

## THE GENERIC POSITION OF *CARALLUMA* *DODSONIANA*

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The generic position of *Caralluma dodsoniana* Lavranos (Asclepiadaceae) is investigated. It is concluded that a monotypic genus to accommodate it is unnecessary and that it should be incorporated into the genus *Pseudolithos* P. R. O. Bally as *P. dodsonianus* (Lavranos) Bruyns & Meve.

### INTRODUCTION

The generic position of *Caralluma dodsoniana* Lavranos has always been somewhat controversial. Lavranos (1971) proposed that it 'appears to belong to the same group as *Caralluma europaea* but differs from all its relatives by its rugose stems . . . reminiscent . . . of *Pseudolithos* which grows in the same general area'. Gilbert (1990) suggested that it is 'a relict with no close affinities to existing species or even genera' and that it deserves to be placed in a monotypic genus. Bruyns (1990) suggested that it might be a hybrid between a species of *Pseudolithos* P. R. O. Bally and *Echidnopsis* Hook. f. As pointed out by Gilbert (1990), this hypothesis would explain many of its unusual features but it utterly fails to explain the fact that a taxon very similar to *C. dodsoniana* has recently been found in Oman, southern Arabia, where *Pseudolithos* is not known to occur.

Plowes (1993) acted on Gilbert's suggestion and moved *C. dodsoniana* to a new genus, *Anomalluma* Plowes. Here he mentions that it 'differs from all other genera in the Asclepiadaceae by the combination of cymose peduncles, short branched stems that are irregularly rugose and follicles that are widely divergent in a straight line or even directed downwards'. Plowes also mentions that 'there are certain stem features which are reminiscent of *Pseudolithos*'. Nevertheless he felt that 'these do not appear to be sufficient to justify the incorporation of this species into an expanded' *Pseudolithos*.

This paper is an attempt to clarify the position. We list firstly the various characters shared by *C. dodsoniana* and *Pseudolithos*; those characters which are partly shared by the two are then given and finally those characters which are found in only one are enumerated and discussed. We also give some indication of the occurrence of these characters elsewhere in the Stapelieae. The evidence that we put forward shows that many of the arguments presented by Plowes in support of his new genus *Anomalluma* are not consistent with the facts. We show that the creation of a monotypic genus is unnecessary and that *Caralluma dodsoniana* should be incorporated

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into *Pseudolithos* P. R. O. Bally. *Pseudolithos* then contains the five species *P. caput-viperae* Lavranos, *P. cubiformis* (P. R. O. Bally) P. R. O. Bally, *P. horwoodii* P. R. O. Bally & Lavranos, *P. migiurtinus* (Chiov.) P. R. O. Bally and *P. dodsonianus* (Lavranos) Bruyns & Meve.

## MATERIALS AND METHODS

Material, originating from different sources, is under cultivation in Cape Town (PB) or the Botanic Garden, Münster University (UM).

For morphological investigations fresh material and specimens fixed in alcohol were studied under the dissecting microscope. For SEM investigations samples were dehydrated, critical point dried, sputtered with gold and scanned with a Hitachi S530 at 10–20kV.

For chromosome counts, mitotic preparations were made from tips of adventitious roots using 0.002M 8-hydroxyquinoline solution (4 hours) as pretreatment and Carnoy (24 hours) as fixative. Squash preparations for microscopic investigations were done from carmine-stained (24 hours) root tips (Snow, 1963).

## RESULTS

### A. Characters shared with *Pseudolithos*

1. *Gross stem morphology.* The stems in the four species of *Pseudolithos* and *C. dodsoniana* are 4-angled with larger tubercles along the angles and the intervening surface covered with smaller convex polygons tightly pressed against one another (Fig. 1A, C).

Macroscopic rugosities on the stems of stapeliads are comparatively rare. They are found in *Rhytidocaulon* P. R. O. Bally (unpublished data), *Echidnopsis leachii* Lavranos (Bruyns, 1988) and some species of *Stapelianthus* Choux (unpublished data). In the case of *Rhytidocaulon* they take the form of longitudinal rounded ridges separated by 'valleys', while in *E. leachii* and *Stapelianthus* one finds  $\pm$ isodiametric 'hills' separated by troughs. In all of these the rugosities could be termed 'bullate' (i.e. blistered) and they bear no resemblance to those in the taxa under discussion here.

