; Vollesen 2000). According to Gutterman (1994) and Van Rheede van Oudtshoorn and Van Rooyen (1999), the mucilage could increase the buoyancy of the seed in some cases and therefore improve dispersal by water – this may well be the case in *A. disperma*, an annual species often occurring in dry, sandy washes, depressions or flats.

Environmental conditions in arid areas, as those inhabited by the genus *Acanthopsis*, are highly unpredictable. Plants adapted to these conditions have evolved an array of functional traits to enhance their chances of survival. The present contribution focuses on a select few of these traits, with discussion centred around them. Given the anticipated climate change, it is crucial to comprehend how species within these environments will react to alterations in temperature and precipitation. Kühn et al. (2021) have proposed a set of functional traits that could serve as useful indicators for predicting species responses to climate shifts. This approach operates under the assumption that there exists general relationships between

traits and the environment, and that the proposed traits are closely associated with climatic conditions. However, a detailed analysis of these traits in *Acanthopsis* is not covered in this study and represents a significant avenue for future research.

Acknowledgements

The authors would like to thank the curators from different herbaria for supplying scanned images of specimens; Marinda Koekemoer, Pieter Bester and Pieter van Wyk for collecting herbarium vouchers and supplying images; Dr Hugh Glen and Dr Otto Leistner for help with Latin translations; John Roux (Farm Silverfontein) and the owners of Warmwaterberg Spa near Barrydale for permission to collect specimens on their properties; Daleen Roodt for the line drawings and Elizma Fouché for preparing the photo plates. I gratefully acknowledge the Richtersveld

Cultural and Botanical Landscape for permission to collect plants; SANParks for accommodation and assistance during work in the Richtersveld and Namaqua national parks. Our grateful thanks to CapeNature, as well as the Department of Tourism, Environment and Conservation: Northern Cape, for plant collecting permits, and the Botanical Education Trust for financial support.

Competing interests

The authors declare that they have no financial or personal relationship that may have inappropriately influenced them in writing this article.

Authors' contributions

HMS (SANBI) performed the research and wrote the manuscript and AEW (University of Pretoria) made conceptual contributions and edited the manuscript.

References

- Adler, P.B., Salguero-Gomez, R., Compagnoni, A., Hsu, J.S., Ray-Mukherjee, J., Mbeau-Ache, C. & Franco, M., 2014, 'Functional traits explain variation in plant life history strategies', *Proceedings of the National Academy of Sciences of the United States of America* 111(2), 740–745, <https://doi.org/10.1073/pnas.1315179111>.
- Balkwill, M.-J., 1993, 'A reappraisal of the generic limits and subdivision of *Barleria* L. (Acanthaceae)', PhD thesis, University of the Witwatersrand, Johannesburg.
- Balkwill, K. & Getliffe Norris, F., 1988, 'Classification of the Acanthaceae: a southern African perspective', *Monographs in Systematic Botany – Missouri Botanical Garden* 25, 503–516.
- Beentje, H., 2016, *The Kew plant glossary, an illustrated dictionary of plant terms*, 2nd ed. Kew Publishing, Kew.
- Bornhofen, S., Barot, S. & Lattaud, C., 2011, 'The evolution of CSR life-history strategies in a plant model with explicit physiology and architecture', *Ecological Modelling* 222(1), 1–10, <https://doi.org/10.1016/j.ecolmodel.2010.09.014>.
- Bremekamp, C.E.B., 1944, 'Materials for a monograph of the Strobilantheae (Acanthaceae)', *Verhandelingen der Koninklijke Nederlandsche Akademie van Wetenschappen* 2, 1–306.
- Bremekamp, C.E.B., 1965, 'Delimitation and subdivision of the Acanthaceae', *Bulletin of the Botanical Survey of India* 7, 21–30.
- Chaloner, W.G., 1986, 'Electrostatic forces in insect pollination and their significance in exine ornament', in S. Blackmore & I.K. Ferguson (eds.), *Pollen and spores: form and function*, 103–108. Academic Press, London.
- Cooper, S.M. & Ginnett, T.F., 1998, 'Spines protect plants against browsing by small climbing mammals', *Oecologia* 113, 219–221, <http://doi.org/10.1007/s004420050371>.
- Corbet, S.A., Williams, I.H. & Osborne, J.L., 1991, 'Bees and the pollination of crops and wild flowers in the European community' *Bee World* 72, 47–59.
- Dellinger, A.S., 2020, 'Pollination syndromes in the 21st century: where do we stand and where may we go?', *New Phytologist* 228(4), 1193–1213.
- Faegri, K. & Van der Pijl, L., 1979, *Principles of pollination ecology*, 3rd ed., Pergamon Press, Oxford.
- Finch-Savage, W.E. & Leubner-Metzger, G., 2006, 'Seed dormancy and the control of germination', *New phytologist* 171(3), 501–523.
- Furness, C.A., 1990, 'Pollen morphology of *Crossandra* Salisbury and *Crossandrella* C.B. Clarke (Acanthaceae: Acanthaceae)', *Grana* 29, 161–176.
- Furness, C.A., 1991, 'The pollen morphology of *Sclerochiton* (Acanthaceae: Acanthaceae)', *Kew Bulletin* 46, 51–59.
- Furness, C.A., 1995, 'A pollen morphological study of *Dyscoriste* Nees and *Chaetacanthus* Nees (Acanthaceae: Ruellieae)', *Review of Palaeobotany and Palynology* 84, 331–345.
- Furness, C.A., 1996, 'Pollen morphology of *Acanthopsis* Harvey, *Acanthus* L. and *Blepharis* Jussieu (Acanthaceae: Acanthaceae)', *Review of Palaeobotany and Palynology* 92, 253–268.
- Gess, S.K. & Gess, F.W., 2010, 'Pollen wasps and flowers in southern Africa', *SANBI Biodiversity Series* 18. South African National Biodiversity Institute, Pretoria.
- Gess, S.K. & Gess, F.W., 2014, 'Wasps and bees in southern Africa', *SANBI Biodiversity Series* 24, South African National Biodiversity Institute, Pretoria.
- Goldblatt, P., 2000, 'Champion pollinators: long-proboscid flies in a biological system unique to southern Africa', *Veld & Flora* Sept., 118–121.
- Goldblatt, P. & Manning, J.C., 2015, 'Systematic biology of *Lapeirousia*, *Codonorhiza*, *Psilosiphon* and *Schizorhiza* in southern Africa', *Strelitzia* 35. South African National Biodiversity Institute, Pretoria.
- Graham, V.A.W., 1988, 'Delimitation and infra-generic classification of *Justicia* (Acanthaceae)', *Kew Bulletin* 43, 551–624.

