CHAPTER 6: PALYNOLOGY

6.1 Introduction

Pollen of the Nyctaginaceae is documented regularly in the fossil record (Hueber *et al*., 1991; Dominique *et al*., 1998; Yu *et al*., 2000; Pickett *et al*., 2004). The earliest occurrence of pollen of the Nyctaginaceae is reported to be Eocene (Hueber *et al*., 1991). The Nyctaginaceae pollen records are used, together with other pollen records, to illustrate climate change over geological time e.g. the presence of Nyctaginaceae pollen in Late Quaternary deposits in the Transvaal (that is North West, Gauteng, Mpumalanga and Limpopo Provinces), South Africa, suggest the absence of very cold conditions (Scott, 1982), and it is often used at continental scale for biome reconstruction (Dominique *et al*., 1998; Yu *et al*., 2000; Pickett *et al*., 2004).

6.1.1 Palynology of the Nyctaginaceae

The pollen morphology of the existing Nyctaginaceae varies (Nowicke, 1970; Nowicke & Skvarla, 1979; Bittrich & Kühn, 1993) and was one of the criteria used by Heimerl (1934) to divide the family into tribes and subtribes. The pollen grains of members of the Nyctaginaceae are 17–200 µm in diameter, spheroidal, prolate or oblate and 3 (–4)-colpate, pantocolpate or pantoporate (Bittrich & Kühn, 1993). The pores are covered by a pore plate which can either be roughened or spinulose. The exine is very thick and varies in its pattern and the muri are spinulose (Nowicke, 1970).

6.1.2 Palynology of *Boerhavia* and *Commicarpus*

The pollen grains of 13 *Boerhavia* and three *Commicarpus* species were described by Nowicke (1970). She described the grains as spheroidal, pantoporate and the sexine as tubuliferous and spinulose. The spinules are 1–2.5 µm long. The grains of *Boerhavia* are 70–138 µm in diameter with 18–40 pores. The pores are 2.4–7 µm in diameter and the pore plates have a roughened base with 1 or 2 spinules. The sexine is 2.5–6 µm thick and the nexine is 4–7 µm. The grains of *Commicarpus* are 84–112 µm in

diameter with 27–39 pores. The pores are 3–5.5 µm in diameter and the pore plates have 1 or 2 spinules. The sexine is 2.5–5.5 µm thick and the nexine is 2.5–5.5 µm.

The pollen of southern African *Boerhavia* and *Commicarpus* species has not been studied in detail, except for the naturalised *B*. *diffusa* var. *diffusa* and *B*. *erecta*, and the native *B*. *repens* subsp. *repens*, *C*. *fruticosus*, *C*. *helenae* var. *helenae* and *C*. *pentandrus* (Nowicke, 1970; Perveen & Qaiser, 2001).

6.2 Aim

The aim of this chapter is to describe the pollen morphology of the southern African *Boerhavia* and *Commicarpus* species in detail for all the species and to report on the taxonomic significance of these characters.

6.3 Materials and Methods

6.3.1 Collecting of plant material

Pollen from herbarium specimens and fresh plant material collected *in situ* during 2009 and 2010 in Namibia and South Africa was investigated (Table 6.1). Voucher specimens of all the collected material were deposited in the A.P. Goossens Herbarium (PUC), Potchefstroom, South Africa. Duplicates of specimens collected in South Africa were deposited in the National Herbarium, Pretoria (PRE), South Africa and duplicates collected in Namibia in the National Herbarium (WIND), Windhoek, Namibia.

6.3.2 Scanning Electron Microscopy

Pollen grains were acetolized according to the method of Erdtman (1969) and Coetzee (1975) with slight modifications. Pollen from herbarium material and material collected in 70% ethanol was centrifuged at 5 000 rpm for 10 min in glacial acetic acid. The glacial acetic acid was replaced with an acetolysis mixture (acetic anhydride and sulphuric acid, 9:1) and heated to 96 °C in a water bath for 20 min, after which it was centrifuged for 10 min at 5 000 rpm. This was followed by two washes in

distilled water and centrifugation for 10 min at 5 000 rpm. The pollen was then washed in an ethanol series of 50%, 70% and 96% and centrifuged at 5 000 rpm for 10 min each. A drop of 96% ethanol/pollen mixture was placed on specimen stubs and sputter-coated with gold/palladium. Specimens were examined and micrographs taken with a FEI Quanta 200 environmental scanning electron microscope (ESEM) or a JEOL JSM 840 SEM using Orion version 6.60.4 to take the micrographs. A minimum of eight pollen grains per species were used to measure the diameter of grain, the diameter of the pores and the length of the spinules (except for *C. decipiens* for which only three grains were measured due to limited available pollen).

6.3.3 Transmission Electron Microscopy

Anthers fixed in 4% aqueous paraformaldehyde were washed three times in 0.05 M cacodylate buffer for 15 min each followed by three rinses with distilled water for 15 min each. The material was then immersed in 2% uranyl acetate (pH 2) for 30 min followed by three rinses with distilled water for 15 min each. The material was dehydrated in an ethanol series of 50%, 70%, 90% and twice in 100% ethanol for 15 min each followed by 15 min in 100% resin (L.R. White™ Wirsam/London Resin Company). This was followed by two changes in resin for 60 min each and then left over night at 20 °C before being imbedded and polymerised overnight at 65 °C. Embedded material was cut with a Reichert-Jung Ultracut E microtome into sections of 180 nm which were then contrasted with 2% uranyl acetate (pH 2) for 4 min and lead citrate (Anala R) for 1 min. Sections were examined and micrographs taken with a Philips CM10 transmission electron microscope.

6.3.4 Light microscopy

Pollen grains were prepared as in section 6.3.3 and embedded material were cut with a Reichert-Jung Ultracut E microtome into sections of 1.4 µm and stained with aqueous 0.5% toluidine blue in 1% boraxs and 0.1% aqueous neufuchsin for 15 sec. Micrographs were taken with a Nikon Digital Camera DXM 1200 F fitted on a Nikon Eclipse E 800 at 40x and 60x magnification. The exine of three to fourteen pollen grains per species was measured with Nikon NIS Elements software.

Terminology used for the palynological descriptions follows Punt *et al*. (2007).

6.4 Results

The pollen grains of the *Boerhavia* and *Commicarpus* species are spheroidal, pantoporate and the tectum is tubuliferous and spinulose. The spinules are (1.12–) 2.70 (–5.43) µm long and the pores are covered with a pore plate with one to two spinules (Fig. 6.1 & Fig. 6.2). The exine is (3.35–) 6.55 (–11.45) µm thick. The tectum is thick and tubuliferous, the collumellae are short, the foot layer is thick and the endexine is thin (Fig. 6.3 & Fig. 6.4).

The pollen grains of the *Boerhavia* species are (51.59–) 64.59 (–91.48) µm in diameter; the pores are (2.77–) 4.46 (–7.67) µm in diameter and the exine (3.35–) 6.99 (–11.45) µm thick (Table 6.2). The pollen grains of *B*. *deserticola* are the largest [(65.42–) 74.55 (–82.54) µm] and those of *B*. *repens* subsp. *repens* the smallest [(45.07–) 57.89 (–68.25) µm]. The exine of *B*. *diffusa* var. *diffusa* is the thickest [(7.75–) 8.78 (–9.69) µm] and that of *B*. *repens* subsp. *repens* the thinnest [(3.35–) 4.02 (–4.96) µm].

The pollen grains of the *Commicarpus* species are (51.59–) 79.80 (–129.28) µm in diameter; the pores are (2.59–) 5.62 (–10.64) µm in diameter and the exine (4.05–) 6.16 (–9.10) µm thick (Table 6.2). The pollen grains of *C*. *chinensis* subsp. *natalensis* [(70.26–) 97.04 (–121.04) µm], *C*. *decipiens* [(97.40–) 116.61 (–129.28) µm], *C*. *pentandrus* [(63.74–) 84.23 (–100.12) µm] and *C*. *plumbagineus* [(71.99–) 85.26 (–105.27) µm] are the largest and those of *C*. *helenae* var. *helenae* [(53.76–) 60.60 (–71.29) µm] and *C*. *squarrosus* [(45.55–) 65.49 (–82.54) µm] the smallest. The exine of *C*. *pilosus* is the thickest [(6.69–) 7.45 (–9.06) µm] and that of *C*. *helenae* var. *helenae* the thinnest [(3.57–) 4.26 (–5.11) µm].

