THE RELATIONSHIPS OF *WHITESLOANEA CRASSA*

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It is shown that the monotypic genus *Whitesloanea* (Asclepiadaceae, *Stapelieae*) is closely allied to *Duvalia* and *Huernia* but nevertheless should remain separate from them. The basionym, *Caralluma crassa* N.E. Br., is lectotypified.

Keywords. Asclepiadaceae, Somalia, *Stapelieae*, *Whitesloanea*.

INTRODUCTION

Whitesloanea crassa (N.E. Br.) Chiov. is one of the rarest of the stapeliads. It was discovered by Ralph E. Drake-Brockman in northern Somalia during or just before 1914. The next record is that of Bally (1959). Bally did not manage to locate plants in the wild. His information was obtained from plants that he cultivated, which had been collected by Roy Tribe in northern Somalia in November 1957. Most recently, it was collected in eastern Somalia (Lavranos, 1986). From these recent collections, some plants have been brought into cultivation and, from these, material has become available in some specialist collections.

Brown (1935) described this species as *Caralluma crassa*. The description was compiled and a drawing made when the plant sent by Drake-Brockman in 1914 eventually flowered in 1919. However, it was not published until 1935, somewhat after Brown's death, when J. Hutchinson sent the description and figure to the *Gardener's Chronicle*. White & Sloane (1937) remarked that the flowers 'with their large, campanulate corolla-tube, recall those of *Caralluma speciosa* . . . but they grow singly or in succession, and not in terminal umbels. Their unique character is found in the stipitate inner corona'. Apart from this remark, there is no suggestion as to what might be its closest ally. White & Sloane separated it from both *Caralluma* and *Stapelia* on the nature of the corona, deciding to place it in a new genus *Drakebrockmania*. As pointed out by Chiovenda (1937), this name is illegitimate, being a later homonym of *Drakebrockmania* Stapf (Poaceae) and so he created a new name *Whitesloanea* Chiov. for it. Chiovenda (1937) described another species of *Whitesloanea*, *W. migiurtina* Chiov., but this is now *Pseudolithos migiurtinus* (Chiov.) P.R.O. Bally (Bruyns, 1990) and is not closely allied to *W. crassa*.

Now that material of this species has become available, it has been possible to examine living plants and flowers. This has enabled clarification of its systematic position within the *Stapelieae* which, until now, has remained uncertain (Eggli, 1994).

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CHARACTER ASSESSMENT

Plant

Gross morphology. In *Whitesloanea* the whole plant usually consists of a single, thick, quadrangular stem narrowing very much to the base. The stem is glabrous, pale grey-green (almost ivory-coloured) to pale brownish, speckled faintly with purple-red, erect, up to 200 × 55mm and relatively hard. The tubercles on the stem are arranged into four continuous wings up the sides of the stem and the area between these four wings becomes somewhat convex if the plant is turgid. Each tubercle is a laterally flattened structure with a broadened, bifid upper end into which the base of the next tubercle fits (Fig. 1A). Leaves are absent and there are no stipules.

Micromorphology of the epidermis (Fig. 1). The surface is made up of small, isodiametric cells whose outer walls are almost all raised into a low, rounded papilla shorter than its basal diameter. Scattered cells are raised above their surroundings. Away from the tubercle the surface becomes smoother. Stomata are sunken into pits which are sometimes remarkably deep but may also be rather shallow and they are fewest along the outer edge of the tubercle. The surface is sometimes somewhat crevassed.

