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A REVISION OF SCHWEINFURTHIA

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ABSTRACT. A synopsis, including keys and descriptions, is given of *Schweinfurthia* A. Braun (Scrophulariaceae) and the affinities of the genus are discussed. The species are distributed from western India and Pakistan through S Iran and Arabia to the shores of the Red Sea, with distant outliers in Tanzania and the Comoro Islands. Six species are recognized of which two, both from Oman, are described for the first time: *S. imbricata* Miller, Short & Sutton and *S. spinosa* Miller, Short & Sutton.

INTRODUCTION

Schweinfurthia is a small genus of annual or perennial, suffrutescent herbs found in desert or semi-desert communities, commonly growing in sand, gravel or amongst rocks. They occur where there has been standing or flowing water, in depressions, gulleys, or the beds and sides of wadis. The genus is distributed (see fig. 1 & 2) from western India, Pakistan through Afghanistan, southern Iran, southern and western Arabia, to Egypt, Sudan, Ethiopia and Somalia with outliers in Tanzania and the Comoro Islands: this corresponds to what Zohary (1973) terms the Nubo-Sindian province of the Sudanian region. *Schweinfurthia* is included in the tribe Antirrhineae of the Scrophulariaceae, on the basis of the porose capsule dehiscence. Within the tribe it is generally considered to be related to *Antirrhinum* L. and *Chaenorhinum* (DC.) Reichenb.

During a recent collecting trip to Oman (by A.G.M.) two new *Schweinfurthia* species were collected. One, *S. spinosa*, was discovered in South Oman; the other, *S. imbricata*, had been found by previous collectors in North Oman but generally confused with the more widespread *S. papilionacea*.

The seeds of *Schweinfurthia* were examined by one of us (D.A.S.), using the scanning electron microscope. This was part of a wider study of seed morphology and classification of the tribe Antirrhineae which will appear in a future publication.

HISTORICAL ACCOUNT

The first species of *Schweinfurthia* was described by Linnaeus as *Antirrhinum papilionaceum* in 1767; this has priority over Burman's description using the same name a year later in *Flora Indica* (Merrill, 1921). Linnaeus included all species now in the tribe Antirrhineae in the single genus *Antirrhinum*, but most later authors subdivided it into a number of genera. In the only monograph of the Antirrhineae, Chavannes (1833) excluded *A. papilionaceum* from the tribe. Rafinesque-Schmaltz (1840) adopted narrow generic limits, describing further genera and also indicating '4 doubtful G. not seen by me'. The first three of these are without description and referable to species no longer included in the tribe. The last is cited thus: '4. *Etornotus* [cordate back] diff. ad *Termontis* cal. inequaliss. lac. sup. cordata magna, ceteris lanceol. cor. lab. sup. bifido, inf. trifido, fol. carnosis alt. fl. axil, type *E. persicus* Raf. *Antir. papilionaceum* L.'.

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This description clearly corresponds to the Linnean species and constitutes a prior name for the genus. The fact that Rafinesque had not seen material is probably irrelevant as he was in the habit of naming genera relying purely on bibliographical references (Merrill, 1949: 28). However, if Rafinesque had accepted the genus fully, it would have been included in the normal text and numbered. Instead he wrote that he must 'indicate besides (four) doubtful (genera)' included under the genus *Antirrhinum*. As these generic names were clearly intended as provisional, under article 34: 1b of the *International Code of Botanical Nomenclature* (Stafleu *et al.*, eds 1978) they are invalid and must be considered *nomina provisorii*, as are many other comparable Rafinesque genera (Merrill, 1949: 51).

Bentham in De Candolle's *Prodromus* (1846), like Chavannes, excluded *A. papilionaceum* L. from the tribe Antirrhineae; at the same time he described *Linaria sphaerocarpa* in sect. *Chaenorhinum*. These two species were later combined by Boissier in *Flora Orientalis* (1879) as *Schweinfurthia papilionaceum* Burm. f. The next two species referable to *Schweinfurthia* were *Antirrhinum pterospermum* described by Richard (1851) from Ethiopia and *Anarrhinum pedicellatum* described by Anderson (1861) from Aden. It is evident from the list of specimens examined by Braun (1867), when he published his account of the new genus *Schweinfurthia*, that he considered these two species as conspecific. Bentham (1876) accepted Braun's genus but treated *Anarrhinum pedicellatum* as a distinct species; it was not until 1888 that Balfour made the new combination under *Schweinfurthia*. A fourth species, *S. latifolia*, was described by Oliver (1895). Rothmaler (1943) considered this to be the same as *S. pterosperma* and also included *S. pedicellata* as a variety of the polymorphic *S. pterosperma*.

Discussion

The facies of the six *Schweinfurthia* species varies considerably. *S. pedicellata, S. pterosperma* and *S. latifolia* are erect, annual or perennial, suffrutescent herbs branched from the base or above, with narrowly spathulate to oblong-orbicular leaves; *S. papilionacea* is a decumbent or ascending perennial with somewhat woody stems and leaves with narrow hyaline margins; *S. imbricata* is a prostrate, suffrutescent herb with imbricate leaves with hyaline margins; and, lastly, *S. spinosa* is a spinescent shrub up to 1 m tall, with reduced leaves.

Though there is this variety of facies in *Schweinfurthia* there are a number of distinctive features which unify the genus. The corolla is distinctly bilabiate, the lower lip with a pronounced fold or palate which includes the mouth of the tube (fig. 3B), as in *Antirrhinum*. There is no spur at the base of the corolla-tube as in *Chaenorhinum* or *Linaria*. The calyx is asymmetrical with a large adaxial lobe and two smaller abaxial lobes which overlap the two median lobes (fig. 3E). The capsule is also asymmetrical with the adaxial locule much smaller than the abaxial, few-seeded, and more or less indehiscent. The abaxial locule has an irregular pattern of dehiscence as a result of the capsule-wall structure. Examination of the inner face of a *Schweinfurthia* capsule reveals that the cells are mostly uniformly polygonal in outline (plate 3 E), that the line of rupture follows a random course between cells, and that the edges of the cells are frequently damaged (plate 3 F). Most other genera of the Antirrhineae (cf.

Sutton, 1981) have rows of elongated cells laid down in the capsule-wall during development, resulting in more precise dehiscence with less cell damage. The seeds of *Schweinfurthia* are basically ovoid with an apical hilum and are usually cristate with five main ridges. The seeds of *S. latifolia* are somewhat anomalous being tuberculate rather than cristate (plate 2 B).

The affinities of the genus are far from clear, but the capsule and seed characters suggest that *Chaenorhinum* is probably the most closely related genus, as suggested by Bentham (1846). The capsule in *Chaenorhinum* has unequal locules, though not to the same degree as in *Schweinfurthia*, and the irregular dehiscence of the capsule in the asiatic species of *Chaenorhinum* is similar to that found in *Schweinfurthia*. The seeds of the asiatic *Chaenorhinum* species also show a similar pattern, i.e. ovoid with an apical hilum, five main ridges, and similar large papillae. Finally the calyx lobes are also uneven with the adaxial lobe longest, though this is less marked than in *Schweinfurthia*.

In the following account all specimens seen have been cited, except where otherwise stated.

Acknowledgements

We should like to thank the following staff of the British Museum (Natural History): Norman Robson for assistance with the Latin descriptions, Arthur Chater for much helpful discussion, and Dorothy Hillcoat for bringing to our attention various Arabian collections. We are also grateful to Ian Hedge of the Royal Botanic Garden, Edinburgh, for much helpful discussion and criticism. We wish to acknowledge loans of material from the following instititions: B, BM, CAI, E, FI, K, KUH, & MOG.

Schweinfurthia A. Braun in [Sitzungs-Ber. Ges. Naturf. Freunde Berlin 1866 (9): 24 (1866), nom. nud.] Monatsber. königl. Preuss. Akad. Wiss. Berlin 1866: 875 (1867).