2. *Stem epidermis.* The surface of the stem of both *P. caput-viperae* Lavranos and *C. dodsoniana* is made up of isodiametric cells with conspicuously convex (dome-shaped) outer walls (Fig. 1B, D). Each of these outer walls is often raised into a central papilla in *C. dodsoniana*, but rather less frequently so in *Pseudolithos*.

Most stapeliad stems are microscopically sculptured by variously shaped outer walls of the epidermal cells and similar outer walls to those here are found in such otherwise unrelated genera as *Lavrana* Plowes (Bruyns, 1993), *Pectinaria* Haw. and many species of *Quaqua* N. E. Br. (unpublished data). The important point here is that microscopically the surfaces in *C. dodsoniana* and *Pseudolithos* are very similar.

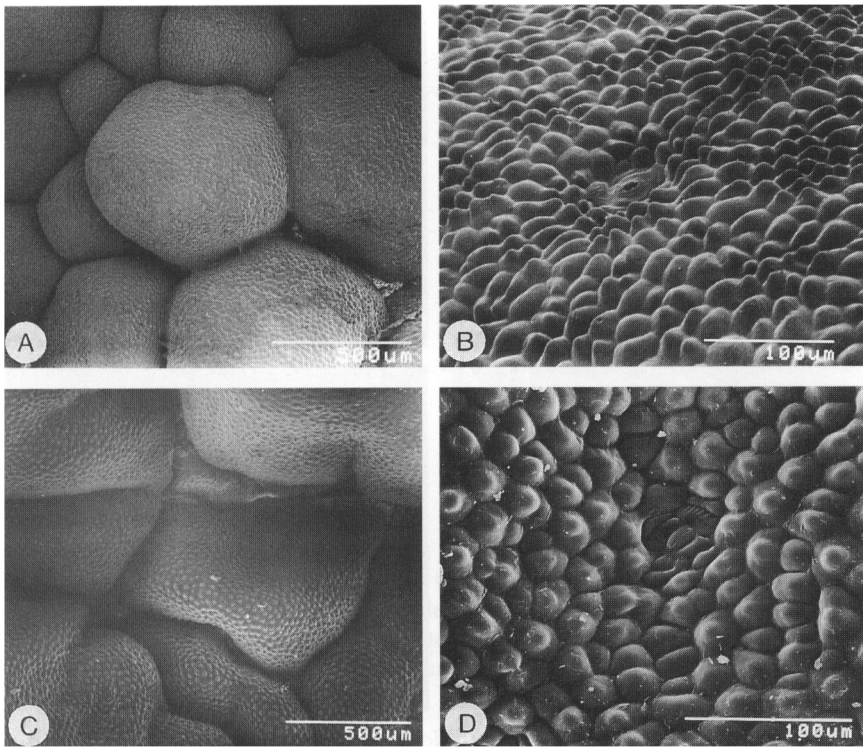


FIG. 1. SEM views of epidermis of stem. A, C, convex polygons covering stem between angles; B, D, epidermal patterns. A, B, *Pseudolithos caput-viperae* (ex hort. de Boer); C, D, *Pseudolithos dodsonianus* (ex hort. Bosma).

They bear, for example, no resemblance at all to that in *Rhytidocaulon*, where the epidermal cells have  $\pm$  flat outer walls and there are short, multicellular hairs scattered over the surface.

3. *Stipules*. In the species under consideration there is no trace of stipules.

Meve & Albers (1990) have tabulated the occurrence of stipular rudiments in the Stapelieae. Once more the situation here is found in several groups of species (e.g. one section of *Tridentea* Haw. (Meve & Albers, 1990), *Lavrania* (Bruyns, 1993)) and is quite different to the position in *Rhytidocaulon* where glandular stipules are present (unpublished data).

4. *Corolla epidermis*. SEM investigations of the corolla epidermis show a pattern of rather loose, though regularly oriented cells with elongated dome-shaped outer walls and granulate apices (Fig. 2).