6.5 Discussion

The pollen grain size range of the southern African *Boerhavia* species is (51.59–) 64.59 (–91.48) µm in diameter, which is smaller than, but overlapping the range determined by Nowicke (1970) (70–138 µm), who studied *Boerhavia* species from

the Americas. Nowicke (1970) studied *B. erecta*, which also occurs naturalized in southern Africa, and recorded the diameter of the grains to be 121–138 µm, which is nearly twice as large as that measured [(57.09–) 64.15 (–69.15) µm] for *B. erecta* in the present study. The description of the shape and sculpturing are however the same. Nowicke (1970) also studied three *Commicarpus* species; *C. brandegei* from Mexico, and *C. fruticosus* and *C. pentandrus* from southern Africa. The shape and sculpturing of the pollen grains of *C. fruticosus* and *C. pentandrus* studied in this chapter is the same as the description of *C. fruticosus* and *C. pentandrus* given by Nowicke (1970), although the size range measurements of the pollen grain diameter are slightly smaller [(63.74–) 82.11 (–100.12) µm] than that measured by Nowicke (1970) (84–110 µm) and the pore diameter is larger [(3.47–) 6.46 (–10.64) µm] than that measured by Nowicke (1970) (2.4–7 µm).

Similarly, Perveen & Qaiser (2001) studied the pollen morphology of the Nyctaginaceae in Pakistan including *B. diffusa* var. *diffusa*, *B. repens* subsp. *repens* and *C. helenae* var. *helenae*, which also occur in southern Africa. The descriptions of the pollen shape and sculpturing of the three species described in this chapter is the same as their description, but the diameter of the pollen grains, the pore diameter and the exine thickness differ. The diameters of the pollen grains of *B. diffusa* var. *diffusa* [(51.99–) 63.26 (–76.19) µm] and *C. helenae* var. *helenae* [(53.76–) 60.60 (–71.29) µm] are larger than that measured by Perveen & Qaiser (2001) [(50–) 56.44 (–62.5) µm and (50–) 56.6 (–60) µm respectively]. The diameter of *B. repens* subsp. *repens* [(45.09–) 57.89 (–68.25) µm] is smaller than that measured by Perveen & Qaiser (2001) [(61.03–) 84.50 (–100.5) µm]. The pore diameter of *B. diffusa* var. *diffusa* [(3.13–) 4.31 (–4.73) µm] is smaller and *B. repens* subsp. *repens* [(2.77–) 4.03 (–5.41) µm] is larger than that measured by Perveen & Qaiser (2001) [(2.5–) 5.02 (–7.5) µm and (3.23–) 3.59 (–3.94) µm respectively] while the pore diameter of *C. helenae* var. *helenae* is the same as that measured by Perveen & Qaiser (2001) [(2.59–) 4.35 (–5.00) µm]. The exine of *B. diffusa* var. *diffusa* (7.75–) 8.78 (–9.69) µm) is larger than that measured by Perveen & Qaiser (2001) [(4.25–) 5.0 (–5.25) µm], the exine of *B. repens* subsp. *repens* [(3.35–) 4.02 (–4.96) µm] is smaller and the exine of *C. helenae* var. *helenae* is the same than that measured by Perveen & Qaiser (2001) [(3.59–) 5.83 (–7.18) µm and (3.57–) 4.26 (–5.11) µm respectively]. The slight differences in

measurements between this study and that of Perveen & Qaiser (2001) can be ascribed to natural variation within the species and between geographical areas.

The columellae of the studied species are short, the foot layer is thick and the endexine is thin. This is in accordance with studies done by Skvarla & Nowicke (1976) and Nowicke & Skvarla (1979), who studied *Salpianthus arenarius* Humb. et Bonpl., *Pisonia aculeata* L. and *B. erecta*. Skvarla & Nowicke (1976) noted that the endexine of *B*. *erecta* is barely perceptible.

The Nyctaginaceae has a wide range in pollen morphology (Nowicke & Skvarla, 1979) and Heimerl (1934) split the Nyctaginaceae into five tribes and used pollen morphology to divide the Nyctagineae into four subtribes (Nowicke, 1970; Nowicke & Luikart, 1971). Subtribe Nyctagininae (to which *Boerhavia* and *Commicarpus* belonged) is characterized by large, spheroidal, pantoporate pollen grains with thick walls and a tubuliferous and spinulose exine (Nowicke, 1970; Nowicke & Luikart, 1971). Nowicke (1970) found that the shape, the size of the grains and the thickness of the exine form a continuum within genera and species of the subtribe Nyctagininae, so much so that these characters are of no taxonomic significance. Nowicke & Luikart (1971) came to the same conclusion for the other subtribes. Recently, a phylogenetic study (Douglas & Manos, 2007) of the family found that pollen morphology is homoplasious among genera and can therefore not support the tribal and subtribal divisions of Heimerl (1934).

The pollen grains of the southern African *Boerhavia* and *Commicarpus* species are uniform in shape and sculpturing (Struwig *et al.,* in press). The pollen morphology cannot be used to distinguish between the two genera, nor the individual species. The pollen grains of the *Boerhavia* species are smaller [(51.59–) 64.59 (–91.48) µm] than the *Commicarpus* species [(51.59–) 79.80 (–129.28) µm], but the ranges overlap making it impossible to distinguish between the genera with the aid of numerical measurements alone. The pore diameter of the *Commicarpus* species is larger [(2.59–) 5.62 (–10.64) µm] than that of the *Boerhavia* species (2.77–) 4.46 (–7.67) and the exine of the *Commicarpus* species is thinner [(4.05–) 6.16 (–9.10) µm] than the exine of the *Boerhavia* species [(3.35–) 6.99 (–11.45) µm]. Once again the size ranges overlap. The numerical values of the size of the pollen grains, the pore diameter and

the thickness of the exine cannot be used to distinguish between the two genera nor the individual species.

6.6 Future research

As described above, the southern African *Boerhavia* and *Commicarpus* species cannot be distinguished palynologically. Apart from the preparation methods used in this study, there are numerous other techniques (Skvarla, 1973; Lynch & Webster, 1975; Daghlian, 1982; Bredenkamp & Hamilton-Attwell, 1988; Smith & Tiedt, 1991; Shivanna & Rangaswamy, 1992) with which to prepare the samples for study, but these methods will probably not uncover any other significant features or characters not already observed and further research in this regard is therefore unnecessary. Pollen information of the family should rather be used for phylogenetic inferences at order level and higher (e.g. Moon *et al*., 2008; Wortley *et al.,* 2008; Furness & Banks, 2010), in genetic (e.g. Slavov *et al.,* 2009) or evolutionary studies (e.g. Scott *et al.,* 2006) or studies which use pollen to infer past climatic conditions and vegetation changes (e.g. Anderson *et al.,* 2011).

6.7 Summary

The pollen morphology of most of the southern African *Boerhavia* and *Commicarpus* species was described for the first time and is uniform in shape and sculpturing. The pollen grains are spheroidal, pantoporate and the tectum is tubuliferous and spinulose. The spinules are 2.70 µm long and the pores are covered with a pore plate with one to two spinules. The exine is 6.55 µm thick. The tectum is thick and tubuliferous, the collumellae are short, the foot layer is thick and the endexine is thin. The pollen grains of the *Boerhavia* species are smaller (64.59 µm) than that of the *Commicarpus* species (79.80 µm). The pore diameter of the *Commicarpus* species is larger (5.62 µm) than the *Boerhavia* species (4.46 µm) and the exine of the *Commicarpus* species thinner (6.16 µm) than that of the *Boerhavia* species (6.99 µm). Although this study can distinguish broadly between the genera, the shapes and sizes show too much variation between species to meaningfully distinguish between the southern African *Boerhavia* and *Commicarpus* species.

Table 6.1. Specimens used for the palynological study of the southern African *Boerhavia* and *Commicarpus* spesies as well as the specimens examined for light microscopy (LM), scanning electron microscopy (SEM) and transmission electron microscopy (TEM).