Syn.: *Antirrhinum* L., Sp. Pl. 2: 612 (1753), pro parte.
Orontium Pers., Syn. Pl. 2: 158 (1806), pro parte.
Etornotus Rafin., Autikon Bot.: 155 (1840), nom provis.
Linaria sect. *Chaenorhinum* DC. sensu. Bentham in DC., Prodr. 10: 287 (1846) pro min. parte non DC. in Chavannes (1833).

Annual herbs or suffrutescent perennials. *Leaves* entire, pinnately veined, petiolate or subsessile, the lowermost opposite, alternate above. *Inflorescence* usually lax, the bracts resembling the foliage leaves or somewhat smaller, occasionally subtending axillary shoots. *Flowers* zygomorphic, pedicellate. *Calyx-lobes* unequal, imbricate; adaxial lobe exceeding and overlapping the four lateral lobes; abaxial pair usually exceeding and overlapping the two median lobes. *Corolla-tube* broad, ecalcarate; lips more or less equal, the upper reflexed, the lower with a conspicuous palate. *Capsule* globose, glabrous, thin-walled with the septum oblique; adaxial locule small, few-seeded, indehiscent; abaxial locule large, many-seeded, dehiscing by a transverse split near the base, then becoming divided into several broad valves and eventually rupturing irregularly. *Seeds* usually oblong-ovoid to somewhat conical, truncate-cristate or tuberculate, blackish brown, the hilum apical; ridges (4–)5–6 separated by irregularly anastomosed tubercles or low secondary ridges, rarely absent; interstitial cells

papillate, cells of the ridge apices reticulate; epicuticular wax granules sparse or abundant.
Type species. *S. sphaerocarpa* (Benth.) A. Braun (under *S. papilionacea* (L.) Boiss.).

Braun did not indicate a type for the genus but listed *Schweinfurthia pterosperma* and *S. sphaerocarpa*. However, the specimens listed under *S. pterosperma* undoubtedly include both *S. pterosperma* and *S. pedicellata*. To avoid confusion *S. sphaerocarpa* would be a better choice of type. *S. papilionacea*, the taxon in which *S. sphaerocarpa* is now included, was also the first taxon of this genus to be described (as *Antirrhinum papilionaceum*) and Rafinesque used this species as the type of his segregate genus *Etornotus*.

KEY TO THE SPECIES

1. Flowers 12 mm or more long; adaxial lobe of calyx 9–18 mm 2
\+ Flowers up to 10 mm long; adaxial lobe of calyx 3–9 mm 3
2. Pedicels 4.5–7.5 mm in flower; calyx-lobes not glandular-pubescent; seeds cristate ..... 1. *papilionacea*
\+ Pedicels 8–12 mm in flower; calyx-lobes densely glandular-pubescent; seeds tuberculate ..... 3. *latifolia*
3. Leaves 1.5–13 mm long, less than 3 × as long as broad, orbicular to broadly spathulate 4
\+ Leaves 8–45 mm long, more than 3 × as long as broad, linear or narrowly spathulate to oblong-ovate 5
4. Plant erect; stems spinescent; corolla 6–7 mm ..... 6. *spinosa*
\+ Plant prostrate; stems not spinescent; corolla 8.5–10 mm ..... 2. *imbricata*
5. Branches narrowly divergent; leaves oblong-ovate to narrowly spathulate; pedicels 3–13 mm, becoming recurved in fruit ..... 4. *pterosperma*
\+ Branches divaricate; leaves linear to oblong-elliptic; pedicels 10–17 mm, the distal portion becoming deflexed in fruit ..... 5. *pedicellata*

1. S. papilionacea (L.) Boiss., Fl. Or. 4: 387 (1879). Fig. 1, Plate 1A–C.
Syn.: *Antirrhinum papilionaceum* L., Mantissa: 86 (1767).
Orontium papilionaceum (L.) Pers., Syn. Pl. 2: 158 (1806).
Etornotus persicus Rafin., Autikon Bot.: 155 (1840), nom provis.
Linaria sphaerocarpa Benth. in DC., Prodr. 10: 287 (1846).
Antirrhinum glaucum [Stocks ex] Wight, Ic. Pl. 4(3): 10, tab. 1459 (1850).
Schweinfurthia sphaerocarpa (Benth.) A. Braun in [Sitzungs-Ber. Ges. Naturfr. Freunde Berlin 1866 (9): 25 (1866), nom. nud.] Monatsber. königl. Preuss. Akad. Wiss. Berlin 1866: 875 (1867).
Etornotus papilionaceus (L.) Speta in Pl. Syst. Evol. 132: 4 (1979).
[*Asarina persica nummulariae facie* Garcin, in sched.]

Decumbent or ascending, rarely erect perennial up to 45 cm, glaucous, glabrescent, the young shoots densely covered with short, somewhat curled hairs; stems becoming woody, usually branched below. *Leaves* 7–55(–85) × 7–29(–40) mm, spathulate to orbicular, obtuse, mucronate, hyaline, attenuate,

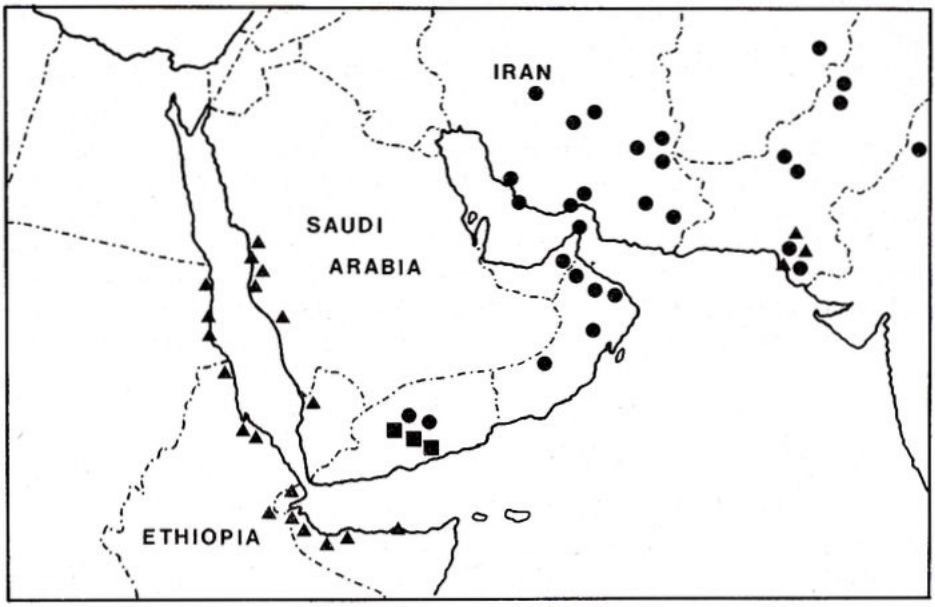


FIG. 1. Distribution of *S. papilionacea* ●, *S. latifolia* ■, *S. pterosperma* ▲.

succulent, strongly muricate below; petiole 2–3(–10) mm. *Inflorescence* lax, with 2–10(–20) flowers. Pedicels 4.5–7.5 mm in flower, 8–14 mm in fruit, becoming reflexed. *Calyx-lobes* with a narrow hyaline margin; adaxial lobe 9–17 × 7–15 mm, cordate to broadly ovate, obtuse with a short mucro; median lobes 4.5–9 × 1.5–2.5 mm, lanceolate, acute; the abaxial lobes 5–10 × 2.5–4 mm, ovate, acuminate. *Corolla* 12–14 mm, whitish, often with purple veins, the palate yellow. *Capsule* 7–10 mm, adaxial locule with 3–4(–9) seeds. *Seeds* 1.5–1.8 mm, oblong ovoid, truncate, cristate; the ridges acute, transversely sulcate, interstices with irregularly anastomosing tubercles; interstitial cells with large, conical papillae, cells of ridge-base transversely banded and with small, wrinkled papillae, wax granules sparse.

Fl. 1–12. Arid sandy and gravelly plains, slopes and wadi beds, nr s.l.–1450 m.