Various kinds of indumentum of the corolla (such as cilia, trichomes or papillae) occur randomly in many stapeliad genera (e.g. *Orbea* Haw. (Leach, 1978), *Piarranthus* R. Br. (Meve, 1994)) and cilia and trichomes occur in three of the four species of *Pseudolithos* (Bruyns, 1990). If one disregards these, the overall similarity in the

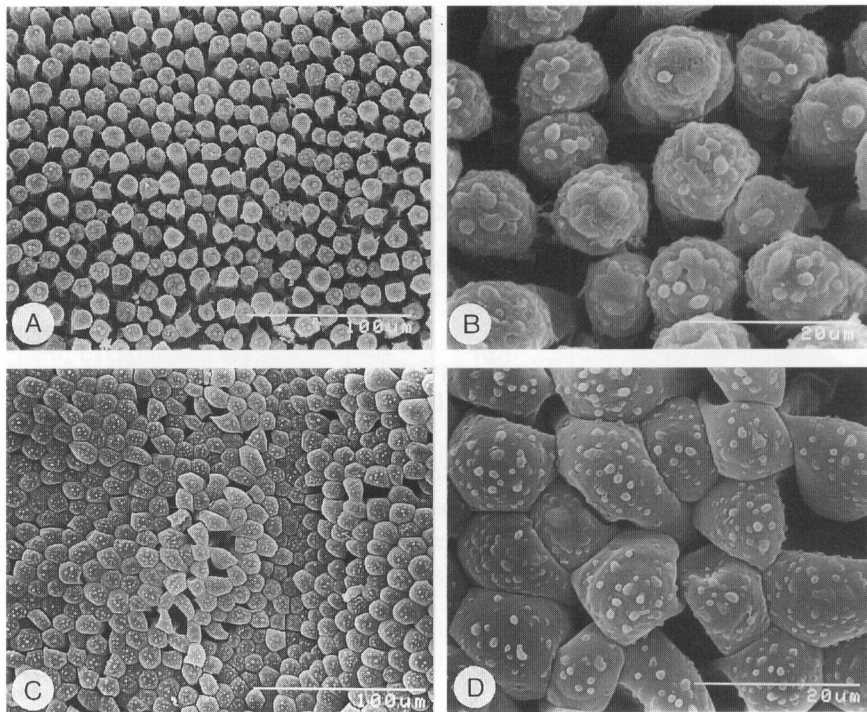


FIG. 2. SEM views of epidermis of corolla. A, C, epidermal patterns; B, D, granulate apices of epidermal cells. A, B, *Pseudolithos migiurtinus* (ex hort. de Boer); C, D, *Pseudolithos dodsonianus* (ex hort. Bosma; photograph by K. Seidler).

basal epidermal pattern of the corolla of both species investigated (*P. migiurtinus* and *C. dodsoniana*) is of considerable significance.

5. *Flower size and corolla/corona ratio, corona shape.* In comparison to the size of their vegetative parts, all species under consideration possess rather small flowers. However, in contrast, the diameter of their coronas is very large in proportion to the diameter of the corolla.

Moreover, the general structure of the corona of *C. dodsoniana* and that of *P. cubiformis* P. R. O. Bally and *P. migiurtinus* (Chiov.) P. R. O. Bally is very similar: in particular the inner corona lobes have a much expanded dorsal part reaching almost to the extremities of the outer lobes (this much expanded part is clearly visible in Fig. 3A as a thin, membranous area (hatched)). The coronas in *P. caput-viperae* and *P. horwoodii* are rather different.

6. *Pollinaria.* In the four species of *Pseudolithos* and *C. dodsoniana* the pollinaria have a proportionately large corpusculum and pollinia usually wider towards the apex than the base (Fig. 4G and Bruyns, 1990).