Taxon	Specimens examined	LM, SEM or TEM
Boerhavia coccinea var. *coccinea*	Struwig, M. 55	LM, SEM, TEM
	Struwig, M. 110	SEM
Boerhavia cordobensis	Struwig, M. 122	SEM, TEM
	Struwig, M. 132	LM
	Straub, C.C. 499	SEM
Boerhavia deserticola	Struwig, M. 38	LM, SEM
	Struwig, M. 42	SEM
	Struwig, M. 43	SEM, TEM
Boerhavia diffusa var. *diffusa*	Struwig, M. 88	SEM, TEM
	Struwig, M. 117	LM, SEM
Boerhavia erecta	Struwig, M. 23	LM
	Struwig, M. 133	SEM
	Struwig, M. 143	TEM
*B*oerhavia *hereroensis*	Struwig, M. 34	SEM, TEM
	Struwig, M. 35	LM, SEM
	Struwig, M. 40	SEM
Boerhavia repens var. *repens*	Acocks, J.P.H. 1978	SEM
	Acocks, J.P.H. 21788	SEM
	Leistner, O.A. 1783	SEM
	Struwig, M. 168	LM,TEM
Commicarpus chinensis subsp.	Struwig, M. 61	SEM, TEM
natalensis	Struwig, M. 62	LM, SEM
	Struwig, M. 63	SEM
Commicarpus decipiens	Struwig, M. 54	SEM
	Struwig, M. 176	LM, TEM
	Struwig, M. 181	SEM
Commicarpus fallacissimus	Struwig, M. 33	SEM
	Struwig, M. 46	LM, SEM, TEM
Commicarpus fruticosus	Struwig, M. 160	SEM
	Struwig, M. 163	SEM
	Struwig, M. 164	LM, TEM
Commicarpus helenae var. *helenae*	Struwig, M. 44	LM, SEM, TEM
Commicarpus pentandrus	Struwig, M. 48	SEM
	Struwig, M. 52	SEM
	Struwig, M. 57	LM, SEM, TEM
Commicarpus pilosus	Struwig, M. 111	LM, SEM, TEM
	Straub, C.C.609	SEM
Commicarpus plumbagineus	Siebert, S.J. 3970	LM, SEM, TEM
	Struwig, M. 106	SEM
Commicarpus squarrosus	Struwig, M. 36	SEM
	Struwig, M. 41	LM, TEM

Table 6.2. Pollen diameter, pore diameter, spinule length and exine thickness of pollen grains of *Boerhavia* and *Commicarpus* species.

Taxon	Diameter of grains (µm)	Diameter of pores (µm)	Length of spinules (µm)	Thickness of exine (µm)
Boerhavia coccinea var. *coccinea*	(53.08–) 66.48 (–91.48)	(3.48–) 4.44 (–5.97)	(1.72–) 2.61 (–3.75)	(6.30–) 6.70 (–7.74)
Boerhavia cordobensis	(56.34–) 66.59 (–80.65)	(3.38–) 4.08 (–4.71)	(1.77–) 2.71 (–3.61)	(6.50–) 7.02 (–7.46)
Boerhavia deserticola	(65.42–) 74.55 (–82.54)	(4.67–) 5.34 (–6.12)	(1.83–) 3.58 (–5.43)	(4.48–) 6.58 (–8.10)
Boerhavia diffusa var. *diffusa*	(51.99–) 63.26 (–76.19)	(3.13–) 4.31 (–4.73)	(1.82–) 3.04 (–3.84)	(7.75–) 8.78 (–9.69)
Boerhavia erecta	(57.09–) 64.15 (–69.15)	(3.08–) 4.23 (–4.59)	(1.83–) 2.16 (–2.86)	(4.76–) 6.81 (–10.22)
Boerhavia hereroensis	(49.06–) 60.77 (–74.62)	(3.30–) 4.79 (–7.67)	(1.47–) 2.70 (–4.01)	(5.64–) 8.57 (–11.45)
Boerhavia repens subsp. *repens*	(45.07–) 57.89 (–68.25)	(2.77–) 4.03 (–5.41)	(2.03–) 3.05 (–3.98)	(3.35–) 4.02 (–4.96)
Commicarpus chinensis subsp. *natalensis*	(70.26–) 97.04 (–121.04)	(3.40–) 5.46 (-7.37)	(1.78–) 2.76 (–3.43)	(4.13–) 5.30 (–6.71)
Commicarpus decipiens	(97.40–) 116.64 (–129.28)	(4.81–) 5.03 (–5.37)	(1.45–) 2.43 (–3.01)	(5.79–) 7.35 (–9.10)
Commicarpus fallacissimus	(63.88–) 76.62 (–88.46)	(4.35–) 5.25 (–5.92)	(2.18–) 3.18 (–3.78)	(4.76–) 4.81 (–4.93)
Commicarpus fruticosus	(64.64–) 76.23 (–87.89)	(4.36–) 7.11 (–10.64)	(1.95–) 2.49 (–4.02)	5
Commicarpus helenae var. *helenae*	(53.76–) 60.60 (–71.29)	(2.59–) 4.35 (–5.00)	(1.12–) 1.72 (–1.87)	(3.57–) 4.26 (–5.11)
Commicarpus pentandrus	(63.74–) 84.23 (–100.12)	(3.47–) 5.76 (–8.45)	(2.39–) 3.36 (-4.84)	(4.65–) 6.40 (–8.28)
Commicarpus pilosus	(67.55–) 71.97 (–77.66)	(4.55–) 5.04 (–5.49)	(1.88–) 2.55 (–3.26)	(6.69–) 7.45 (–9.06)
Commicarpus plumbagineus	(71.99–) 85.26 (–105.27)	(3.70–) 5.82 (–8.30)	(1.19–) 1.95 (–2.77)	(4.93–) 6.02 (–6.99)
Commicarpus squarrosus	(45.55–) 65.49 (–82.54)	(3.30–) 4.77 (–6.12)	(1.47–) 2.89 (–5.43)	(3.88–) 5.23 (–6.16)