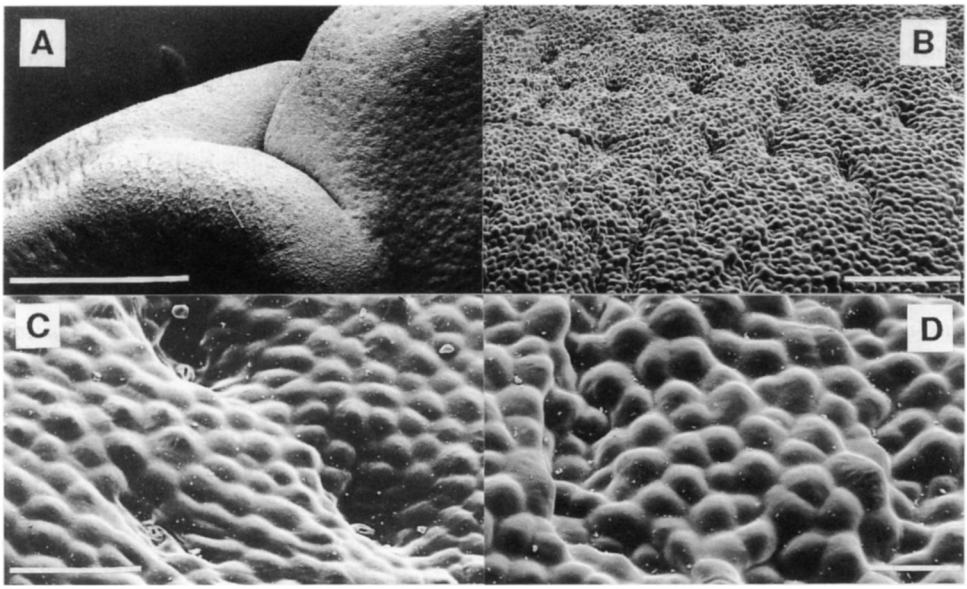

FIG. 1. SEM views of stem/leaf epidermis of *Whitesloanea crassa*: A, v-shaped apex of tubercle with broad base of next one above; B, papillate surface of tubercle with some crevices and deep pits for stomata; C, stomata in pits on tubercle; D, crevices and papillae on outer walls of epidermal cells of tubercle. Scale bars (approx.): A, 2mm; B, 250μm; C, 100μm; D, 50μm.

Flowers

Inflorescence. In *Whitesloanea* the primary stem bears flowers. Inflorescences develop near the base of the stem, often in positions slightly hidden by the bulk of the plant. Each inflorescence arises exactly out of the tiny gap present at the top of the broadened bifid upper end of a tubercle. There are usually several inflorescences arranged in a vertical series at the apices of several successive tubercles. The position of the inflorescence seems to be axillary. However, this would be very unusual indeed in the *Stapelieae* and it is more likely that it is terminal but has been forced into the apparently axillary position, as is also the case in some species of *Caralluma*. The paucity of material has so far precluded an anatomical investigation to clarify this aspect.

Each inflorescence develops a small peduncle which persists for several seasons. There are several, very small, concave-deltoid bracts on each peduncle which are devoid of stipules. On each peduncle flowers develop in gradual succession. The pedicels are spreading to ascending and are extremely variable in length even on one