Type. Iran. *Garcin*.

Selected specimens:

INDIA. Punjab, Kiri Golewala, 300 m, *Kabir* 14583 (K).

PAKISTAN. Bannu, Salt Range, NWFP, *Rahman* 25869 (BM). W Sibi, 100 m, *Watt* 4098 (E); Rocks in Scinde, *Stocks* 521 (type *Antirrhinum glaucum*, K); 22 miles from Thano Bula Khan towards Karachi, *Qaiser et al.* 538 (KUH).

AFGHANISTAN. In Regno Cabulico [nr Kandahar], *Griffith* 609 (type *Linaria sphaerocarpa*, K).

IRAN. Khorassan, S of Dasht-e-Lut, 33°10′ N 57°40′ E, dry wadi bed, 950 m, *Parris* 75.162 (E); Baluchistan, Khash to Iranshahr road, 1450 m, *Rechinger* 54921 (B,W); 30 km E of Bandar Khomyer, 10 m, *Davis & Bokhari* 56145 (K,E); Bandar Abbas, E end of Kuh-e Genou, 200 m, *Wendelbo & Foroughi* 15721 (E).

SULTANATE OF OMAN. Musamdam peninsula, Khasab, 26°11′ N 56°15′ E, disturbed ground around camp, 5 m, *Mandaville* 7182 (BM); Iski, 22°57′ N 57°46′ E, outside oil camp area, *Mandaville* 3436 (BM); 40 km S of Adam, open stony desert, 200 m, *Miller* 2025 (E); 40 km SW of Mugshin, flat sandy desert, 150 m, *Miller* 2046 (E).

UNITED ARAB EMIRATES: ABU DHABI. Al Ayn, ridge nr sports stadium, ungrazed enclosure, limestone, 300 m, *Edmondson* 3012 (E).
PDRY: S YEMEN. Nr Sai'un [Saywun], Hadramaut, 600 m, *Popov* 518 (BM, K).

Probably the best-known species of the genus, represented in herbaria by many specimens. However, the typification of this species is not very clear. Linnaeus (1767) cited Burman's forthcoming *Flora Indica* (1768) but no specimens. Linnaeus received the majority of the plates for Burman's Flora in 1765 (Stearn, 1961: ix) and it is almost certain that he saw the illustration of Burman's *Antirrhinum papilionaceum*. Thus the type of *Antirrhinum papilionaceum* is the illustration in *Flora Indica* (Burman, 1768: tab. 39). This illustration is based on a Garcin specimen, the only material cited by Burman, and represents the type of the type illustration or 'typotype' according to J. E. Dandy (Stearn, 1957: 129). We have not seen the Garcin specimen but believe it to be in the Geneva herbarium. Linnaeus did not give any suggestion of having seen the Garcin specimen, contrary to the suggestion of Merrill (1921: 380).

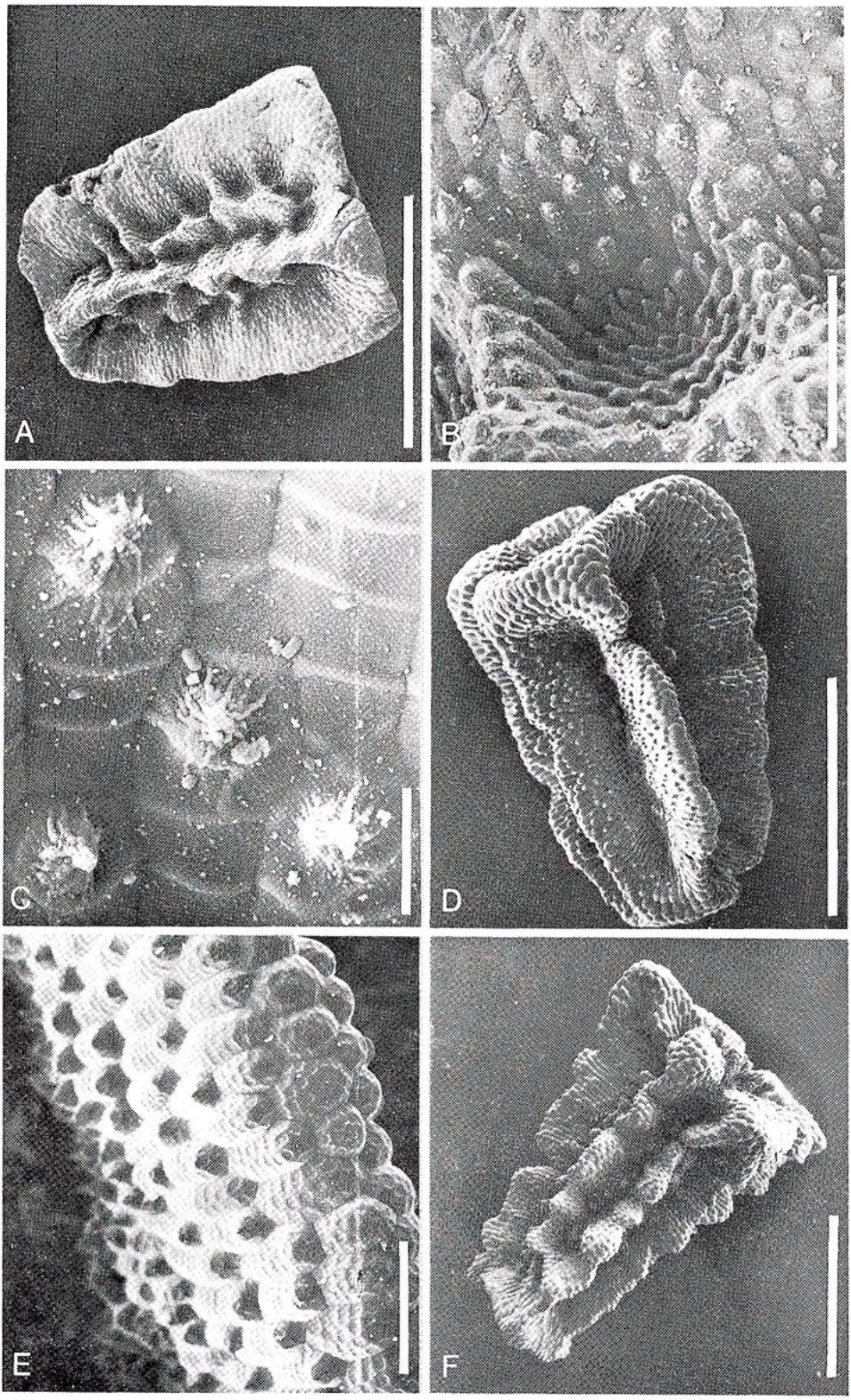
2. S. imbricata Miller, Short and Sutton, **sp. nov.** Fig. 2, 3, Plate 1D–F.

S. papilionaceae affinis, sed habitu prostrato, foliis imbricatis, inflorescentia densa floribusque parvis imprimis differt.

Herba annua vel perennis prostrata suffrutescens glauca glabrescens ad 14 cm alta; surculi juveniles pilibus albis parum crispis vestiti; caules plerumque e base et aliquando versus apicem ramosi. Folia 4–13 × 4–13 mm, orbicularia vel late spathulata, apice obtusa vel mucronata, margine anguste hyalino, basi truncata vel attenuata, parum succulenta; petiolus 2–7 mm longus. Inflorescentia densa multiflora; pedicelli 3.5–6.5 mm longi, post anthesin vix elongati sed recurvescentes. Calycis lobi parum scariosi; lobus adaxialis 7–9 × 6–8 mm longus, late ovatus vel suborbiculatus, obtusus mucronatus; lobi mediani 5–7.5 × 1.2–2.8 mm longi, lineari-lanceolati acuminati; lobi abaxiales 5.5–8 × 2–3 mm longi, lanceolati acuti. Corolla 8.5–10 mm longa, alba vel cremea venis purpureis notata, palato luteolo. Capsula 5–10 mm longa, loculo adaxiali 0–1-seminali. Semina 1.5–2.5 mm longa, oblongo-ovoidea vel plus minusve conica, truncata, cristata cristis laevibus vel irregulariter dentatis obtusis ad apicem inflatis; interstitia tubercula irregulariter anastomosantia instructa cellulis interstitialibus papilla grandes conica ferentibus cristarum cellulis basi reticulatis et papilla parva marginales ferentibus; granula ceracea sparsa.