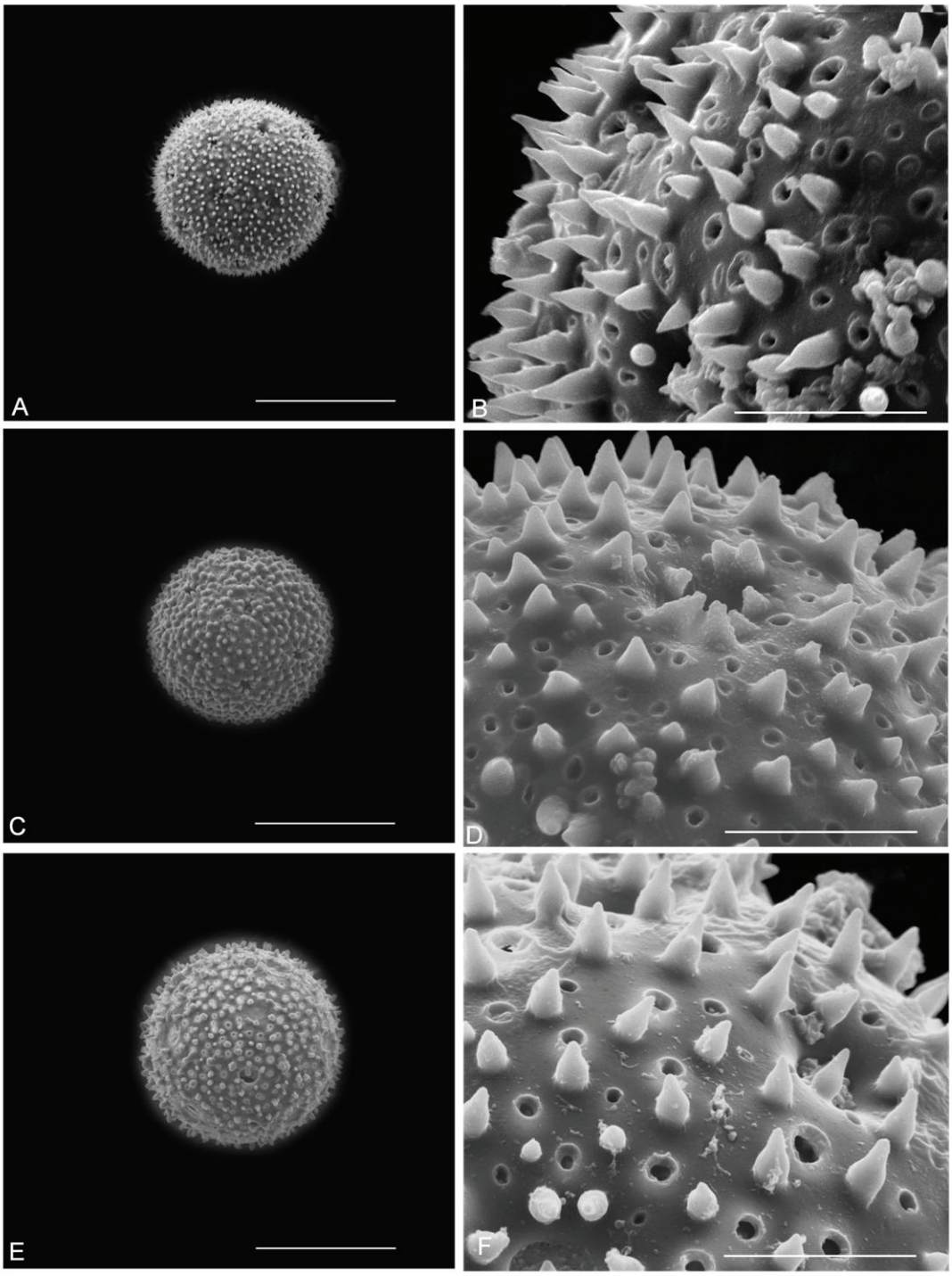

Figure 6.1: Scanning electron micrographs of pollen grains of southern African *Boerhavia* species. A, B: *B. coccinea* var. *coccinea* (*Struwig 55*); C, D: *B. cordobensis* (*Straub 499*); E, F: *B. deserticola* (*Struwig 42*). Scale bars A, C, E: 50 µm; B, D, F: 10 µm.

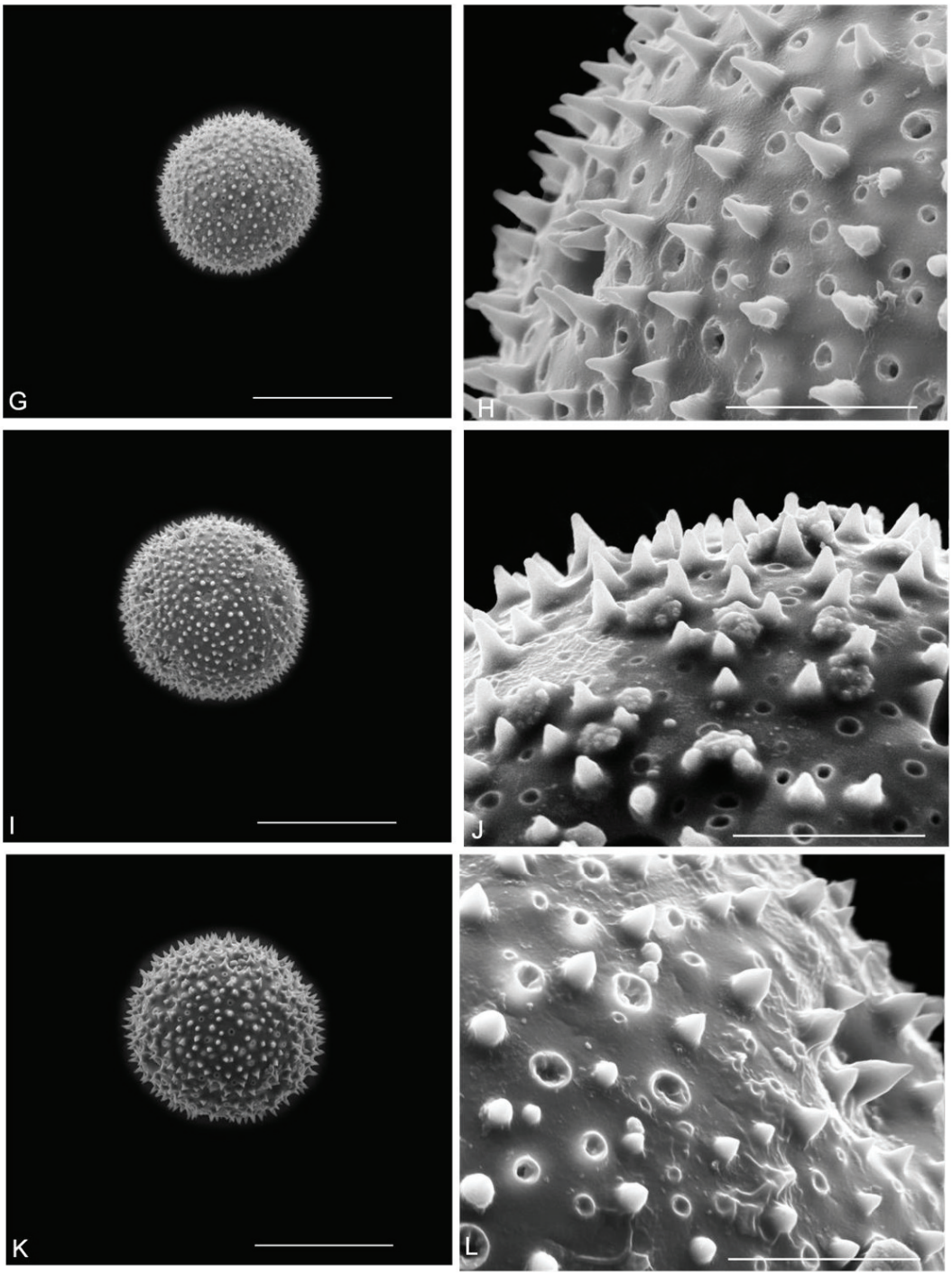

Figure 6.1: Scanning electron micrographs of pollen grains of southern African *Boerhavia* species. G, H: *B. diffusa* var. *diffusa* (*Struwig 88*); I, J: *B. erecta* (*Struwig 133*); K, L: *B. hereroensis* (*Struwig 34*). Scale bars G, I, K: 50 µm; H, J, L: 10 µm.

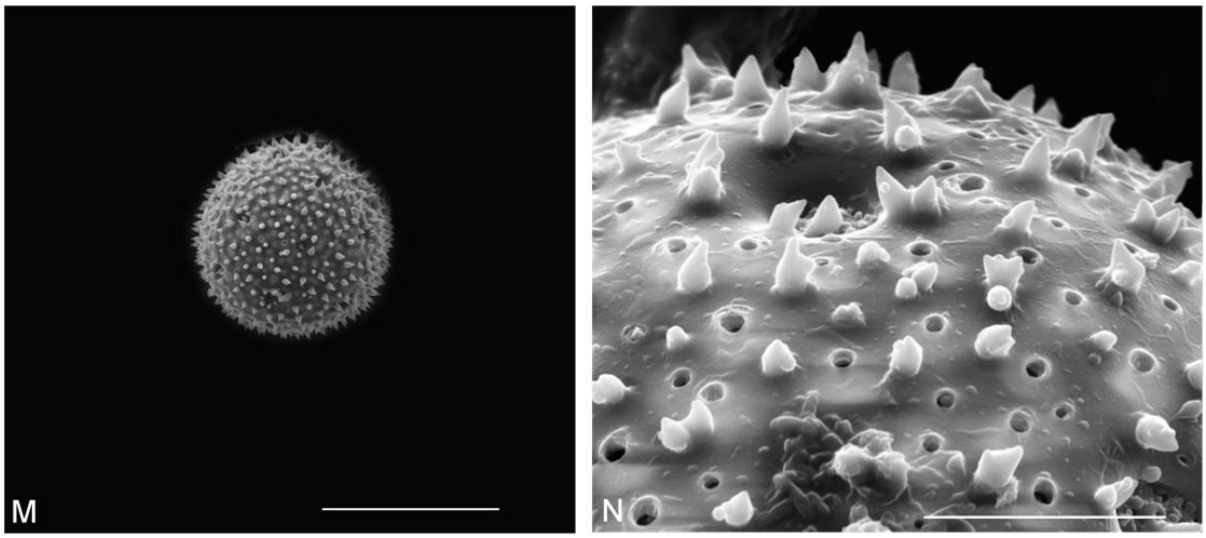

Figure 6.1: Scanning electron micrographs of pollen grains of southern African *Boerhavia* species. M, N: *B. repens* subsp. *repens* (*Acocks 21788*). Scale bar M: 50 µm; N: 10 µm.

