ZYGOCACTUS TRUNCATUS OR SCHLUMBERGERA TRUNCATA?

A PROBLEM IN TAXONOMY

by A. J. S. McMillan

Zygocactus truncatus as a species has had a somewhat chequered career. First described by Haworth in 1819 as *Epiphyllum truncatum*, it was later called *Cactus truncatus* by Link and *Cereus truncatus* by Sweet, and in 1890 Schumann erected the genus *Zygocactus* for it.[1]

In 1892 Schumann had second thoughts and transferred *Zygocactus truncatus*, *Schlumbergera russelliana* and *Epiphyllanthus obovatus* (*opuntioides*) to *Epiphyllum* (the plants we now know as *Epiphyllum* were then called *Phyllocactus*). Löfgren revived the genus *Zygocactus* in 1918 and this was adopted by Britton and Rose, Borg and other writers.

In 1953 Moran,[2] in a review of *Schlumbergera*, *Rhipsalidopsis* and allied genera, referred *Zygocactus truncatus* to *Schlumbergera* with the following comment: " . . . *Schlumbergera truncata* differs from *S. bridgesii* and *S. russelliana* in several characters whose total may, in this family, seem impressive. Nevertheless, they are more similar to each other than to any other species and they are said to hybridise with each other, though none of them is known to hybridise with any other species. The Christmas cactus, *S. bridgesii*, though agreeing with *S. russelliana* in most characters, is similar enough to *S. truncata* to have been confused with it for years. Here, then, is a place where genera may well be consolidated."

Let us have a look at the differences to which Moran refers (we compare *Zygocactus truncatus* only with *Schlumbergera russelliana* because the Christmas cactus, recognised as a species (*S. bridgesii*) by Moran, has now been shown to be a hybrid under the name *S. x buckleyi* by Tjaden [3, 4]):

It is interesting to note that several of these differences resemble the opposed character pairs observed by Mendel when he was studying inheritance in the garden pea, e.g. tall/dwarf habit, green/yellow seeds, smooth/wrinkled seed coats, etc. For example, in *russelliana* and *truncatus* we have angled/terete pericarpel and fruit, regular/zygomorphic flower, carmine/yellow anthers and pollen, etc. It is not claimed that these are Mendelian character pairs, this can of course only be determined by breeding experiments, but that they appear to be of a similar nature, and *S. x buckleyi* is scored in relation to such pairs later in this article.

This raises the interesting point that, in the garden pea such differences are barely sufficient to be recognised as varieties, and all the different sorts of garden peas are contained within the one species *Pisum sativum;* whereas, in the *Cactaceae*, such differences have been considered sufficient to erect, not merely different species, but different genera. The ordinary man in the greenhouse may wonder what useful purpose is served by the multiplication of species and genera, and whether there is any special reason why the *Cactaceae* should be treated differently from other families of plants.

Throughout the history of cacti, from the earliest days when the few species were all known as *Cactus*, every botanist who has studied the family has (up to fairly recently) found it necessary to subdivide the family into more and more genera. The splitting approach, as it is often called, was justified by its prime exponent, Curt Backeberg[5]: "Britton and Rose were the first to develop the principle of separating the cacti into small genera." "I am working towards small genera that are drawn on the most precise lines and which form distinct limits."