Prostrate, suffrutescent annual or perennial up to 14 cm, glaucous, glabrescent, young shoots densely covered with white, somewhat curled hairs; stems usually branched from the base, occasionally above. *Leaves* 4–13 × 4–13 mm, orbicular or broadly spathulate, obtuse or mucronate, with narrow hyaline margins, truncate or attenuate, somewhat succulent; petiole 2–7 mm. *Inflorescence* dense, with 5–30 flowers. Pedicels 3.5–6.5 mm, scarcely elongating in fruit, becoming recurved. *Calyx-lobes* somewhat scarious; adaxial lobe 7–9 × 6–8 mm, broadly ovate to suborbicular, obtuse, mucronate; median lobes 5–7.5 × 1.2–2.8 mm, linear-lanceolate, acuminate; abaxial lobes

PLATE 1. Scanning electron micrographs of *Schweinfurthia* seeds. A–C, *S. papilionacea*: A, whole seed showing transversely anastomosed ridges, scale = 1 mm; B, interstitial region with conical papillae, scale = 0.1 mm; C, cells of ridge-base with low, wrinkled papillae and transversely banded thickening, scale = 10 μm. D–F, *S. imbricata*: D, whole seed of *Whitcombe* 347 with more or less entire ridges, scale = 1 mm; E, ridge-cells showing conical papillae and reticulate thickening, scale = 0.1 mm; F, whole seed of *Thesiger* s.n. (4 iv 1949) with irregular ridges, scale = 1 mm.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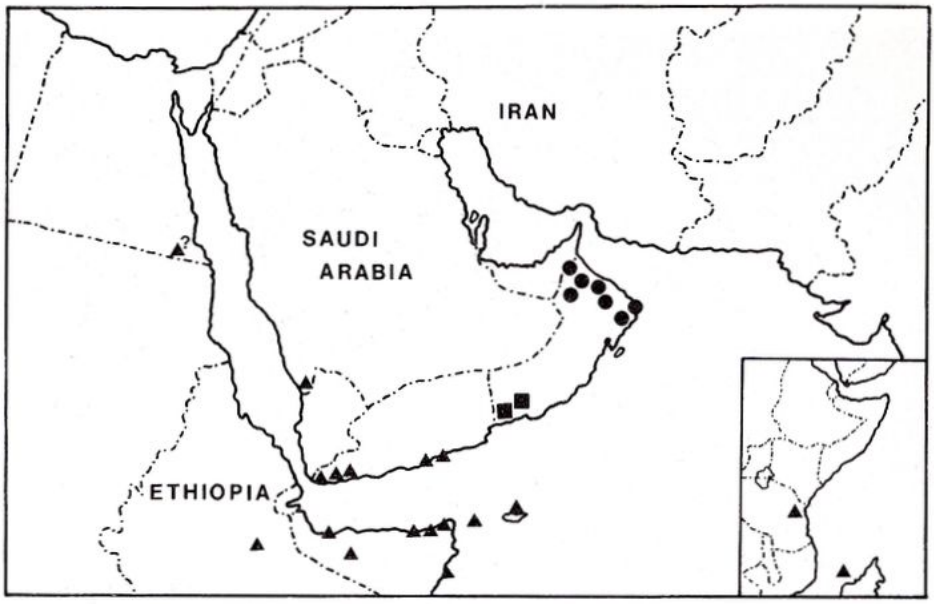


FIG. 2. Distribution of *S. pedicellata* ▲, *S. imbricata* ●, *S. spinosa* ■.

5.5–8 × 2–3 mm, lanceolate, acute. *Corolla* 8.5–10 mm, white or cream with purple veins, the palate pale yellow. *Capsule* 5–10 mm; adaxial locule with 0–1 seeds. *Seeds* 1.5–2.5 mm, oblong-ovoid to conical, truncate, cristate; ridges smooth or irregularly dentate, obtuse, inflated towards the apex, the interstices with irregularly anastomosed tubercles; interstitial cells with large conical papillae, the cells of ridge-base reticulate with small marginal papillae, wax granules sparse.

Fl. 1–9. Arid sandy and gravelly slopes, wadi beds and sides, 60–650 m.

Type. Sultanate of Oman, Jabal Akhdar, Al Hijir, Wadi Bani Kharus, 11 km S of Anabi, nr Rustaq, 700 m, 24 x 1979, *Miller & Whitcombe* 2804 (holo. E, iso. BM).

SULTANATE OF OMAN. Halfway between Ras al Hadd and Bilad Bani Bu Ali, 70 m, *Whitcombe* 354 (E); Nr Ras al Hadd in direction of Bilad Bani Bu Ali, 60 m, *Whitcombe* 347 (E); 10 km N of Al'Ulya, 600 m, *Radcliffe-Smith* 3921 (K); Mahadha, *Popov* GP/520 (BM); Wadi Ghaur, *Guichard* KG/65/Oman (BM); Below Dhank W bu Karba, 4 iv 1949, *Thesiger* s.n. (BM); Ruashid, Wadi Hinna, Drua Steppe, 600 m, 19 ii 1949, *Thesiger* s.n. (BM); W Hajar mtns, J. Akhdar, in Wadi Beni Ghafir, 1 km W of Sidaq, volcanic rocks, 23°56′ N 57°02′ E, 950 m, *Edmondson* 3474 (E).

A highly distinctive species which can be distinguished from all other *Schweinfurthia* species by its prostrate habit and closely overlapping leaves (fig. 3). It is probably most closely related to *S. papilionacea*, both species having similar broad leaves with narrow hyaline margins and relatively large flowers and seeds. The seeds of *S. imbricata* differ from those of *S. papilionacea* in that the main ridges are not connected by transverse ridges to produce the transversely sulcate pattern of the latter taxon. Also, the sides of the ridges bear larger papillae in *S. imbricata*. There is considerable variation in the seeds of the new species. The *Miller & Whitcombe* type specimen has smaller seeds with broader