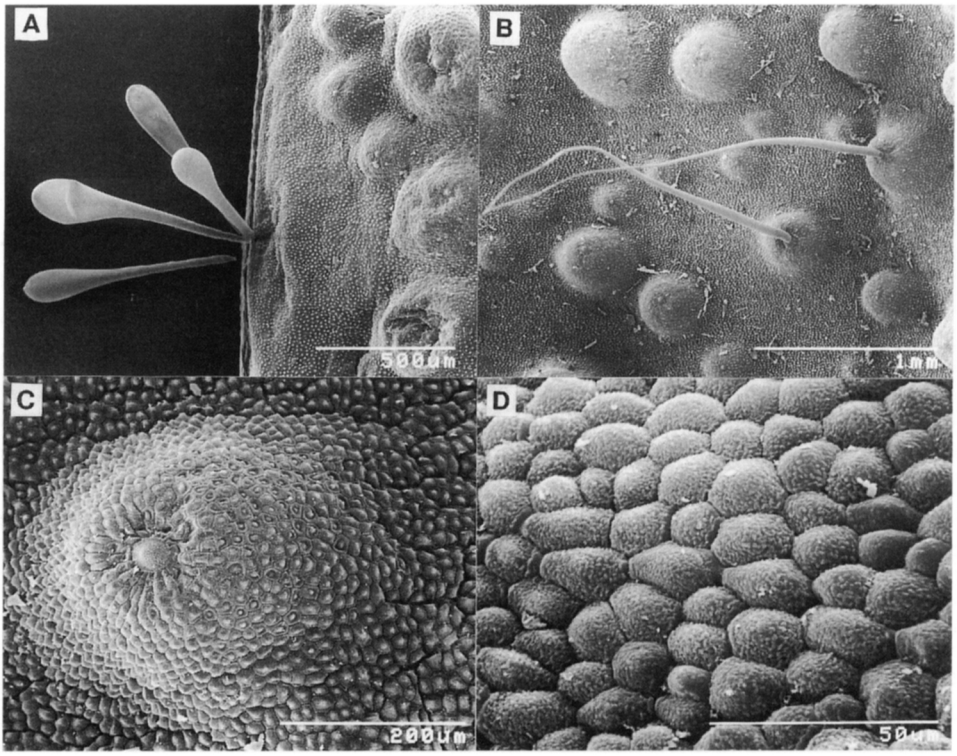

FIG. 2. SEM views of inner surface of corolla: A, edge of corolla lobe with cilia; B, papillae on inner surface of corolla, some with a long apical seta, others without; C, individual papilla with apical seta reduced to a bump; D, basal cells of inner surface of corolla.

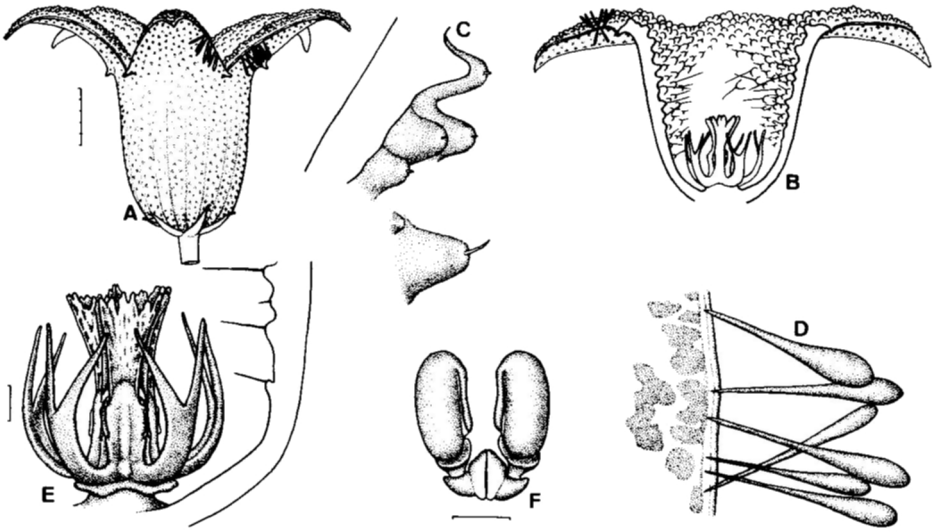

FIG. 3. *Whitesloanea crassa*: A, side view of flower; B, flower dissected; C, papillae taken from base of tube; D, cilia near base of corolla lobes along margin; E, side view of gynostegium; F, pollinarium. Scale bars: A, B, 5mm; C, D, 0.5mm (at F); E, 1mm; F, 0.25mm.

plant: their length depends on how hidden the peduncle is, with those on the most buried peduncles up to twice as long as those on the upper, exposed peduncles.

Corolla (Figs 2, 3). The corolla is about 30mm long with 10–15mm of this taken up by a deep, cylindrical tube. The lobes are deltoid and spread from the mouth of the tube. The exterior of the corolla is glabrous, finely spotted with red-pink, with slightly raised, longitudinal veins becoming more prominent towards the base. The entire inner surface of the flower is densely covered (except in the base around the gynostegium) with obtuse, columnar papillae each of which has a spreading to ascending, apical seta. These setae are of very variable length, reaching a maximum of up to 4mm at about the middle of the tube, decreasing both towards the base and towards the mouth and onto the lobes, where they are hardly visible. Conspicuous maroon cilia line the margins near the base of the corolla lobes. These are initially clavate but their contents rapidly evaporate and they soon become flattened.

The basal epidermal cells (Fig. 2D) are densely packed and more or less isodiametric with raised, rounded, outer walls.

