Xylose is a major nectar sugar in *Protea* and *Faurea*

Glucose, fructose and sucrose have been called the 'big three' and are thought to be the only major nectar sugars in flowering plants. We have now found the pentose sugar xylose at concentrations of up to 39% of total sugar in the nectar of 36 species of Protea *and three species of* Faurea. *It is interesting that morphological similarities between these two genera of the Proteaceae are also reflected in the nectar composition, therefore supporting the idea that nectar sugars have value as taxonomic characters. Xylose has never been considered as a nectar sugar and little is known about its ecological significance.*

In an extensive chemotaxonomic study of sugar compositions in the nectar of more than 1 000 plant species (van Wyk, unpublished), only three major nectar sugars – glucose, fructose and sucrose – were detected. These results agree with previous surveys where the same three sugars were found as the only major nectar sugars in plants.[1-4] Minor sugars[3] include arabinose, galactose, mannose, gentiobiose, lactose, maltose, melibiose, trehalose, melezitose, raffinose and stachyose, but these rarely occur in more than trace amounts. Xylose has never been reported from floral nectar before, but there is one reference to small amounts found in the extrafloral nectar of a grass.[9]

The sugar compositions of nectar from all the *Faurea* samples and the first seven species of *Protea* (Table 1) are illustrated schematically in Fig. 1, showing the variation found in the larger sample. Xylose is present in virtually all of the species and often represents more than 10% of total sugar. *Faurea speciosa* (Fig. 2) was a convenient source of nectar for the isolation and identification of xylose, which was present only in *Protea* and *Faurea* and not in any of the other genera of the family investigated so far: *Banksia, Dryandra, Grevillea, Hakea, Leucospermum, Mimetes,*

Table 1. Nectar sugar compositions in species of *Faurea* and *Protea*.

			Percentage of total sugar			
Sample	Genus and species		xylose	fructose	glucose	sucrose
1a.	*Faurea macnaughtonii*	sample 1	17	38	30	15
1b.		sample 2	15	37	29	19
1c.		sample 3	12	36	28	24
2a.	*F. saligna*	sample 1	27	35	33	5
2b.		sample 2	17	38	40	5
3a.	*F. speciosa*	sample 1	7	45	48	-
3b.		sample 2	4	49	47	-
3c.		sample 3	29	35	36	-
3d.		sample 4	36	35	29	-
3e.		sample 5	39	30	31	-
1.	*Protea acaulos*		9	48	29	14
2.	*P. amplexicaulis*		5	29	22	43
3.	*P. aristata*		trace	50	49	1
4.	*P. aspera*		25	36	37	trace
5a.	*P. aurea* subsp. *aurea*	sample 1	7	49	39	5
5b.	*P. aurea* subsp. *aurea*	sample 2	8	51	34	6
5c.	*P. aurea* subsp. *potbergensis*		trace	50	50	-
6.	*P. burchellii*		2	21	22	55
7a.	*P. caffra*	sample 1	23	40	37	trace
7b.		sample 2	20	21	58	1
7c.		sample 3	10	34	56	
7d.		sample 4	7	35	50	8
7e.		sample 5	32	22	46	-
8.	*P. compacta*		2	47	51	-
9.	*P. coronata*		-	3	1	96
10.	*P. cynaroides*		3	47	50	-
11.	*P. eximia*		3	44	51	2
12.	*P. glabra*		11	42	47	-
13a.	*P. grandiceps*	sample 1	3	2	2	93
13b.		sample 2	trace	14	10	76
14.	*P. lacticolor*		3	46	49	2
15.	*P. laetans*		3	47	50	-
16.	*P. lanceolata*		36	30	33	1
17.	*P. laurifolia*		trace	84	8	8
18.	*P. lepidocarpodendron*		trace	45	46	9
19a.	*P. longifolia*	sample 1	3	30	32	35
19b.		sample 2	2	30	34	34
19c.		sample 3	2	36	36	26
20.	*P. lorifolia*		4	43	49	4
21.	*P. magnifica*		-	47	47	6
22.	*P. montana*		7	44	40	9
23.	*P. mundii*		trace	51	49	-
24.	*P. nana*		1	30	5	64
25.	*P. neriifolia*		2	45	50	3
26a.	*P. nitida*	sample 1	6	46	48	trace
26b.		sample 2	4	46	48	2
26c.		sample 3	3	46	48	3
26d.		sample 4	4	47	48	1
27.	*P. obtusifolia*		trace	42	39	19
28.	*P. pityphylla*		6	10	5	79
29a.	*P. pruinosa*	sample 1	6	29	31	34
29b.		sample 2	7	24	28	41
29c.		sample 3	7	20	22	51
30.	*P. pudens*		4	34	37	25
31.	*P. punctata*		-	trace	trace	100
32.	*P. repens*		5	46	49	-
33.	*P. roupelliae*		2	43	48	7
34.	*P. rubropilosa*		4	39	45	12
35.	*P. scabra*		6	28	23	43
36.	*P. speciosa*		6	46	48	-
37.	*P. stokoei*		-	50	50	-
38.	*P. sulphurea*		5	31	23	41
39a.	*P. suzannae*	sample 1	1	36	36	27
39b.		sample 2	2	38	41	19
39c.		sample 3	1	36	40	23
40a.	*P. venusta*	sample 1	7	35	35	23
40b.		sample 2	4	47	48	1
40c.		sample 3	4	46	48	2