- Grime, J.P., 1977, 'Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory', *The American Naturalist* 111(982), 1169–1194.
- Gutterman, Y., 1972, 'Delayed seed dispersal and rapid germination as survival mechanisms of the desert plant *Blepharis persica* (Burm.) Kuntze', *Oecologia* 10, 145–149.
- Gutterman, Y., 1994, 'Strategies of seed dispersal and germination in plants inhabiting deserts', *The Botanical Review* 60, 373–425.
- Gutterman, Y. 2002, *Survival strategies of annual desert plants*, Berlin, Springer.
- Gutterman, Y., Witztum, A. & Evenari, M., 1967, 'Seed dispersal and germination in *Blepharis persica* (Burm.) Kuntze', *Israel Journal of Botany* 16, 213–234.
- Gutterman, Y., Witztum, A. & Heydecker, W., 1973, 'Studies of the surfaces of desert plant seeds. II. Ecological adaptations of the seeds of *Blepharis persica*', *Annals of Botany* 37, 1051–1055.
- Holmgren, P.K., Holmgren, N.H. & Barnett, L.C., 1990, *Index herbariorum, Part I. The herbaria of the world*, 8th ed., The New York Botanical Gardens, New York.
- House, A. & Balkwill, K., 2016, 'Labyrinths, columns and cavities: new internal features of pollen grain walls in the Acanthaceae detected by FIB–SEM', *Journal of Plant Research* 129, 225–240, <http://doi.org/10.1007/s10265-015-0777-9>.
- Immelman, K.L., 1987, 'A study of the genera *Justicia* L. and *Siphonoglossa* Oerst. (Acanthaceae) in southern Africa', PhD thesis, University of Natal, Pietermaritzburg.
- Kühn, N., Tovar, C., Carretero, J., Vandvik, V., Enquist, B.J. & Willis, K.J., 2021, 'Globally important plant functional traits for coping with climate change', *Frontiers of Biogeography* 13(4), e53774, <https://doi.org/10.21425/F5FBG53774>.
- Ladd, P.G. & Donaldson, J.S., 1993, 'Pollen presenters in the South African flora', *South African Journal of Botany* 59, 465–477.
- Lindau, G., 1893, 'Beiträge zur sytematik der Acanthaceen', in A. Engler (ed.), *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 18, 36–64, Verlag von Wilhelm Engelmann, Leipzig.
- Lindau, G., 1895, 'Acanthaceae', in H.G.A. Engler & K.A.E. Prantl (eds.), *Die natürlichen Pflanzenfamilien* 4, 274–354, Verlag von Wilhelm Engelmann, Leipzig.
- Liu, Y, Walck, J.L. & El-Kassaby, Y.A., 2017, 'Roles of the environment in plant life-history trade-offs', in J.C. Jiminez-Lopez (ed.), *Advances in Seed Biology*, InTech, <http://doi.org/10.5772/intechopen.70312>.
- JSTOR, 2018, 'Global Plants', available from: <http://plants.jstor.org/search?asf> [accessed continuously].
- Manktelow, M., 1996, '*Phaulopsis* (Acanthaceae) – a monograph', *Symbolae Botanicae Upsalienses* 31. Acta Universitatis Upsaliensis, Uppsala.
- Menzel, R. & Schmida, A., 1993, 'The ecology of flower colours and the natural colour vision of insect pollinators: the Israeli flora as a study case', *Biological Review* 68, 81–120.
- Munday, J., 1980, 'The genus *Monechma* Hochst. (Acanthaceae Tribe Justiceae) in southern Africa', M.Sc thesis, University of the Witwatersrand, Johannesburg.
- Nonogaki, H., Bassel, G.W. & Bewley, J.D., 2010, 'Germination – still a mystery', *Plant Science* 179(6), 574–581, <https://doi.org/10.1016/j.plantsci.2010.02.010>.