Gynostegium. Perhaps the most remarkable feature of the flower in this species is its extraordinary gynostegium. In its early stages (Fig. 4A) it is unremarkable: early on the stamens are relatively well developed, each consisting of an anther with traces of where the pollen is developing already visible and a short, broad base as long as the fertile part; the lower margins are already fashioned into spreading wings which later form the guide rails. The inner corona is visible already as a small outgrowth

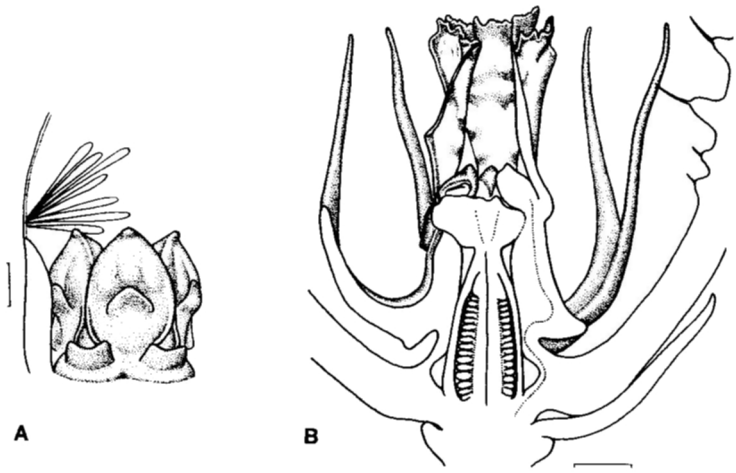

FIG. 4. *Whitesloanea crassa*: A, side view of gynostegium in bud 4mm long (cilia at base of lobes already well developed); B, half-flower. Scale bars: A, 0.5mm; B, 1mm.

on the back of the anther at the base of the fertile part (just above the top of the guide rails) and the outer corona is present (in fact already slightly more advanced in its development) just beneath the guide rails on the staminal tube.

The half-flower (Fig. 4B) and sketches of the whole gynostegium (Fig. 3E) show a very different structure at maturity. It is seated on a short stipe and immediately above this is a short skirt encircling the column. The half-flower shows that this arises on the dorsal surface of the outer corona near its base. The outer corona-lobes are initially horizontal, then rise up more or less to form a cage around the centre of the gynostegium. By maturity the staminal tube has elongated considerably along with the ovaries, keeping the guide rails alongside the style-head, and the anthers have become more horizontal on top of the style-head. The guide rails have a distinctly flared base and an inner rail (Kunze, 1982) is also clearly present. There is no nectarial orifice or cavity. The inner corona-lobes have also elongated massively into a very unusual shape: from a base as broad as the anthers, they expand to their very deeply notched apex.

Pollinarium (Figs 3F, 5). The pollinarium consists of a squat, dark brown corpusculum, very slightly longer than broad with short, lateral wings, to the rear of which the caudicles are attached. The caudicle begins from a narrow base, widening to a broad, spathulate apex. The upper, thin part of this broad area is fused to the underside of the pollinium and just below the pollinium it has a noticeably thickened ridge. The pollinium is long and rectangularly elliptical with germinating zone exactly along its outer edge: when inserted in the guide rail the pollinium projects out along a radius of the flower.