The pollinia are comparatively small, similar in size to those of *Caralluma* R. Br. subg. *Caralluma* (Gilbert, 1990), *Echidnopsis* (Bruyns, 1988) and *Rhytidocaulon*

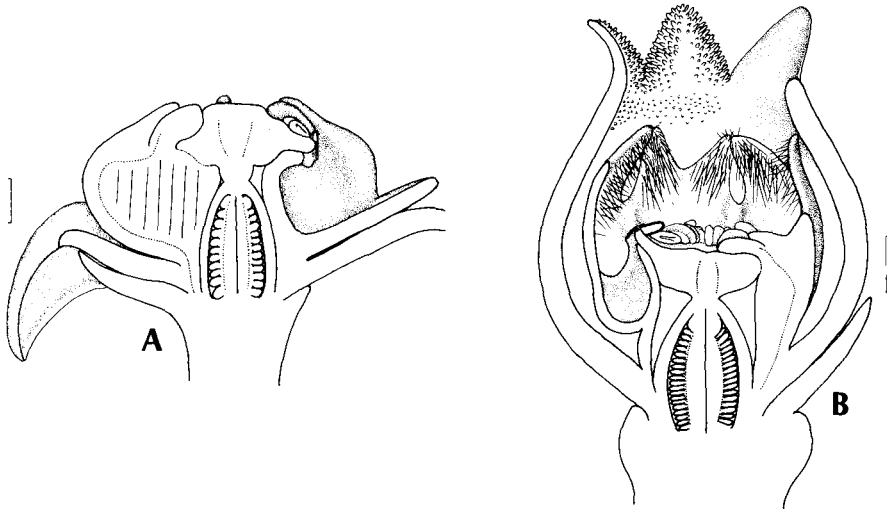


FIG. 3. Half flowers showing differences in style-head, orientation of anthers, guide rails and corpuscula. A, *Pseudolithos dodsonianus*, Oman, Miller 9376 (E). The vascular trace of the anther (dotted line on left) is much expanded laterally, dragging the underlying tissue with it and leaving a thin membranous area (hatched). B, *Pseudolithos caput-viperae*, ex hort. Heunis. (Both drawn from live material, January 1994. Scales in both cases are 0.5mm.)

(unpublished data). In *Echidnopsis* the pollinia are almost always circular in outline, in *Rhytidocaulon* they are much broader than long. In *Caralluma* subg. *Caralluma* they are mostly broader than long but occasionally longer than broad (*C. sinaica* (Decne.) Benth. & Hook. f., *C. peschii* Nel) and in *C. sinaica* they are distinctly broader towards the base. In all, the corpusculum is much smaller than it is here and the pollinia do not narrow towards the base.

7. *Follicles*. It is well known that in *C. dodsoniana* the follicles usually diverge from one another at 180° or more (Gilbert, 1990: 30). The same is recorded in several *Pseudolithos* (Bally et al., 1975: fig. 18, p. 89 under *P. caput-viperae*). Such widely spreading follicles are rare (most diverge at 30–60°) and are otherwise known only in a few species of *Lavrania* (Bruyns, 1993) and occasionally in *Caralluma*, *Stapelianthus* and *Tridentea* (unpublished data).

8. *Chromosomes*. Somatic chromosomes of *C. dodsoniana*, *P. caput-viperae* and *P. migiurtinus* (Reese, 1971 and own investigations) were counted. All three were found to be diploid with  $2n=22$ .

It has been found that around 90% of stapeliad species investigated are diploids (Albers & Meve, 1991) and therefore the situation here is not of great significance. However, in all three the sizes of the chromosomes were fairly homogeneous, with the total length for the single karyotype measuring 22–26µm. This fact is more significant because stapeliad karyotype lengths mostly do not vary significantly in groups of closely related species (unpublished data).

*B. Characters partly common to C. dodsoniana and Pseudolithos*

1. *Habit.* In *C. dodsoniana* the plant is tufted with sometimes more than 40 quite loosely packed stems which may be as long as 150mm. In *P. caput-viperae* the stems may be up to 12 per plant and 40mm long. They are rather thicker and quite tightly packed. In *P. cubiformis*, *P. horwoodii* and *P. migiurtinus* the stem is solitary and  $\pm$  cubiform.