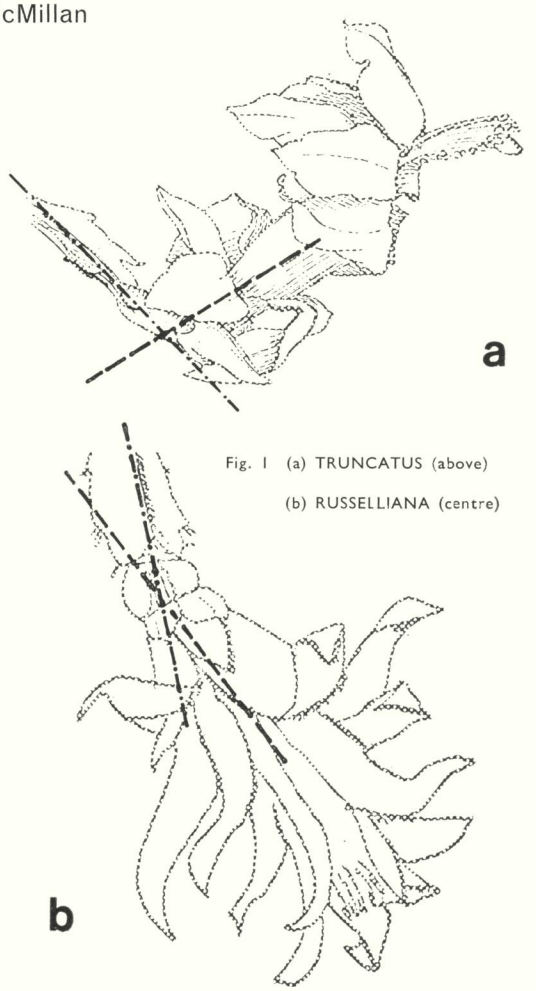

Fig. 1 (a) TRUNCATUS (above)
(b) RUSSELLIANA (centre)

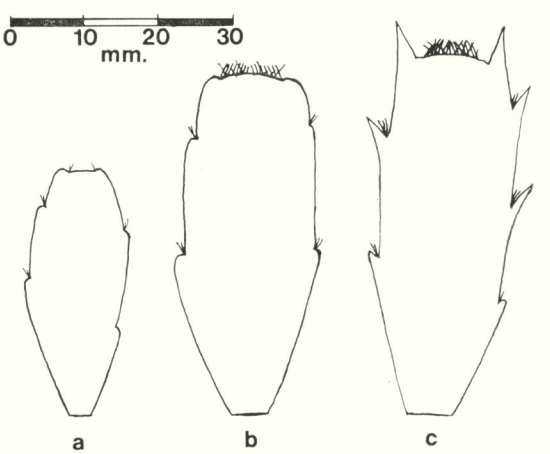

Fig. 2 Outlines of stem segments
(a) RUSSELLIANA (b) BUCKLEYI (c) TRUNCATUS

The opposite view, that of the "lumpers", is well exemplified by Donald and Rowley in a recent article[6]: "In what might be called the post-Backeberg era of cactus taxonomy it seems inevitable that the pendulum will swing over towards fewer genera and larger species. Oversplitting has taken place, and perhaps Hutchinson's great 'Genera Plantarum', with less than 90 genera in Cactaceae, will lead the way in the future. Already *Opuntia*, *Rebutia*, *Ariocarpus* and *Borzicactus* have been consolidated: the present paper suggests the same amalgamation for several 'genera' under the oldest name, *Neoporteria*."

The lumpers have been aided by the recent development of a computer-based technique, numerical taxonomy, briefly described by Donald and Rowley, and in more detail by Sokal[7]. This technique enables the taxonomist to examine all possible combinations of a much larger number of characters than has been practicable before. From this statistical analysis groupings emerge that can be plotted as a matrix and suitable deductions made.

Before we are blinded by science and accept such results quite uncritically, there are several facts we should bear in mind. The first and most important of these is that the concept of a species (and therefore of a genus as a group of similar species) is an artificial one which cannot be precisely defined (though one can do rather better than the rather unhelpful 'a species is whatever a competent taxonomist decides to call a species'.). Such ideas as the ability of the individuals to breed among themselves, similarity of form, particularly of flowers, a common geographical area, are all criteria that have been used to a greater or lesser degree in differentiating species. Nevertheless, in nature there is often a more or less continuous gradation necessitating the division of species and genera at arbitrary points, and nowhere has this been more marked than among the *Cactaceae*.