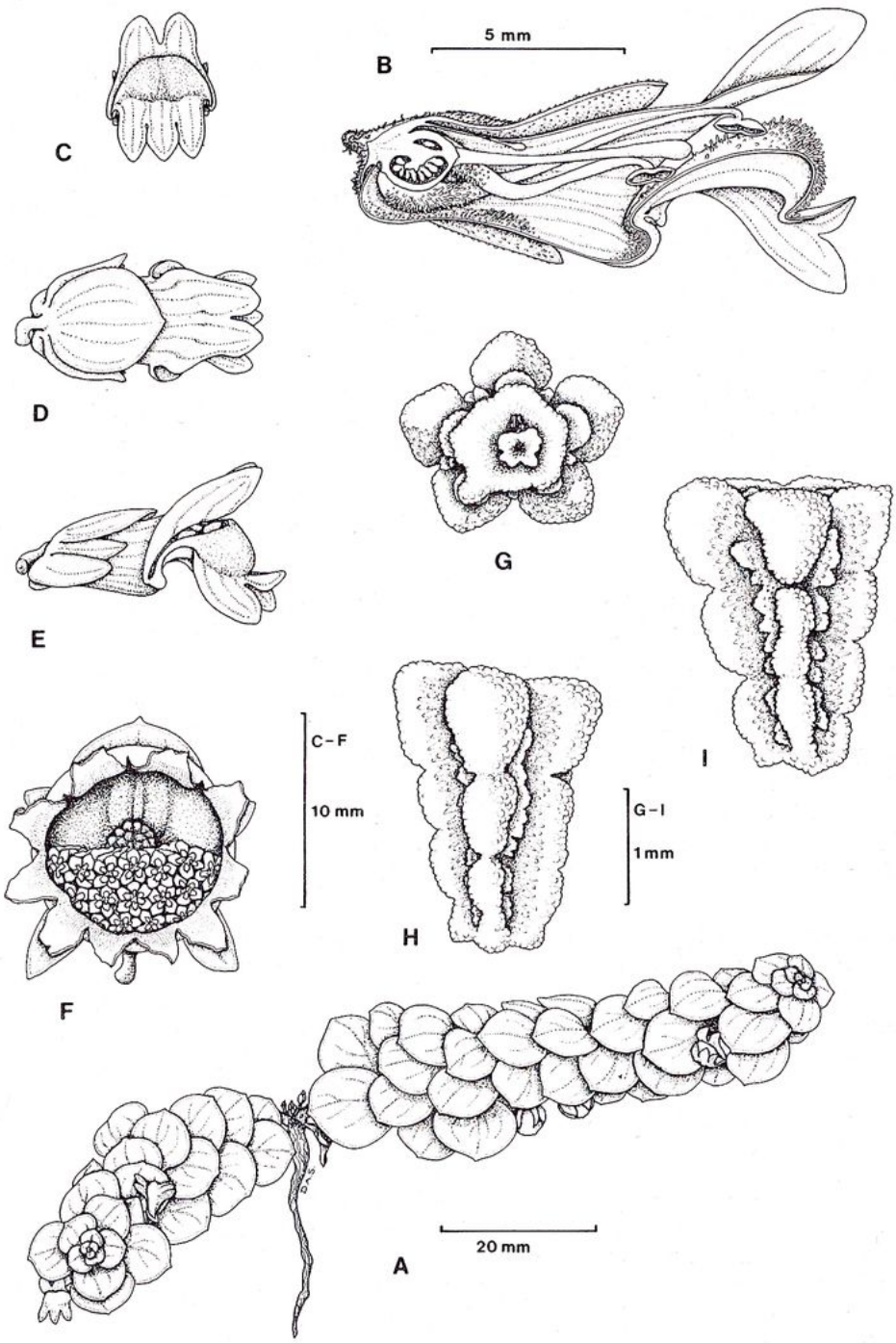


FIG. 3. *Schweinfurthia imbricata*: A, habit; B, half-flower; C, flower, front view; D, flower, top view; E, flower, side view; F, capsule; G, seed, basal view; H, seed, lateral view; I, seed, dorsal view.

ridges (plate 2A) than those of the *Whitcombe* 347 specimen (plate 1D). Both *Thesiger* specimens have even larger seeds than the *Whitcombe* specimen and more uneven ridges (plate 1F). Further collecting is required to determine the pattern of this variation before the use of infraspecific taxa can be investigated.

3. S. latifolia [Baker ex] Oliver in Hooker's Ic. Pl. 24: pl. 2362 (1895). Fig. 1, Plate 2B, C.

Syn.: *S. latifolia* Baker in Kew Bull. 93: 338 (1894), nom. nud.

S. pterosperma (A. Rich) A. Braun var. *latifolia* (Bak.) Rothm. in Feddes Repert. 52: 32 (1943) nom. illegit., pro parte.

Erect, suffrutescent perennial up to 45 cm, glabrescent, young shoots densely covered with soft, multicellular, glandular hairs; stems branched from the base, occasionally above. *Leaves* 23–43 × 16–37 mm, broadly ovate to oblong-orbicular, obtuse or shortly apiculate, cordate to truncate; petiole 4.5–8 mm. *Inflorescence* somewhat lax, with 8–30 flowers. Pedicels 8–12 mm in flower, up to 16 mm in fruit and becoming recurved. *Calyx-lobes* somewhat thickened at the margins, densely glandular pubescent; adaxial lobe 15–18 × 8–17 mm, broadly ovate to deltoid, acute; median lobes 11–14 × 2–5 mm, linear-lanceolate, acuminate; abaxial lobes 12–16 × 4–6.5 mm, ovate, acute. *Corolla* 20–30 mm, pale yellow with a mauve upper lip. *Capsule* 9–11 mm; adaxial locule with 3–5 seeds. *Seeds* 0.9–1.2 mm, elliptic to oblong-ovoid, tuberculate; tubercles slender, acute; interstitial cells with large conical papillae, wax granules abundant.

Fl. 5–6. Arid gravel plains, rocky slopes and wadi beds, 60–900 m.

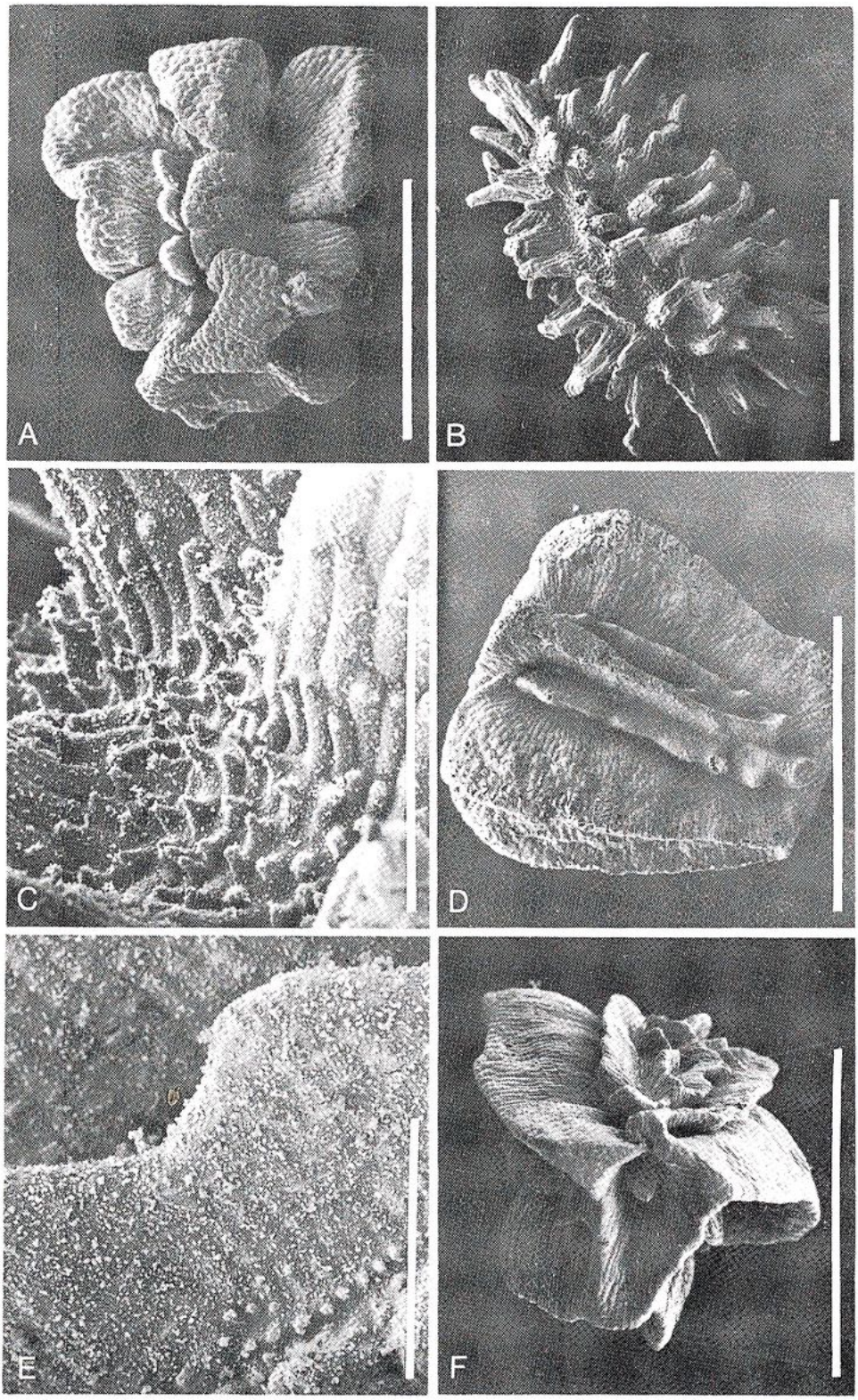
Type. [PDRY: S Yemen] Hadramaut, Mokalla, Shari Burrock Valley, 60–90 m, 21 xii 1893, *Lunt* 58 (holo. K).