2. *Leaves.* *C. dodsoniana* develops a well-differentiated leaf rudiment from the furrowed upper surface of the tubercle (Fig. 4A). In *P. caput-viperae* exactly the same tubercle morphology can be observed in young stages of growth. In *P. migiurtinus* the leaves are rarely present and then in an even more reduced form. The furrow on the upper surface of the leaf is often still present.

*C. Characters not shared*

1. *Inflorescence morphology.* In *C. dodsoniana* many small inflorescences are grouped around the apex of the stem and 1–3 flowers open in succession on each of them. In *Pseudolithos* the inflorescences are few per stem, produced at the apex or lower down and in an inflorescence all flowers open simultaneously. In *C. dodsoniana* the inflorescence possesses a small, caducous peduncle which survives only one flowering season and then falls off in the manner of a wilting pedicel. In *Pseudolithos* stout and very short peduncles are formed and, as is usual in most stapeliads, they are long-lived.

2. *Style-head morphology.* In *C. dodsoniana* the style-head is very thick towards the centre. From this thick centre it descends beneath the anthers which are consequently

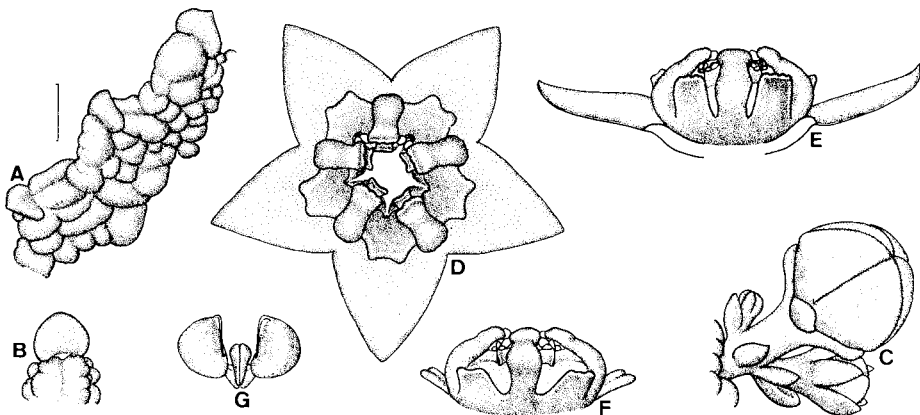


FIG. 4. *Pseudolithos dodsonianus*, Dhofar Province, Oman, Miller 9376 (E). A, part of stem showing larger leaf-bearing tubercles and convex polygons covering stem; B, face view of leaf; C, inflorescence; D, flower; E, side view of dissected flower; F, gynostegium; G, pollinarium. [Scales: A–F, 1mm (at A); G, 0.25mm (at A).]

ascending, and the guide rails descend vertically. Between the anthers it also descends away from the centre becoming  $\pm$  horizontal towards the outer edge on which the corpusculum is then held vertically. This arrangement can be seen in Fig. 3A.

In *Pseudolithos* the centre of the style-head is not much thickened. Beneath the anthers it is  $\pm$  flat and so the anthers are horizontal and the guide rails descend obliquely. Between the anthers the style-head rises up markedly and consequently the corpusculum is held obliquely facing the centre (Fig. 3B).

The style-head in *C. dodsoniana* has the construction found in most stapeliads. However, the peculiar concave construction in *Pseudolithos* is found elsewhere only in *Stapelianthus* and reaches an extreme form in *Tavaresia* Welw. (Bruyns & Forster, 1991: fig. 7B). Oblique rather than vertical guide rails are also found in *Duvalia* Haw. and those species of *Huernia* R. Br. in which the gynostegium is short (e.g. *H. verekeri* Stent, *H. urceolata* Leach). However, in these the style-head is not concave above and has the more common form.

## CONCLUSION

From the above it can be seen that two of the differences listed by Plowes as distinguishing *Anomalluma* from all other genera (short branched stems that are irregularly rugose; follicles widely divergent) are partly or wholly shared with *Pseudolithos*. His statement that 'the stems are superficially similar to those of *Pseudolithos*' is also not correct since they show a surprisingly broad similarity from the macroscopic down to the microscopic level.