We see the occurrence of very similar plant forms and quite different flowers, and vice versa. The former may be seen in the recently discovered gymnocalycoid *Notocactus* spp. such as *N. arachnites* and *N. crassigibbus* while an example of the latter is the genus *Epiphyllanthus*, the flowers of which are closely akin to those of *Zygocactus*, yet the stems are very different. Knebel[8] remarked of *E. obtusangulus:* "The conformity is so pronounced that I believe it would be impossible to distinguish the flower of *Epiphyllanthus* if one mixed it in amongst a number of cut flowers of equally coloured *Epiphyllum* (=*Zygocactus*)." Yet the stem form is very different from *Zygocactus:* the joints are oval, cylindrical or flattened, with areoles scattered over the surface. *E. opuntioides* is like a small *Opuntia* (e.g. *O. microdasys v. albispina*), and the areoles are small and do not have glochids, but one to several white bristles or weak spines.

Another point to bear in mind is that some cactus taxonomists in the past have worked with a few specimens, with dried herbarium material, or even from descriptions. They have seldom had the opportunity of seeing the variability that can occur among members of a species growing in the wild. It is considered that a number of species and genera have been separated on quite inadequate evidence, and that some of Backeberg's species, for instance, are no more than varieties or even forms.

One of the problems confronting the lumpers is this: how far should the lumping go? This difficulty is admitted by Donald and Rowley (loc. cit.) and no really stringent reason for not including *Notocactus s. lat.* (i.e. including *Wigginsia* (*Malacocarpus*)) and *Eriosyce* in their revised genus *Neoporteria* is advanced. Even Moran divides his consolidated genus *Schlumbergera* into two subgenera: *Zygocactus* and *Schlumbergera*, which would seem to put us back to square one, so to speak!

Backeberg[9] rebuts Moran's referral: "To change the name of *Zygocactus* to that of *Schlumbergera*, a fairly normal blooming plant which can hardly be found anywhere today, is therefore no satisfactory solution: it tends, in fact, to disregard the differences in the blossoms and puts the name of a scarcely remembered genus in the place of a widely known one. The blossoms of *Zygocactus* differ from those of *Schlumbergera* in the following characteristics: they have a longer genuine corolla tube and are strongly zygomorphic, the edge is bent backwards, the stamens project, the inner series of stamens have grown together with the bottom of the tube with an inwardly curved thin layer of skin, the ovary and fruit are typically turbinate. Therefore only a more exact distinction regarding the abovementioned characteristics can give sufficient evidence. Actually, there are also *Zygocactus* plants growing in the garden which have ± angular ovaries and fruits; these plants have neither a tubular shape inner circle of stamens nor a fold in the skin."

We can set against this the opinion of a collector resident in Brazil that there is such a wide variation in forms of the plants in habitat that they could all be considered to be one very variable species. (Cf. also Tjaden[4]).

Before considering these opinions further, let us look at the Christmas cactus, referred to by Moran as *S. bridgesii*, and mentioned earlier in this article. This has been exhaustively studied by Tjaden[3] and has been identified as *Schlumbergera x buckleyi*, a hybrid between *Z. truncatus* (*var. ruckerianum*) x *S. russelliana*. It is instructive to score some of the character pairs mentioned earlier on this hybrid:

This analysis shows more characters of the type we have attributed to *russelliana* than those called *truncatus*. Analysis of other cultivars such as 'Frankenstolz', 'Gertrude Beahm', 'Mandy', 'Noris', etc. shows a similar though variable distribution of characters, some showing more *russelliana* characters, others more of *truncatus*.

The characters we have designated *russelliana* are those of one extreme of a range, and those described as *truncatus* as the other end of the range so that, by scoring plants against these character pairs, we can locate them quantitatively within the gamut of forms appearing in this complex. The analysis is effective whether we consider the complex to be one species, two species or two separate genera.

The differences between *Schlumbergera* and *Zygocactus* adduced by Backeberg in support of two separate genera could well be considered to be the dominant or recessive expression of one or several pairs of allelomorphic genes. This can only be determined by breeding experiments, and the writer hopes to test this by scoring several hundred seedlings of various crosses in the genus when they are mature enough to flower.