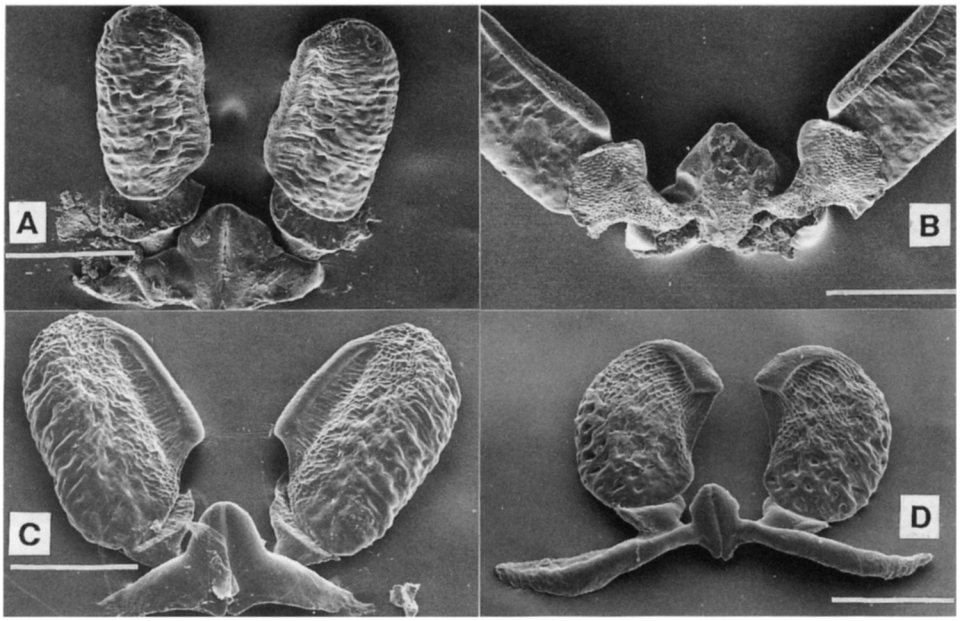

FIG. 5. SEM views of pollinaria of *Whitesloanea* and some allied genera. A, B, *W. crassa*: A, view from above of whole pollinarium with corpusculum in flattened position; B, view of rear of pollinarium showing broad pads joining caudicle to pollinium. C, *Huernia zebrina* (Gt Karas Mtns, Namibia, *PVB* 3533 (BOL)), view from above of whole pollinarium, corpusculum in flattened position. D, *Duvalia maculata* (NE Fraserburg, *PVB* 4788b (BOL)), view from above of whole pollinarium, corpusculum in ±flattened position. Scale bars (approx.): all 200μm.

Follicles and seed

The follicles are paired, erect, with horns diverging from one another at about 60°. The horns are thick, fusiform and glabrous, longitudinally flecked with purple on a pale greenish background.

Seeds are ±4mm diam., very slightly longer than broad and are ±smooth but with a puffy, much inflated margin.

CONCLUSIONS

One fact that emerges from the above examination is that in *Whitesloanea* there is a difference in the earlier stages of the gynostegium from that usually found in the *Stapelieae* (as illustrated in Kunze, 1982, Abb. 5; Bruyns, 1993, fig. 11). In the cases illustrated there the meristem of the inner corona lies a little higher than the outer. However, as the inner lobes begin to develop they become joined dorsally towards the base to the outer series and remain that way throughout their development. This results in the development of a somewhat cupular structure (whose outer wall is formed by the outer corona-lobes fused to the lower dorsal parts of the inner corona-

lobes) and from the inside of this the inner corona-lobes rise. This structure, with various modifications, is found throughout most of the *Stapelieae*. In *Whitesloanea* the two series of corona-lobes develop separately from the beginning and considerable elongation of the staminal tube during the ontogeny of the flower leads to their being even further separated at anthesis. The development of the corona as two quite separate series, whose separation increases as the flower matures, is found also in the genera *Duvalia* Haw. and *Huernia* R. Br. An assessment of character states shows that these two genera share (in the case of *Duvalia*, the sharing is often only partial) a suite of character states with *Whitesloanea*:

1. Leaves absent (present in many species of *Duvalia*).

2. Stipules absent (present in many species of *Duvalia*).

3. Inflorescences borne near base of stems, flowers developing successively from a lengthening peduncle.

4. Corolla with a deep tube, with longitudinal veins on outer surface (both characters absent in *Duvalia*).

5. Inner surface of corolla with seta-tipped papillae (most *Huernia* species, not in *Duvalia*).

6. Outer and inner corona not at all fused, outer corona at least initially horizontal, arising much lower on column than inner.

7. Outer and inner guide rails present and clearly visible in longitudinal section.

8. Pollinia longer than broad (narrowly rectangularly elliptical: much less narrow in *Duvalia*), with germinating zone exactly down outer edge.

9. Corpusculum short and broad with short wings (wings long in *Duvalia*), caudicle with narrow join to wing, widening above this to a spathulate zone onto which the pollinium is fused, with the lower edge of this spathula raised into a distinctly thickened ridge just below pollinium.

Since there are so many characters involved, it seems unlikely that the unusual coronal development that they share is a parallelism. In addition, *Whitesloanea* does not share many character states with any other group of species and thus it may be assumed to be closely allied to *Huernia*, with *Duvalia* also allied but slightly less closely.

From *Huernia*, *W. crassa* is separated by its single, thick, hard stem; by the nature of the tubercles (not attenuated into a point, bifid towards the top); by the inflorescences arising between adjacent tubercles along the angles and the deltoid rather than attenuated bracts; by the longer stipe holding the gynostegium well away from the base of the corolla and by the very different inner and outer corona-lobes (outer ascending, deeply bifid; inner flat and widening right to apex). In all *Huernia* (and *Duvalia*) flowers there is a nectarial cavity bounded on the outside by a thickening

of the outer corona-lobe below the mouth of the guide rail (this cavity is lacking in *Whitesloanea*). In both *Huernia* and *Duvalia* the skirt around the base of the column is lacking. There does not seem to be any reason, therefore, to question the generic status of *Whitesloanea crassa*.