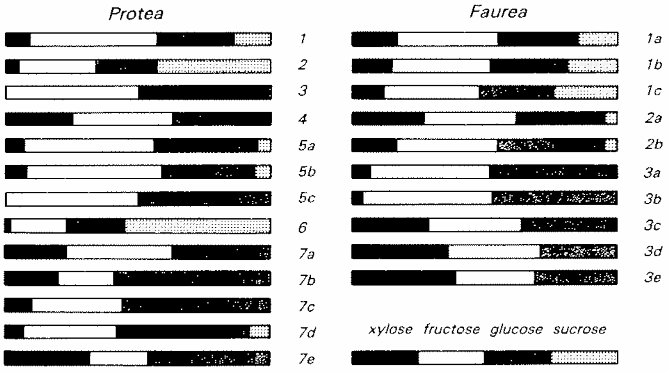

Fig. 1. Nectar sugar compositions in species of *Protea* and *Faurea* showing the variation found in a larger number of samples. Species and samples are numbered as in Table 1, where the complete data set is given. Sugar compositions were determined by analytical HPLC, using a Waters Sugarpack column and acetonitrile:water in the ratio of 83:17 as eluent, with detection by refractive index. Xylose was isolated from the nectar of *Faurea speciosa* (Fig. 2) by repeated semi-preparative runs with the same HPLC system. The isolated xylose (11 mg) was identical to a standard sample of D-xylose (optical rotation; melting point; identical behaviour on TLC in various eluents; inseparable by HPLC with various solvent systems; identical GC retention times of the trimethylsilyl derivatives).

Orothamnus, Paranomus, Stenocarpus and *Telopea.* Previous studies of *Protea* nectar reported only glucose, fructose and sucrose for seven species[10] or, in addition to these, small amounts of melezitose and maltose in five rodent-pollinated species.[11] Although trace amounts of unknown sugars were indeed sporadically detected in some species of *Protea*, sample limitations have not yet allowed us to confirm initial identifications by spectroscopic methods. At the species level, there are some interesting similarities and differences in the sucrose–hexose and fructose–glucose ratios (Table 1). Note, for example, the similarity between *Protea nana* and *P. pityphylla*, two closely related species and the only ones known to have high sucrose–hexose ratios combined with a marked imbalance between fructose and glucose.

Fig. 2. Inflorescence of *Faurea speciosa*, the species which was chosen as a source of nectar for the isolation of xylose by semi-preparative HPLC. The individual flowers are slightly zygomorphic in *Faurea* and *Protea*[5-7] but more or less actinomorphic in other African Proteaceae.

It has long been speculated that *Faurea* and *Protea* are closely related.[5-7] They share distinct features such as entire leaf margins and zygomorphic flowers[7] (Fig. 2), which are regarded as shared derived characters for the two genera. The unique presence of xylose in these two genera provides independent evidence of a close relationship and further supports the idea that nectar sugars may be taxonomically useful.[8]

The ecological significance of xylose in nectar is not clear. Some *Protea* species show interesting adaptations for pollination by non-flying mammals[11-13] but xylose is not rapidly metabolized in mammalian tissues and its excretion in the urine is the basis of the xylose absorption test.[14] Studies on the digestion of nectar sugar in birds[15,16] have not considered xylose. Among the insects, bees can utilize xylose[17] but flies cannot.[18] Proteas are pollinated mainly by insects and birds[19] but the exclusion of birds from flowerheads does not result in a reduction of seed set.[20] Judged by the results in Table 1, the presence of xylose in nectar seems unrelated to pollination syndromes and may be due to enzymatic activities in the plants rather than direct selection.

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Arrowheads or pen knives? A microwear analysis of mid-Holocene stone segments from Jubilee Shelter, Transvaal

Segments are usually assumed to have been used exclusively in stone arrowheads. This interpretation is challenged by a microwear analysis of seven segments from Jubilee Shelter, in the Magaliesberg, Transvaal. The micro-polish on some of those tools resembles polish that is obtained from working vegetal material such as wood and sedge.

Segments as arrowheads

A segment is a crescent-shaped stone tool with a straight, unworked cutting edge (the cord) opposite an arc that has been blunted (backed) by the removal of a series of small facets.