Variation in the numbers of flowers per inflorescence is present within *Hoodia* Sweet ex Decne. (Bruyns, 1993) and *Piarranthus* (Meve, 1994) and variation in the number of inflorescences per axis is known in several genera (e.g. *Lavrana* (Bruyns, 1993), *Stapelia* L. (Leach, 1985), *Piarranthus* (Meve, 1994)) so that the differences in the inflorescences in *C. dodsoniana* and *Pseudolithos* should be assessed in the light of these.

The differences in the morphology of the style-head are significant. However, at the same time it must be stressed that in this group of strictly myiophilous plants such modifications may well represent adaptations to a specific pollinator and should perhaps not be emphasized too strongly at generic level.

The two characters partly common to both (see B above) together provide an excellent example of a morphological cline with the following stages in its derivation:

(1) *C. dodsoniana* with many rather loosely held, longer stems and larger leaf rudiments.

(2) *P. caput-viperae* with fewer, rather more compact, shorter stems and smaller leaf rudiments.

(3) The remaining species of *Pseudolithos* with a single, cubiform stem and leaves mostly absent.

Microscopic characters of the epidermis of both the stem and the corolla have

been found to be helpful in delimiting groups of related species (Bruyns, 1993; Meve, 1994). Both of these characters also correlate well with the above-mentioned cline.

In our opinion there appears to be an overwhelming preponderance of evidence to suggest that *C. dodsoniana* is sufficiently closely related to *Pseudolithos* that congeneric status is justified. Therefore we have:

**Pseudolithos** P. R. O. Bally in *Candollea* 20: 41 (1965). Type: *P. sphaericus* (P. R. O. Bally) P. R. O. Bally.

Syn.: *Lithocaulon* P. R. O. Bally in *Candollea* 17: 55 (1959), *nom. illegit.*

*Anomalluma* Plowes in *Cact. Succ. J. (US)* 65: 167 (1993). Type: *A. dodsoniana* (Lavranos) Plowes.

**Pseudolithos dodsonianus** (Lavranos) Bruyns & Meve **comb. nov.**

Syn.: *Anomalluma dodsoniana* (Lavranos) Plowes in *Cact. Succ. J. (US)* 65: 167 (1993).

*Caralluma dodsoniana* Lavranos in *Cact. Succ. J. (US)* 43: 60–61 (1971). Type: Somalia, Lavranos 7326 (holo. FT).

The genus *Pseudolithos* now consists of five species. Four of these are found in Somalia and Ethiopia and the fifth, *P. dodsonianus*, is known from Somalia and two localities in the Dhofar Province of southern Oman (specimens in E). There is growing evidence of many species of Stapeliaceae which occur in both north-east Africa and on the Arabian Peninsula, especially if one takes a broader view of some species complexes: *Caralluma acutangula* (Decne.) N. E. Br., *C. adscendens* (Roxb.) Haw., *C. edulis* (Edgew.) Benth. & Hook. f., *C. penicillata* (Deflers) N. E. Br., *Ceropegia arabica* H. Huber, *C. aristolochioides* Decne., *C. botrys* K. Schum., *C. bulbosa* Roxb., *C. somalensis* Chiov., *C. tihamana* Chaudhary & Lavranos, *C. variegata* Decne., *Duvalia sulcata* N. E. Br., *Echidnopsis scutellata* A. Berger, *Huernia lodarensis* Lavranos (including *H. boleana* M. G. Gilbert and *H. saudi-arabica* D. V. Field) and possibly *H. somalica* N. E. Br. (including *H. laevis* J. R. I. Wood). Thus the occurrence of *P. dodsonianus* on both sides is not that surprising especially in view of the fact that it is vegetatively the least specialized in the genus.

As with many of the species found on both sides of the Red Sea, there are slight differences between *P. dodsonianus* on the western side (Bruyns, 1990, fig. 6) and plants from Oman (Fig. 4). In Omani specimens the leaves are broader and flatter, the corolla is greenish brown rather than purple-brown, the outer corona lobes are truncate rather than bifid and the dorsal appendage of the inner lobes is rounded and hump-like rather than flattened and slightly grooved.

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