- Parsons, R.F., 2012, 'Incidence and ecology of very fast germination', *Seed Science Research* 22(3), 161–167.
- Perveen, A. & Qaiser, M., 2010, 'Pollen flora of Pakistan – LX–VII Acanthaceae', *Pakistan Journal of Botany* (Special issue) 42, 175–191.
- Poppenwimer, T., Mayrose, I. & DeMalach, N., 2023, 'Revising the global biogeography of annual and perennial plants', *Nature* 624, 109–114, <https://doi.org/10.1038/s41586-023-06644-x>.
- Proctor, M., Yeo, P. & Lack, A., 1996, *The natural history of pollination*, Timber Press, Portland, Oregon.
- Radlkofer, L., 1883, *Ueber den systematischen Werth der Pollen-beschaffenheit bei den Acanthaceen*. Akademische Buchdruckerei von F. Straub, München.
- Raj, B., 1961, 'Pollen morphological studies in the Acanthaceae', *Grana Palynologica* 3, 3–107.
- Rajjou, L., Duval, M., Gallardo, K., Catusse, J., Bally, J., Job, C. & Job, D., 2012, 'Seed germination and vigor', *Annual Review of Plant Biology* 63, 507–533, <https://doi.org/10.1146/annurev-arplant-042811-105550>.
- Raunkiaer, C., 1934, *The life forms of plants and statistical plant geography; being the collected papers of C. Raunkiaer*. Clarendon Press, Oxford.
- Rostás, M. & Tautz, J., 2010, 'Ants as pollinators of plants and the role of floral scents', in Z. Dubinsky. & J. Seckbach (eds.), *All flesh is grass: plant-animal interrelationships*, 151–161, Springer, New York.
- Schmid, R., 1982, 'Descriptors used to indicate abundance and frequency in ecology and systematics', *Taxon* 31, 89–94.
- Scotland, R.W., Endress, P.K. & Lawrence, T.J., 1994, 'Corolla ontogeny and aestivation in the Acanthaceae', *Botanical Journal of the Linnean Society* 114, 49–65.
- Scotland, R.W. & Vollesen, K., 2000, 'Classification of Acanthaceae', *Kew Bulletin* 55, 513–589, <https://doi.org/10.2307/4118776>.
- Steyn, H.M., 2018, 'A taxonomic revision of the genus *Acanthopsis* (Acanthaceae)', PhD thesis, University of Pretoria, Pretoria.
- Steyn, H.M. & Van Wyk, A.E., 2021, 'Taxonomic significance of trichomes in the genus *Acanthopsis* Harv. (Acanthaceae, tribe Acantheae)', *Adansonia* 43(14), 163–176, <https://doi.org/10.5252/adansonia2021v43a14>.
- Steyn, H.M., Von Staden, L., Bellstedt, D.U., Van der Merwe, P.D.W. & Van Wyk, A.E., 2019, 'Notes on the phyto-geography and conservation status of the genus *Acanthopsis* (Acantheae, Acanthaceae)', *Phytotaxa* 415(4), 157–178, <https://doi.org/10.11646/phytotaxa.415.4.1>.
- Thiers, B., 2023, 'Index herbariorum: A global directory of public herbaria and associated staff: New York Botanical Garden's Virtual Herbarium', Available online: <http://sweetgum.nybg.org/science/ih/>.
- Thorp, R.W., 1979, 'Structural, behavioral, and physiological adaptations of bees (Apoidea) for collecting pollen', *Annals of the Missouri Botanical Garden* 66, 788–812.
- Vaknin, Y., Gan-Mor, S., Bechar, A., Ronen, B. & Eisikowitch, D., 2000, 'The role of electrostatic forces in pollination', *Plant Systematics and Evolution* 222, 133–142, <https://doi.org/10.1007/BF00984099>.
- Van Rheede van Oudtshoorn, K. & Van Rooyen, M.W., 1999, *Dispersal biology of desert plants*. Springer, Berlin.
- Vollesen, K., 2000, *Blepharis, a taxonomic revision*. Royal Botanic Gardens, Kew.