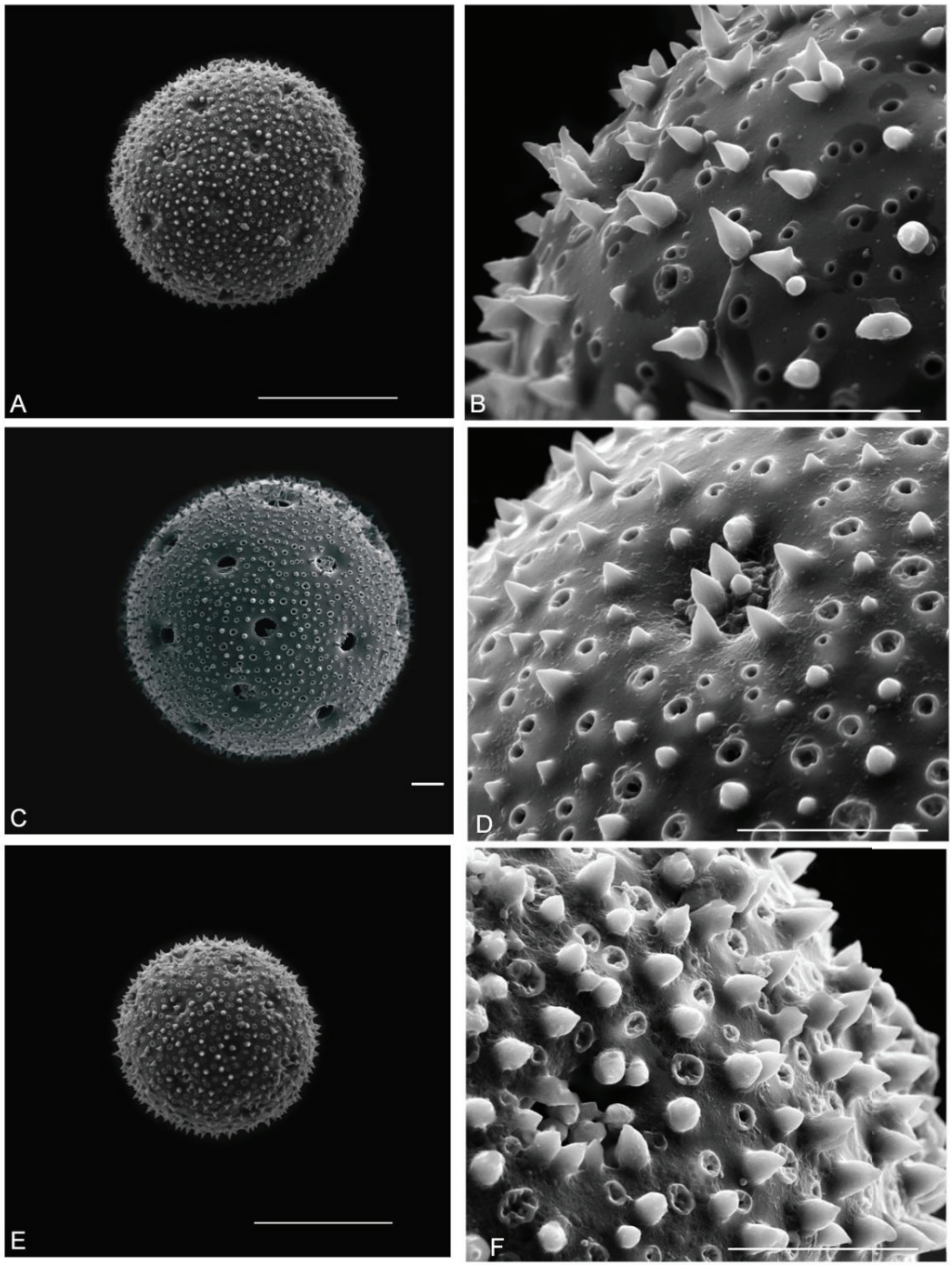

Figure 6.2: Scanning electron micrographs of pollen grains of southern African *Commicarpus* species. A, B: *C. chinensis* subsp. *natalensis* (*Struwig 63*); C, D: *C. decipiens* (*Struwig 181*); E, F: *C. fallacissimus* (*Struwig 46*). Scale bars A, E: 50 µm; B, C, D, F: 10 µm.

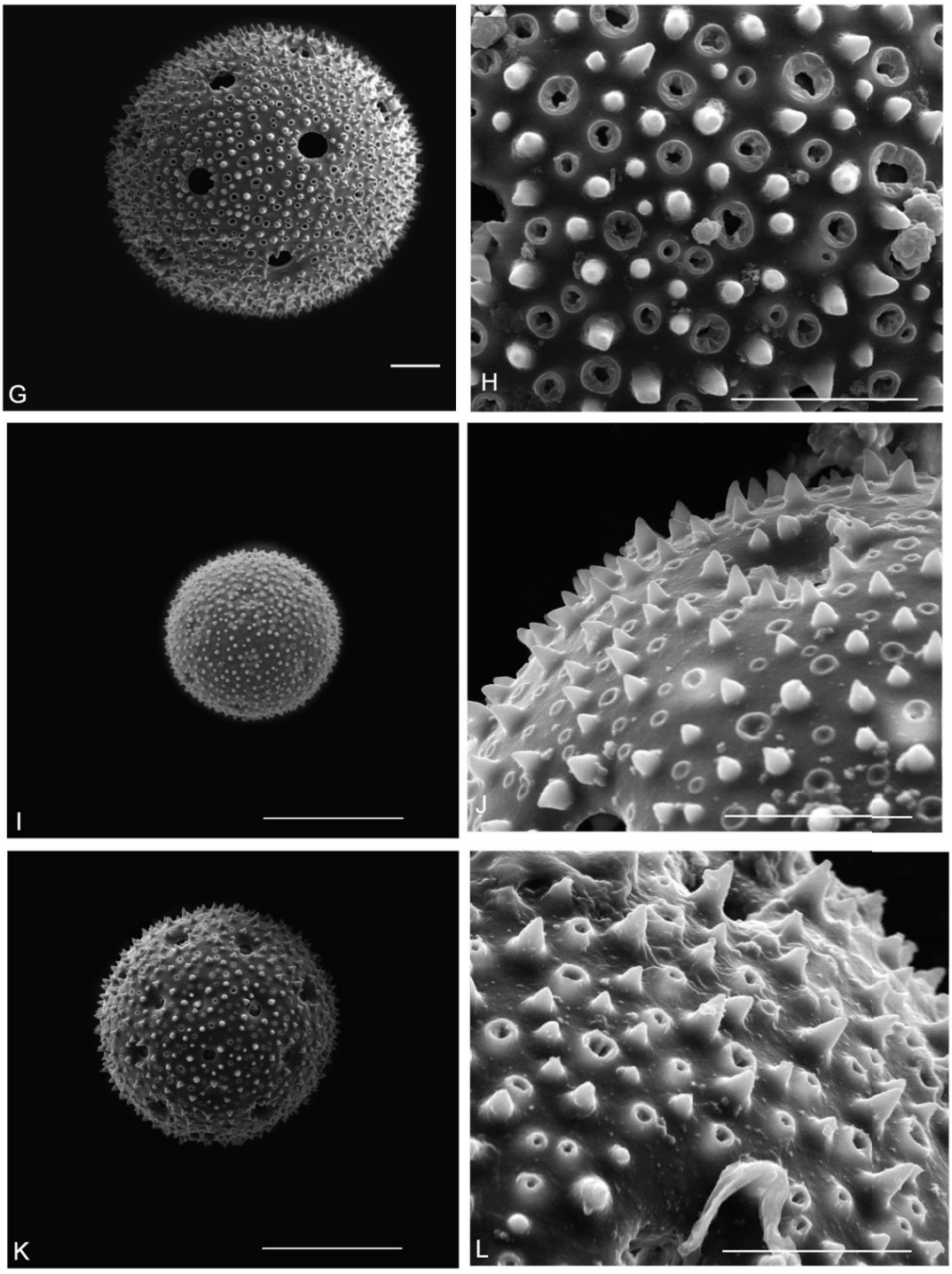

Figure 6.2: Scanning electron micrographs of the pollen grains of southern African *Commicarpus* species. G, H: *C. fruticosus* (*Struwig 160*); I, J: *C. helenae* var. *helenae* (*Struwig 44*); K, L: *C. pentandrus* (*Struwig 52*). Scale bars I, J: 50 µm; G, H, J, L: 10 µm.