PDRY: S YEMEN. Hadramaut, Es Serêre-Harschiyât, Kalkschotter-Terrassen des Küsten-Tieflandes, *Wissmann* 3069 (BM); rocks near Mukalla, *Guichard* KG/HAD/361 (BM); Wadi Bin Ali, upper wadi area on sand, 600 m, *Popov & Gilliland* 4146 (K); Huraidha, 800 m, sandy wadi bed, *Wakefield Expedition* 16 (K).

An uncommon species with a narrow distribution in South Yemen. Most authors have accepted *S. latifolia* as a distinct species although Rothmaler (1943) considered it to be identical with *S. pterosperma*, perhaps as a result of misidentified material. He included the two taxa in *S. pterosperma* var. *latifolia*, an illegitimate name since it includes the type of *S. pterosperma*.

S. latifolia is perhaps the most anomalous species of the genus as it has tuberculate rather than cristate seeds. However, the structure of ridges and tuberculae is basically the same and species with ridges (including those of other *Schweinfurthia* species) often have isolated tubercles. There are several examples in the genus *Linaria* of species with tuberculate seeds and very similar species with longitudinal ridges. It is surprising though, to find the ridge development of *Schweinfurthia latifolia* so completely suppressed. In other respects, however,

PLATE 2. Scanning electron micrographs of *Schweinfurthia* seeds. A, *S. imbricata*, seed of *Miller & Whitcombe* 2804 showing relatively broad, irregular ridges, scale = 1 mm. B,C, *S. latifolia*: B, whole tuberculate seed, scale = 1mm; C, interstitial region showing conical papillae and granular waxy covering, scale = 0.1 mm. D,E, *S. pterosperma*: D, whole seed showing relatively high acute ridges, scale = 1 mm; E, interstitial ridge with minute papillae at base, scale = 0.1 mm. F, *S. pedicellata*, basal (hilar) view of seed of Socotra specimens showing relatively high ridges, scale = 1 mm.



B

particularly in the form of the calyx, corolla and capsule, *S. latifolia* exhibits characters typical of *Schweinfurthia*.

4. S. pterosperma (A. Rich.) A. Braun in [Sitzungs-Ber. Ges. Naturf. Freunde Berlin 1866 (9): 24 (1866), nom. nud.] Monatsber. königl. Preuss. Akad. Wiss. Berlin 1866: 872 (1867). Fig. 1, Plate 2D, E.

Syn.: *Antirrhinum pterosperma* A. Rich., Tent. Fl. Abyss. 2: 115 (1851).

Schweinfurthia pterosperma var. *latifolia* Rothm. in Feddes Repert. 52: 32 (1943), nom illegit., pro parte.

Erect annual or perennant herb up to 38(−45) cm, stems usually densely branched above, the branches usually narrowly divergent, fleshy towards the tips. *Leaves* 8−40 × 1.5−12 mm, oblong-ovate to narrowly spathulate, obtuse to subacute, attenuate; petiole 3−15 mm. *Inflorescence* somewhat lax with 2−10(−20) flowers. Pedicels 3−13 mm, scarcely elongating in fruit, becoming recurved. *Calyx-lobes* ovate, acute, somewhat scarious; adaxial lobe 3−5 × 1.5−2 mm; median lobes 2.5−3.5 × 0.7−1.6 mm; the abaxial lobes 3−4 × 0.7−1.6 mm. *Corolla* 6−8 mm, whitish, the throat pink, the palate yellow with purplish glandular hairs. *Capsule* 4.5−6 mm; adaxial locule with 6−11 seeds. *Seeds* 1−1.5 mm, oblong to oblong-ovoid, truncate, cristate; ridges thin, wing-like, acute, the interstices with small intermediate ridges or rows of elongated tubercles; interstitial cells with minute rounded papillae, wax granules abundant. Fl. 1−6. Arid sandy plains, wadis and depressions, occasionally on saline soils, often by the coast. 15−30 m.

Type. Ethiopia. In regione arenaria Choho dicta, *Quartin, Dillon & Petit* s.n. (holo. P).

Selected specimens:

PAKISTAN. Bund Murad, Karachi, *Aziz* s.n. (KUH).

YEMEN ARAB REPUBLIC. Frequent on sand between Haradh and Meidi especially in shallow depressions, 100 m, *J. Wood* 2677 (E).

SAUDI ARABIA. 8 km S Rabigh, Red Sea Coast, *Mandaville* 3001 (BM); nr Lith, c. 20°10′ N 40°20′ E, *Popov* 69/14 (BM).

SUDAN. Tokar Delta North, also on littoral, Suakin, *Bally* 6989 (K); c. 21° N, sea coast between 900−1200 m, 1896, *Bent* s.n. (K).

ETHIOPIA. 20 miles SE Marsa Fatma, raised coral beaches, *Hemming* 1258 (BM); Wadi Walkat, 120 m, *Bally* 6855 (K).

T.F.A.I. Quassi, *Popov* 1268 (K).

SOMALIA. N Region, 65 miles from Berbera on Las Dureh road, 450 m, *Hemming* 1922 (K, FI); 2 miles from Garissa on tug on road to Sillil, *Glover & Gilliland* 883 (K, FI).

Frequently confused with *S. pedicellata*, to which it is undoubtedly closely related. It can be distinguished from that species by its usually narrowly divergent not divaricate branches, the pedicels which are completely recurved in fruit rather than having the distal portion only deflexed, and lastly by the relatively higher, wing-like ridges on the seeds. The differences in leaf shape used by earlier authors, elliptic-spathulate to linear-oblong in *S. pterosperma* versus usually narrowly linear in *S. pedicellata*, have proved inadequate for separation. Whilst there are basic differences in leaf shape, the ranges of dimensions of the leaves overlap and the shape of the leaves changes between young and old plants.

5. S. pedicellata (T. Anderson) Balfour in Trans. Royal Soc. Edinb. 31: 201 (1888). Fig. 2, Plate 2F, 3 A,B.

Syn.: *Anarrhinum pedicellatum* T. Anderson in Jour. Linn. Soc. London (Bot.), Suppl. 5: 26 (1861).

Antirrhinum apterum Vatke in Österr. Bot. Zeitschr. 26: 96 (1875).

Anarrhinum pedicellare Bentham in Bentham & Hooker, Gen. Pl. 2 (2): 434 (1876), sphalm.

Schweinfurthia pedicellaris (T. Anderson) Wettstein in Engler & Prantl, Natürl. Pflanzenfam. 4(3b): 60 (1891), sphalm.

S. aptera (Vatke) Hemsley & Skan ex Thistleton-Dyer, Fl. Trop. Afr. 4(2): 294 (1906).

S. pterosperma var. *angustifolia* Rothmaler in Feddes Repert. 52:32(1943).

[*Orontium arabicum* [Ehrenb. & Hempr. ex] Braun in Monatsber. königl. Preuss. Akad. Wiss. Berlin 1866: 872 (1867), in syn.]