The morphology of the pollinaria in the three genera *Duvalia*, *Huernia* and *Whitesloanea* is strikingly similar (character states 7, 8) and is partly shared with *Duvaliandra* Gilbert. As usual, there are slight divergences in *Duvalia* (long wings on corpusculum, pollinia less narrow) but in comparison to pollinaria generally in the *Stapelieae*, those here are very characteristic. The unusual orientation of the germinating zone found here is common in genera with small pollinaria (e.g. many species of *Caralluma* R. Br., *Pectinaria* Haw., *Quaqua* N.E. Br., *Rhytidocaulon* P.R.O. Bally) but is absent in all other genera with large pollinaria. In such cases the germinating zone, while starting at the top of the pollinium on the outer edge, lower down becomes folded up towards the upper surface of the pollinium. This allows for the insertion of large pollinia in the guide rail even when the distance between the guide rail and the outer corona is smaller than the width of the pollinium, for the pollinium is no longer inserted along a radius of the flower (for which there isn't room) but nearly perpendicular to it.

It seems very likely, therefore, that the shape of the pollinium in the genera *Duvalia*, *Huernia* and *Whitesloanea* is correlated with the fact that there is no restriction of the space between the outer corona-lobes and the guide rails, this in turn being largely a consequence of the elongation of the staminal tube during the gynostegial ontogeny.

While it is clear that the reduced growth form, lack of leaves and flowering from the primary stem are all advanced characters in *Whitesloanea*, it is not clear whether the coronal structure and the correlated shape of the pollinium of *Duvalia*, *Huernia* and *Whitesloanea* is primitive or advanced. In this regard it might be noted that:

1. *Duvalia*, *Huernia* and *Whitesloanea* are absent from India and Madagascar, which are now assumed to have been well separated from Africa by 118Ma (Scotese et al., 1988).

2. All *Stapelieae* found in Madagascar and India lack this kind of corona.

These facts might indicate that plants with the *Huernia*-type of corona came into existence only after these geological events and have subsequently achieved a wide distribution in Africa and Arabia. It is possible, therefore, that these character states might be derived.

TAXONOMY

Whitesloanea Chiov., Malpighia 34: 541 (1937), Bally (1959, 1960), Bally, Horwood & Lavranos (1975), Lavranos (1986). Type: *W. crassa* (N.E. Br.) Chiov.
Syn.: *Drakebrockmania* White & Sloane, Stap. ed. 2, 1: 401 (1937). Type: as above.