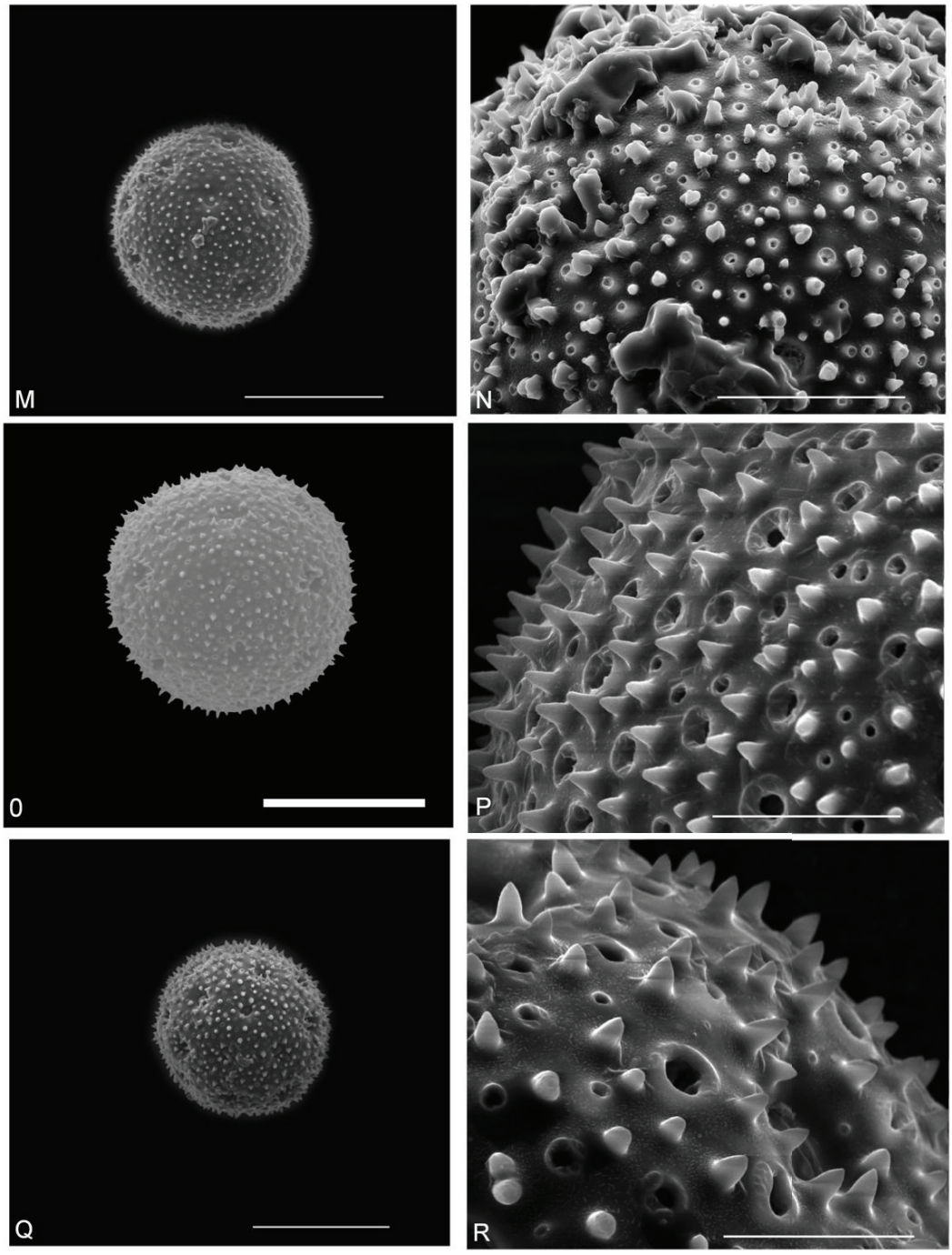

Figure 6.2: Scanning electron micrographs of pollen grains of southern African *Commicarpus* species. M, N: *C. pilosus* (*Straub 609*); O, P: *C. plumbagineus* (*Struwig 106*); Q, R: *C. squarrosus* (*Struwig 41*). Scale bars M: 20 µm; O, Q: 50 µm; N, P, R: 10 µm.

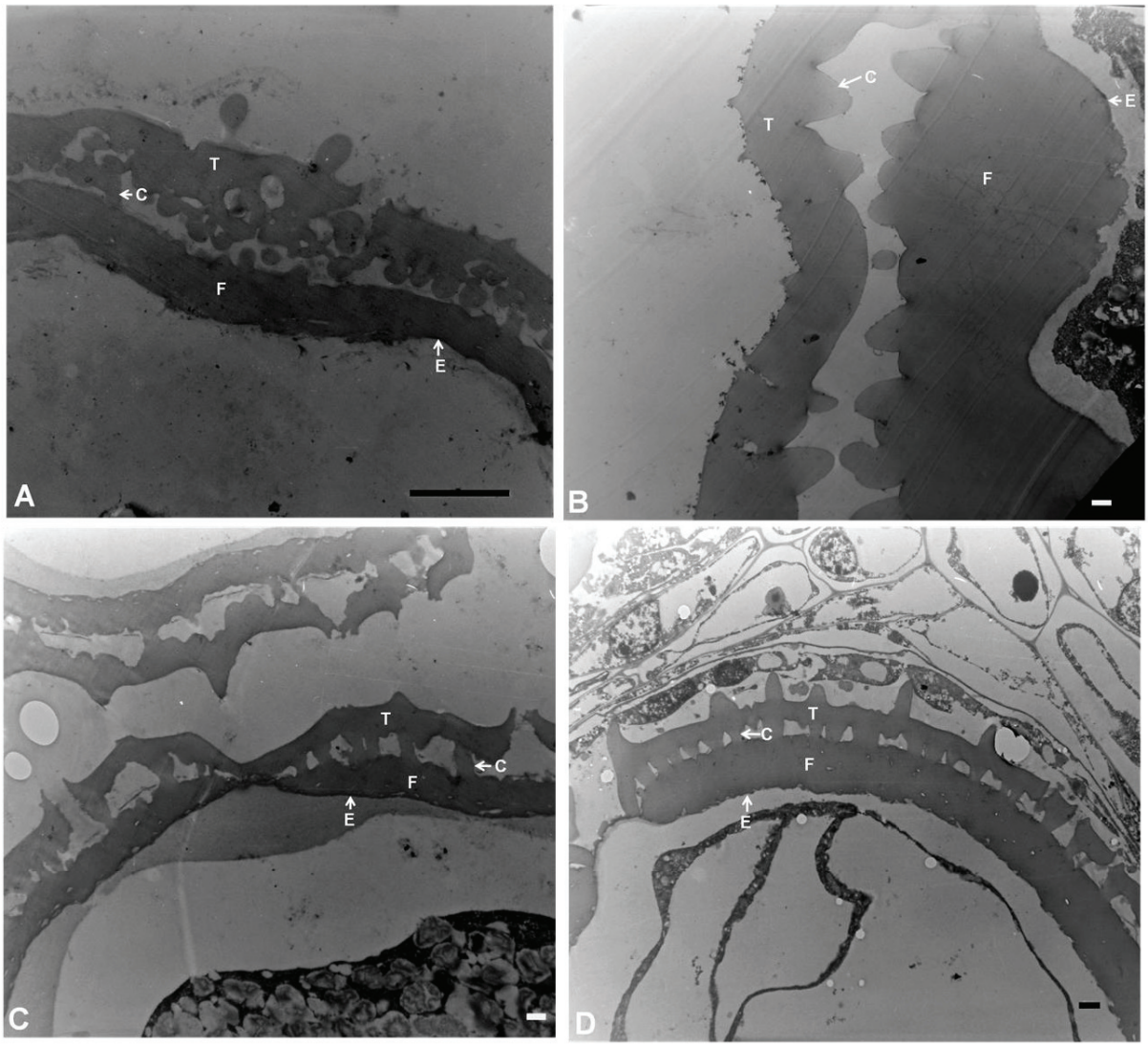

Figure 6.3: Transmission electron micrographs showing the exine of portions of pollen grains of *Boerhavia* species. A: *B. coccinea* var. *coccinea* (*Struwig 55*); B: *B. cordobensis* (*Struwig 132*); C: *B. deserticola* (*Struwig 43*); D: *B. diffusa* var. *diffusa* (*Struwig*, 88) (C, columellae; E, endexine; F, foot layer; T, tectum). Scale bars A: 5 µm; B, C, D: 1 µm.