Erect, subglabrous annual up to 75 cm, usually laxly branched above, the branches divaricate. *Leaves* 10–45 × 0.5–2.5(–6) mm, linear, the lowest oblong-elliptic, obtuse, the base gradually tapering into the petiole or subsessile, the margin somewhat thickened, occasionally revolute, somewhat succulent; petiole 1–5(–8) mm. *Inflorescence* very lax, with 6–30 flowers. Pedicels 10–17 mm, scarcely elongating in fruit; patent, the distal portion becoming deflexed. *Calyx-lobes* ovate-acute, somewhat scarious; adaxial lobe 3.5–5 × 1.3–2 mm; median lobes 2.5–3.5 × 1–1.5 mm; abaxial lobes 3–3.5 × 1–1.5 mm. *Corolla* 6–9 mm, whitish or pale lilac, the palate tinged with yellow. *Capsule* 4–6 mm; adaxial locule with 3–4 seeds. *Seeds* 1–1.5 mm, oblong to oblong-ovoid, truncate, cristate; ridges thin, rounded or somewhat acute, interstices with low secondary ridges or irregularly anastomosed tubercles; interstitial cells with minute rounded papillae, wax granules abundant.

Fl. 3–12. Arid sandy plains, wadis and depressions, rocky slopes, often by the coast. 0–1500 m.

Lectotype (selected here). [PDRY: S Yemen] Aden, low ground, 19 xii 1847, *J. D. Hooker* s.n. (K).

Selected specimens:

PDRY: S YEMEN. Mukalla, *Guichard* KG/HAD/354 (K); Aden, Goldmine Valley, *Lunt* 281 (BM).

SOCOTRA. W end of Hadibu plain, 12°38′ N 54°02′ E, 10 m, *Smith & Lavranos* 343 (K, FI).

SAUDI ARABIA. Valle wadi Djara in arenis prope aquam, ii 1825, *Ehrenberg & Hemprich* s.n. (type *Orontium arabicum* Ehrenb. & Hempr. ex Braun, nom. nud.).

EGYPT. Gebel Elba–n.v. (in Täckholm, 1974).

ETHIOPIA. *Salt* s.n. (BM).

SOMALIA. Senag plains, S of Berbera, *Bally* 7227 (K); Lasgori-Ahlgebirge (Laskhoreh Al hills), *Hildebrandt* 861 (type *Antirrhinum apterum*, BM); Damaleh, 11°04′ N, 48°16′ E, 1200 m, *Newbould* 876 (K).

TANZANIA. Amani, *Toms* 6 (K).

COMORO ISLANDS. viii 1825, *Humboldt* (K).

Many authors (Rothmaler, 1943; Cufodontis, 1963) have included *S. pedicellata* as a synonym or variety of *S. pterosperma*. Braun (1867) listed amongst his specimens of *S. pterosperma* gatherings undoubtedly referable to *S. pedicellata* (i.e. *Wichura* s.n., 1862; *Ehrenberg & Hemprich* s.n., ii 1825). The

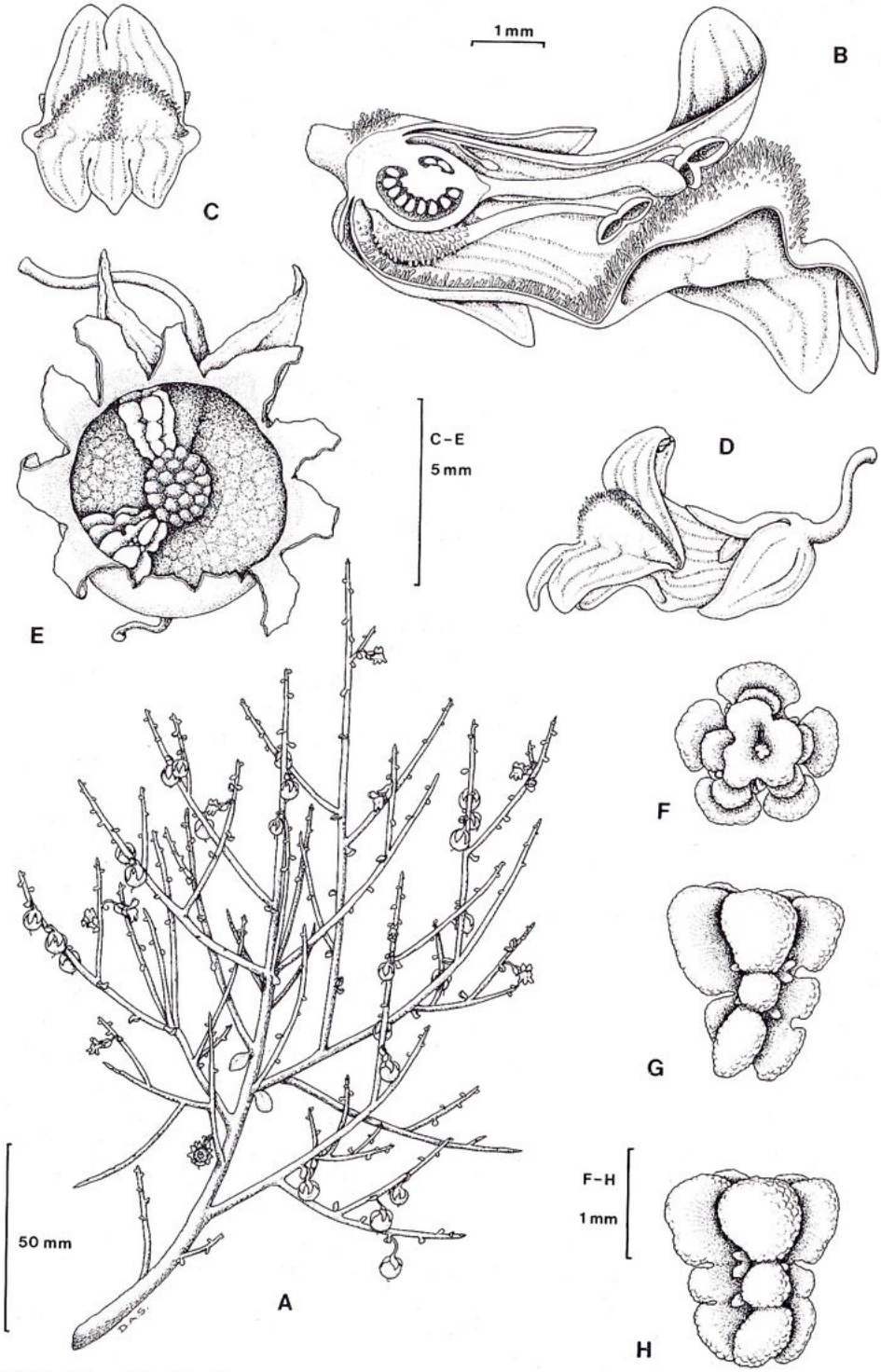


FIG. 4. *Schweinfurthia spinosa*: A, habit; B, half-flower; C, flower, front view; D, flower, side view; E, capsule; F, seed, basal view; G, seed, lateral view; H, seed, dorsal view.

two species can be distinguished by differences in habit, pedicel thickness and orientation in fruit, and the ridges of the seeds. *S. pedicellata* is a taller species with a wider branching angle than *S. pterosperma*. The pedicels are thinner and reflexed in fruit near the capsule, rather than being recurved as in *S. pterosperma*. *S. pedicellata* usually has thicker, more obtuse ridges on its seeds, although in Socotra seeds of this species resemble those of *S. pterosperma*. *S. pedicellata* has the more southern distribution of the two taxa. At present there is no evidence to indicate whether the distant outliers of this species, in Tanzania and the Comoro Islands, are remnants of an earlier, wider distribution or have arisen by chance long-distance dispersal. We have not seen the specimen from Jabal Elba in southern Egypt cited by Täckholm (1974), so cannot state if it is referable to *S. pedicellata* or the geographically closer *S. pterosperma*.

Amongst the specimens cited by Anderson (1861), the Hooker sheet collected in 1847 is the most complete and therefore we have selected this to serve as the lectotype.

6. S. spinosa Miller, Short & Sutton, **sp. nov.** Fig. 2, 4, Plate 3 C–F.

S. pedicellatae affinis, a qua ramis spinescentibus, foliis minutis, pedicellis brevibus et cristis seminum inflatis imprimis differt.