The most obvious difference is the regular versus zygomorphic flower. This zygomorphy is caused by varying amounts of curvature of the petals, tube, stamens and style, without modification of the shape of the petals. In *truncatus* the lower and side petals are strongly reflexed and the top petals are often curved slightly forward, while the stamens and style are curved downwards. As this is not really a very drastic modification of the flower it could, again, be considered as the expression of a not very great genetic difference. In some cultivars the flowers have the more regular appearance of *S. x buckleyi* when they first open, and on the next day the perianth petals become fully reflexed to give the typical *truncatus* appearance.

Rowley[10] shows a sport as an example of zygomorphy in *Bulbine*, normally actinomorphic. He says zygomorphy is considered to be an advanced adaptation, usually to a larger pollinator. Zygomorphy may well be an adaptation to pollination by humming birds in the case of *truncatus*. An interesting feature of the flowers shown in fig. 1 is that the tube and pericarpel align themselves so that the lower part of the tube makes an angle of about 30° above the horizontal which brings the mouth of the flower more or less horizontal. This

alignment of the flowers occurs irrespective of the angle of the stem from which they spring,whether it is pointing up or down, or even when it is twisted through 90°. Preliminary experiments, suggested by D. R. Hunt, seem to indicate that this is due to negative geotropism, and further experiments to clarify this will be made in the next flowering season.

The foregoing analysis shows that there appear to be two extreme character types designated *russelliana* and *truncatus*, and that there are many intermediate forms each showing varying proportions of *russelliana* and *truncatus* characters. Bearing in mind Moran's remark—"Nevertheless, they are more similar to each other than to any other species," we should accept his referral of *Zygocactus truncatus* to the genus *Schlumbergera* as a subgenus with the retention of the two species *S. russelliana* and *S. truncata*, but it is doubtful whether all the intermediate forms should be grouped together as *S. x buckleyi*. Analysis of the seedlings mentioned earlier may disclose one or several clusters of characters sufficiently definite to warrant naming as separate entities.

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	russelliana	*truncatus*
Stem segments	Ovate. (25 -) 40 x 15 mm. 1-2 crenate angles at sides. No teeth at ends Linear areole 3-5 mm. Midrib not prominent.	Oblong, variable from 40x15 to 55x35 mm. 2-3 serrate angles at sides. Teeth at ends. Linear aerole 7-10 mm. Midrib prominent.
Tube	Short and not clearly defined. ± same axis as pericarpel. Flower ± pendent.	~35 mm. long. Axis horizontal to 45° up from axis of pericarpel. Flower held up.
Petals at mouth of tube	10-12 petals 6-7 mm. wide, ascending to spreading. Some petals recurved at tip. ± regular.	8 (-10) petals 10-15 mm. wide, lower petals strongly reflexed. Strongly zygomorphic.
Outer stamens	20-30 inserted in tube, ~35 mm. long.	60+ inserted in tube, ~50 mm. long.
Anthers	Carmine pink.	Yellow.
Pollen	Carmine pink	Yellow.
Style	~40 mm. long, straight.	~60 mm. long, bowed.
Pericarpel	Strongly 4-winged, not at right-angles, 5 mm. long.	Terete, round conical, 10 mm. long.
Fruit	4-6 angled, hard, red.	Terete, red-purple, oval to pear-shaped, 15-20 mm. long.

Character pairs (*russelliana* first)	*S. x buckleyi*	Dominant†
Small/large segments	(35-) 50 x (15-) 30 mm.	t
Crenate/dentate edges	crenate	r
No teeth/teeth at end	no teeth	r
Small/large linear areole	6-8 mm.	t
Short/long tube	long	t
Coaxial/angled tube	coaxial	r
Pendent/horizontal flowers	pendent	r
Spreading/recurved petals	recurved	t
Regular/zygomorphic flowers	regular	r
~30/~60 outer stamens	~30	r
Carmine/yellow anthers	carmine	r
Carmine/yellow pollen	carmine	r
Straight/bowed style	straight	r
Angled/terete pericarpel	5-angled	r
Angled/terete fruit	5-angled, oval	r

†Note. In this column is shown the character, r=*russelliana* or t=*truncatus*, which is partially or completely dominant.