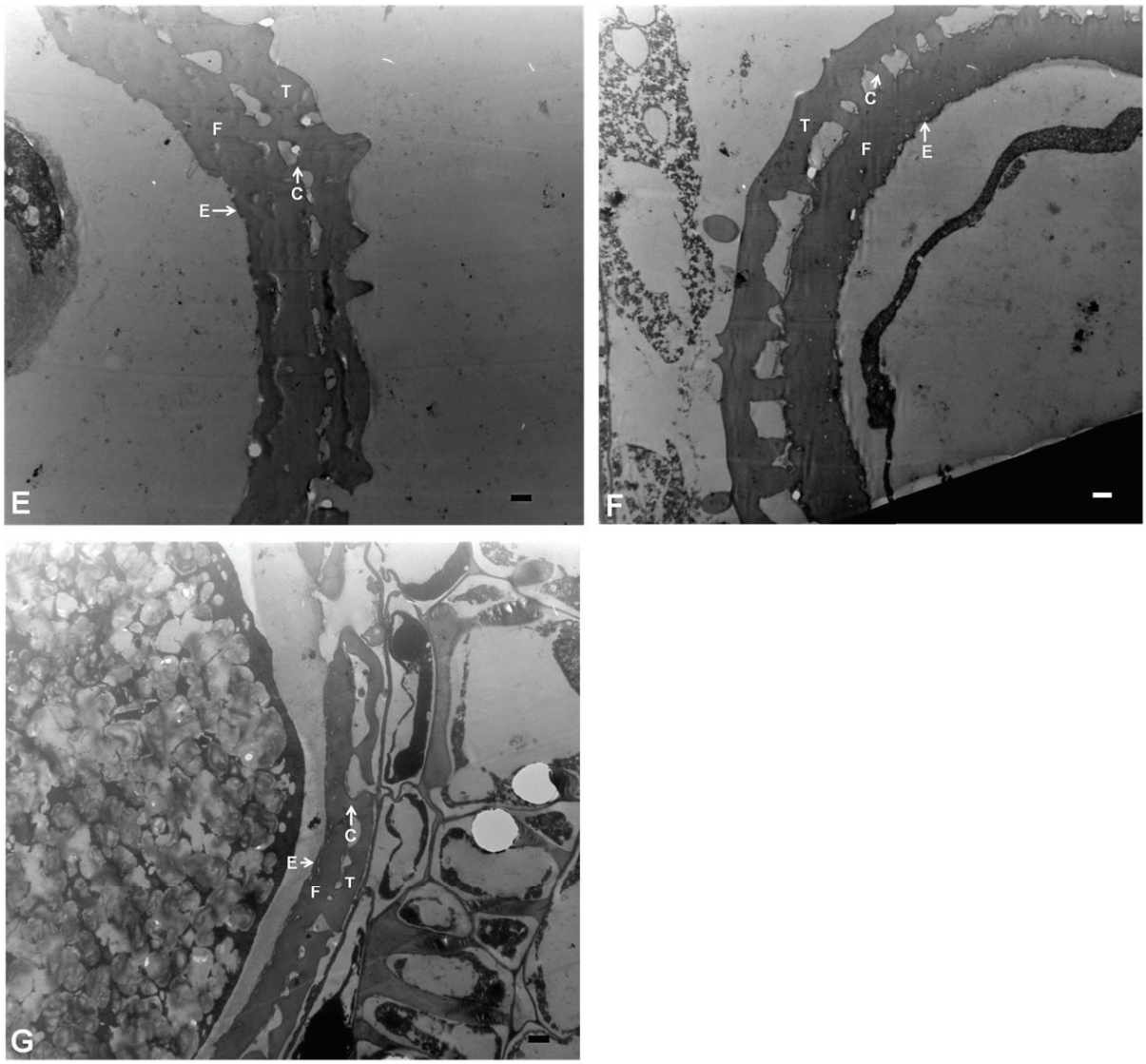

Figure 6.3: Transmission electron micrographs showing the exine of portions of pollen grains of *Boerhavia* species. E: *B. erecta* (*Struwig 143*); F: *B. hereroensis* (*Struwig 34*); G: *B. repens* subsp. *repens* (*Struwig 168*). (C, columellae; E, endexine; F, foot layer; T, tectum). Scale bars E, F, G: 1 µm.