Herba perennis erecta glauca glabrescens ad 1 m alta; surculi juveniles pilibus brevibus albis crispis vestiti; caules lignescentes spinescentes divaricate ramosi. Folia 1.5–8.5 × 1.5–6.5 mm, spathulata vel orbicularia, apice obtusa mucronataque, basi attenuata, parum succulenta; petiolus 0.5–3 mm longus. Inflorescentia laxa pauciflora; pedicelli 2–7 mm longi, post anthesis vix elongati sed recurvescentes. Calycis lobi acuti margine anguste hyalini; lobus adaxialis 3–4 × 2–3 mm, late ovatus; lobi mediani 1.5–2 × 0.4–0.6 mm, lanceolati; lobi abaxiales 2.5–3 × 1–2.3 mm, ovati. Corolla 6–7 mm longa, luteola venis purpureis obscuris notata. Capsula 4.5–6 mm longa, loculo adaxiali 0–2-seminali. Semina 1.3–1.8 mm longa, oblongo-ovoidea vel subglobosa, irregulariter cristata cristis inflatis obtusis reticulatis; interstitia saepe tubercula acuta instructa, cellulis interstitialibus papilla minuta rotundata ferentibus; granula ceracea abundantia.

Erect, glaucous glabrescent perennial up to 1 m, the young shoots covered in short, white, crisped hairs, stems becoming woody, spinescent, branching divaricately. *Leaves* 1.5–8.5 × 1.5–6.5 mm, spathulate to orbicular, obtuse, mucronate, attenuate, somewhat succulent; petiole 0.5–3 mm. *Inflorescence* lax, with 1–5 flowers. Pedicels 2–7 mm, scarcely elongating in fruit, becoming recurved. *Calyx-lobes* acute, the margin narrowly hyaline; adaxial lobe 3–4 × 2–3 mm, broadly ovate; median lobes 1.5–2 × 0.4–0.6 mm, lanceolate; abaxial lobes 2.5–3 × 1–2.3 mm, ovate. *Corolla* 6–7 mm, pale yellow with dull purple veins. *Capsule* 4.5–6 mm, glabrous; adaxial locule with 0–2 seeds. *Seeds* 1.3–1.8 mm, oblong-ovoid to subglobose, irregularly cristate; ridges inflated, obtuse, the interstices often with acute tubercles; interstitial cells with minute rounded papillae, wax granules abundant.

Fl. 9–10. Arid gravelly plain and wadi beds in and to the north of the Frankincense zone. 500–600 m.

Type. Sultanate of Oman. Dhofar, Jabal Qara, 20 km N of Ravens Roost on main Thamrait to Salalah road, bare rocky slopes N of Frankincense zone, 600 m, 13 x 1979, *Miller* 2726 (holo. E, iso. BM).

SULTANATE OF OMAN. Dhofar, Ayun Pools, N Jabal Qara, dry rocky slopes, *Boswellia* zone, 500 m, *Miller* 2243 (E).

A new species represented by two collections from the Dhofar region of Oman. It is easily recognized by the shrubby habit, spinescent branches (fig. 3) and the seeds with broad, inflated ridges (plate 3C). In spite of its spinescent branches the growth habit of *S. spinosa* is very similar to that of *S. pedicellata*. *S. spinosa* resembles *S. imbricata* and *S. papilonacea* in having relatively broad leaves and broadly ridged seeds, although the minute papillae of the seeds (plate 3D) resemble those of *S. pedicellata* or *S. pterosperma* (plate 2E). It grows in the region to the north (inland) of the main area affected by the rains of the SW Monsoon. There is a fairly rich flora in this region dominated by scattered trees of *Boswellia sacra* (Frankincense).

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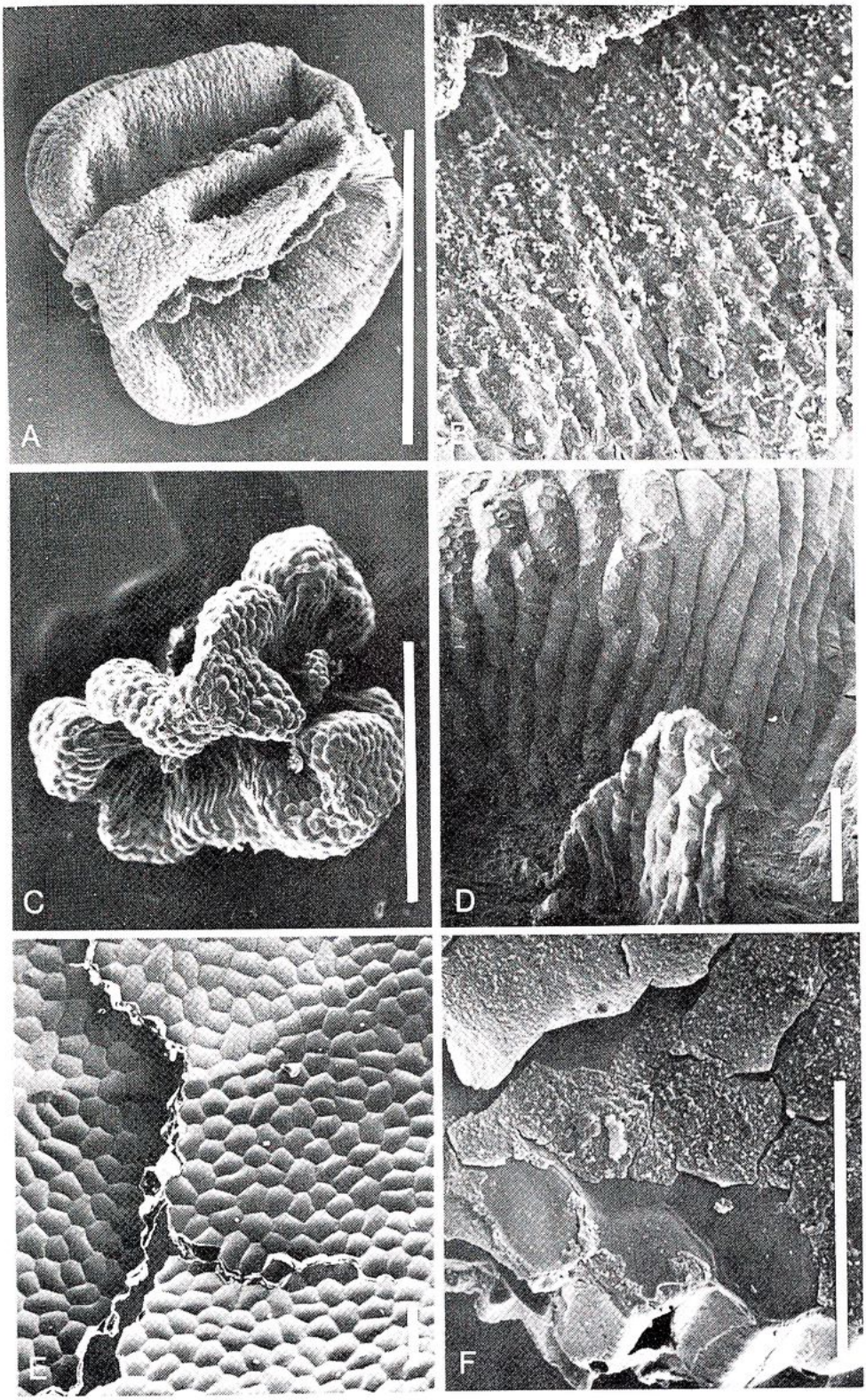
PLATE 3. Scanning electron micrographs of *Schweinfurthia* seeds and capsules. A,B, *S. pedicellata*: A, whole seed from type locality specimen showing relatively low, obtuse ridges, scale = 1 mm; B, side of ridge showing dense waxy covering, scale = 0.1 mm. C–F, *S. spinosa*: C, whole seed showing inflated ridges, scale = 1 mm; D, base of ridge and interstitial region showing minute papillae, scale = 0.1 mm; E, inside of capsule wall showing lack of cellular differentiation and irregular dehiscence, scale = 0.1 mm; F, edge of capsule valve showing damaged cells, scale = 0.1 mm.


A
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D
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