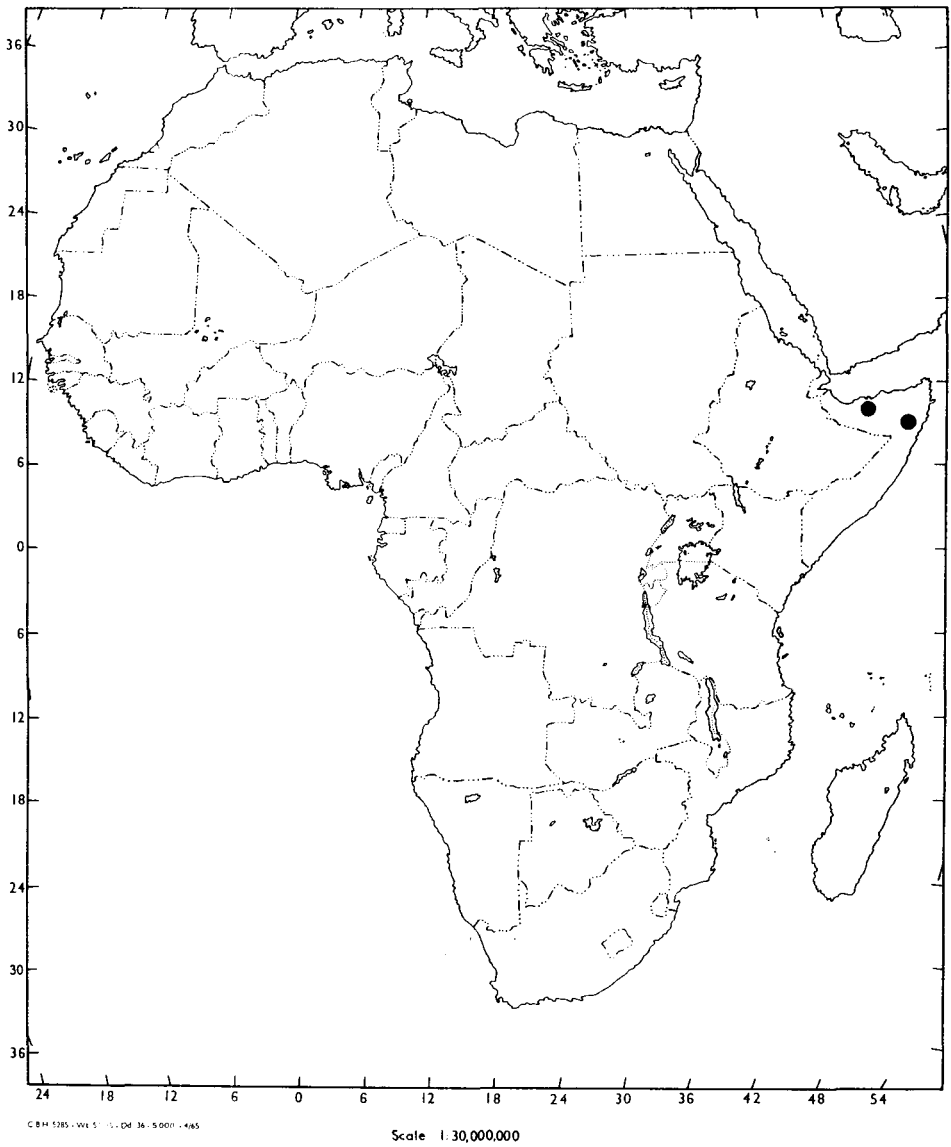

FIG. 6. Known distribution of *Whitesloanea crassa.*

Whitesloanea crassa (N.E. Br.) Chiov., Malpighia 34: 541 (1937).
Syn.: *Caralluma crassa* N.E. Br., Gard. Chron. Ser. 3, 98: 6 (1935). Type: Somalia, Odweina, *Drake-Brockman* 1132 (Fig. only K! This is here designated lectotype).
Drakebrockmania crassa (N.E. Br.) White & Sloane, Stap. ed. 2, 1: 402 (1937).

Plant a much reduced succulent consisting usually of only a single stem. *Stem* erect, squat, 4-angled, 40–200 × 50–55mm, glabrous, pale grey-green or brownish often

speckled faintly with purple-red, tubercles laterally flattened, arranged vertically into 4 wings, leaves absent. *Flowers* developing successively from small peduncles 2–17mm long near base of stem, with numerous small shortly deltoid bracts <3mm long. *Pedicels* 5–15 × ±1.5mm, spreading to ascending, glabrous. *Sepals* 4–5 × 1mm, acuminate. *Corolla* ±20 × 30–33mm, exterior glabrous and finely spotted with red-pink, interior spotted with red on cream and densely covered with obtuse columnar papillae each tipped with an apical seta; *tube* 10–15 × 9–10mm, campanulate; *lobes* 12–14 × 5–8mm, ovate to ovate-lanceolate or deltoid, margins ciliate towards base. *Gynostegium* with a short basal stipe, consisting of two series, the inner arising much above the outer, ±6.5 × 6.0mm; *outer corona-lobes* arising near base of gynostegium, initially spreading then erect and incurved, bifid to the middle into slender slightly divergent lobules, maroon tending to pink at base with narrow ± descending continuum skirt arising dorsally near base; *inner corona-lobes* initially adpressed to anthers then erect and exceeding outer lobes, flattened above with edges folded outwards, widening from base to broad deeply notched truncate apex, apex lined with maroon, rest speckled with maroon on pink background.

Material examined. Somalia: near Sheikh, 17 xi 57, *Tribe* E244 *sub Bally* B 11487 (ZSS); between Garowa and Gardo, x 1985, *Lavranos* (BOL).

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