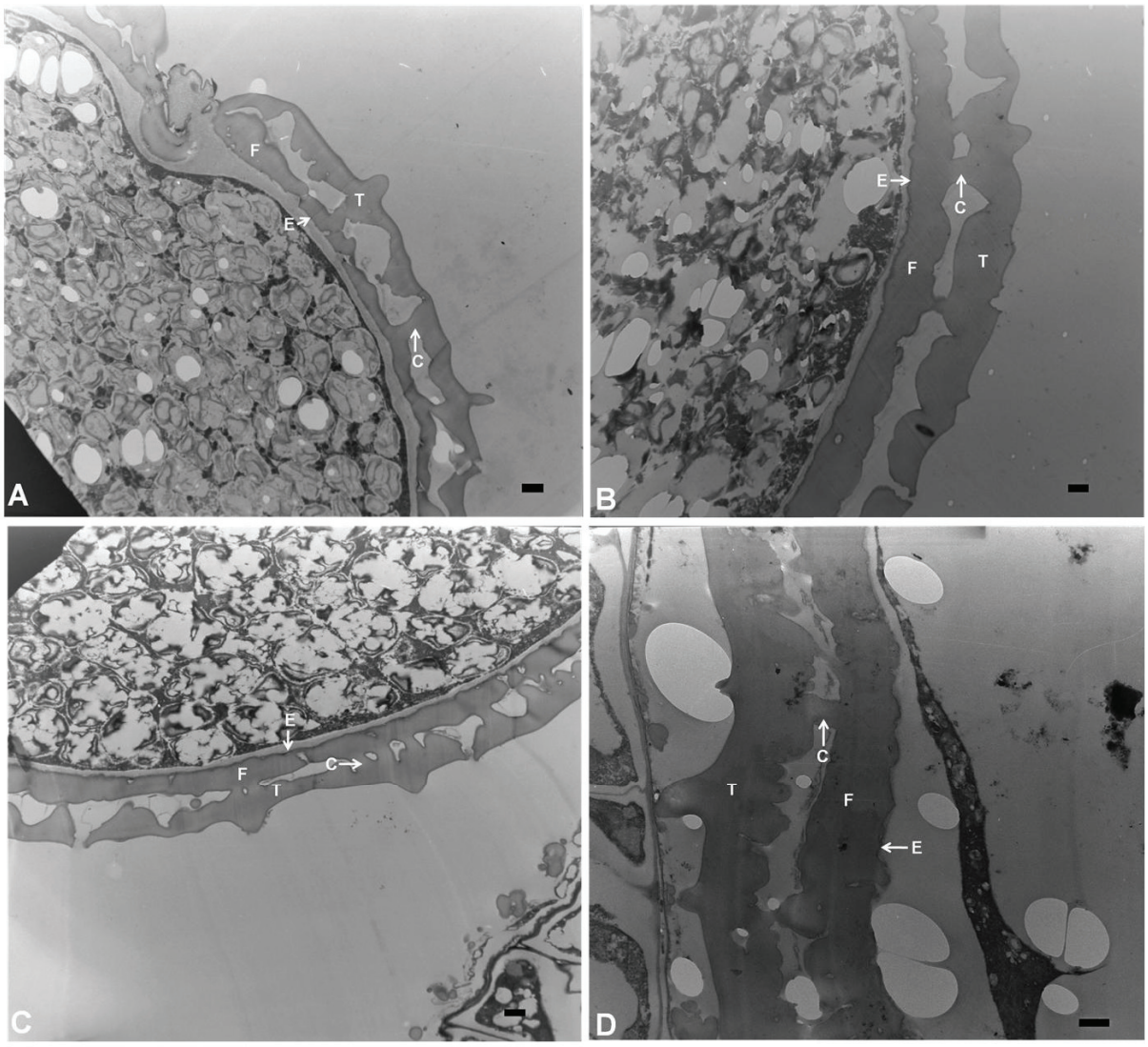

Figure 6.4: Transmission electron micrographs showing the exine of portions of pollen grains of *Commicarpus* species. A: *C. chinensis* subsp. *natalensis* (*Struwig 61*); B: *C. decipiens* (*Struwig 176*); C: *C. fallacissimus* (*Struwig 46*); D: *C. fruticosus* (*Struwig 164*) (C, columellae; E, endexine; F, foot layer; T, tectum). Scale bars A, B, C, D: 1 µm.

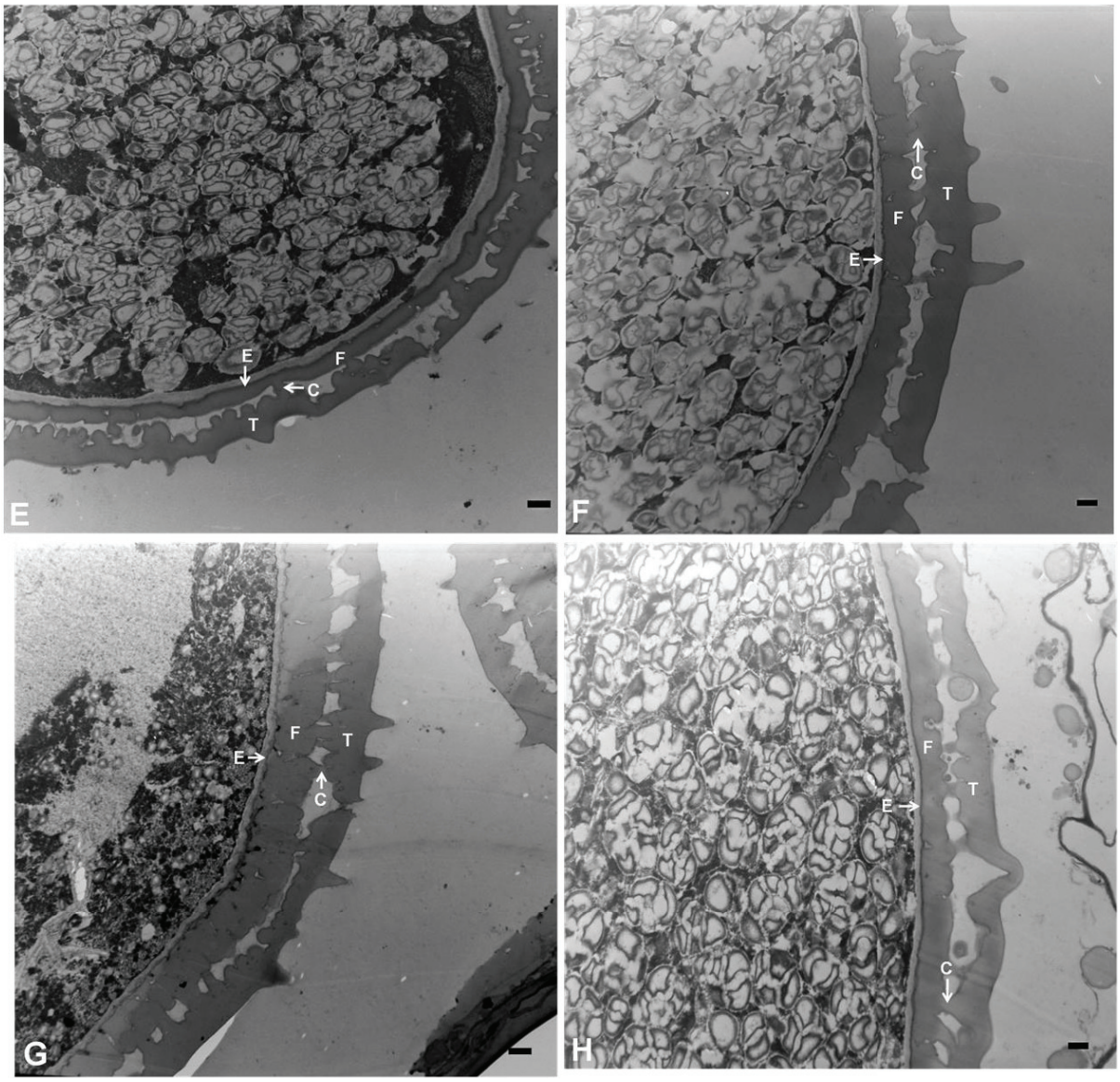

Figure 6.4: Transmission electron micrographs showing the exine of portions of pollen grains of the *Commicarpus* species. E: *C. helenae* var. *helenae* (*Struwig 44*); F: *C. pentandrus* (*Struwig 57*); G: *C. pilosus* (*Struwig 111*); H: *C. plumbagineus* (*Siebert 3970*) (C, columellae; E, endexine; F, foot layer; T, tectum). Scale bars E, F, G, H: 1 µm.

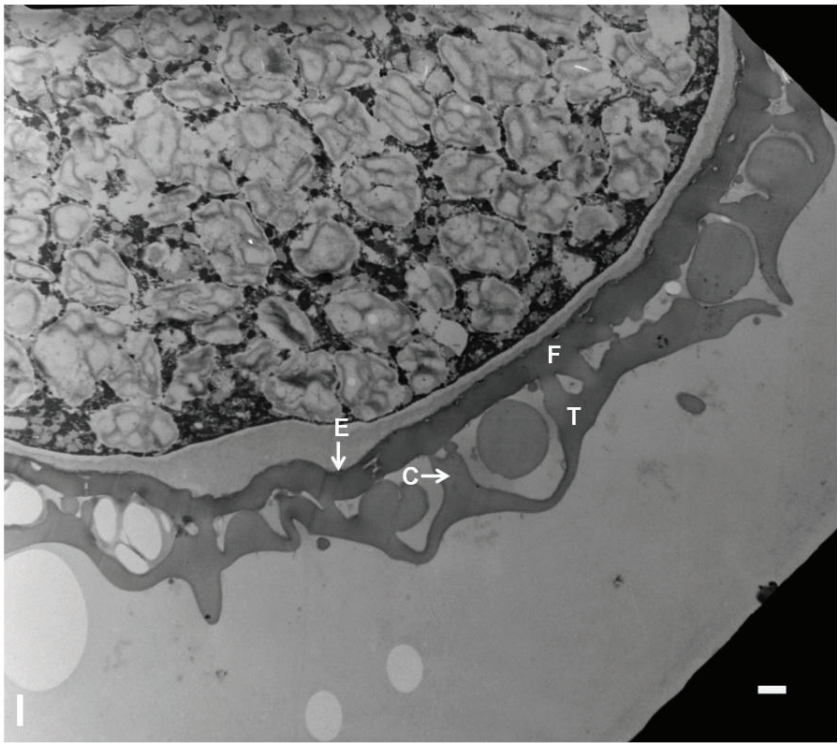

Figure 6.4: Transmission electron micrograph showing the exine of a potion of a pollen grain of *Commicarpus* species. I: *C. squarrosus* (*Struwig*, 41) (C, columellae; E, endexine; F, foot layer; T, tectum). Scale bar 1 μm.