Segments were unequivocally parts of stone arrowheads in Egypt. Three types of segment tipped arrows were found in predynastic and dynastic Egyptian tombs.[1] The first type was an arrow in which the head had a large segment (*c.* 15 mm in length) mounted transversely so that both ends protruded beyond the mastic (Fig. 1*a*). The second type contained a small segment (*c.* 5–8 mm) with mastic that extended up to and sometimes over both ends of the stone (Fig. 1*b*). In the third type of arrowhead, the transverse microlith was augmented by two segments mounted below the head (Fig. 1*c*, *d*).

The Egyptian arrowheads have encouraged archaeologists elsewhere in Africa to interpret unmounted segments as the remnants of stone-tipped arrowheads. Phillipson recovered mastic-encrusted stone tools from Makwe Rock Shelter, eastern Zambia, that he believes were used as arrowheads.[2] From the positioning of the mastic he suggests that pointed and asymmetrical segments were used as spear- and arrow-barbs and that they were hafted diagonally so that the sharp tips and edges were exposed. on the other hand, he suggests that deep segments with a mass of mastic on their ends were mounted as transverse arrowheads.

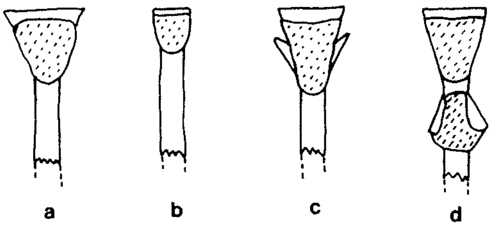

Fig. 1. Segment-tipped arrowheads found in predynastic and dynastic Egyptian tombs (after Clark, Phillips and Staley[1]).

Some southern African segments have mastic on them, which shows that they, too, were part of composite tools. Segments from Melkhoutboom Cave, in the eastern Cape, have mastic traces that are generally restricted to the outer backed arc, but they occasionally extend over the blade.[3] There are, however, no surviving stone-tipped arrows in southern Africa that contain segments, not even those used by Cape San in the last century.[3,4] There is, consequently, no unequivocal evidence for the use of segments as arrowheads in southern Africa. Nonetheless, there is a substantial body of historic and ethnographic evidence for arrowheads made from stone tools other than segments. Arrowheads with barbs made from triangular pieces of agate, chalcedony, glass or quartz crystal were used by /Xam (San) in the Cape.[5,6] The /Xam glass or stone barbs were mounted in mastic as a pair of flaked slivers at the end of the foreshaft. Eighteenth- and nineteenth-century European travellers, such as Wikar, Palgrave, Dunn and Paterson, also described San stone arrowheads.[7,8] A recent archaeological excavation in Adam's Krans Cave, eastern Cape, yielded a unique find in the form of a wooden arrow shaft tipped with a single piece of stone that is secured with mastic and twine.[9] The arrowhead bears a resemblance to the Egyptian Type 2 arrowhead (Fig. 1*b*) but the stone tip has not yet been X-rayed to determine what type of stone tool is buried in the mastic. The level in which the arrow was found has been dated 1 760 ± 50 BP (Pta-6418).

Segments from Jubilee Shelter

Jubilee Shelter is situated in a wooded kloof on the northern slopes of the Magaliesberg (25°42'S; 27°55'E). The rich deposits at the shelter have been extensively excavated to reveal a long occupation sequence, that included the first mid-Holocene occupation discovered in the Transvaal.[10-12]

The mid-Holocene occupations, dated between 3 150 ± 150 BP (Wits-1214) and 6 490 ± 200 BP (Wits-1462), contain assemblages bearing a resemblance to the Wilton Industry of the Cape, and also to the Interior Wilton and the Inland Wilton.[13,14] The Jubilee Shelter assemblages are dominated by small end scrapers, but 52 segments occurred between 6 490 and 3 100 BP and a further 12 were found in younger deposits.[10] Many of the segments were exceptionally small (less than 10 mm in length), particularly those occurring in the younger levels. Unfortunately,

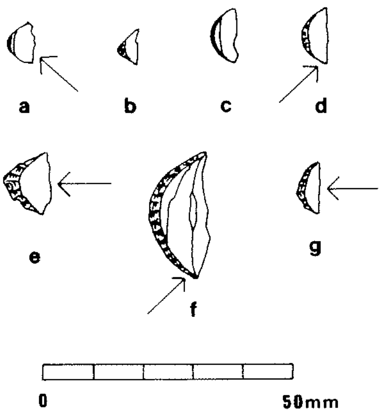

Fig. 2. Jubilee Shelter segments with micro-polish: *a*, segment A from Level G; *b*, segment B from Level G; *c*, segment C from Level G; *d*, segment D from Level BB; *e*, segment E from Level RL; *f*, segment F from Level RL2; *g*, segment G from Level PB. The arrows point to the position of the micro-polish.

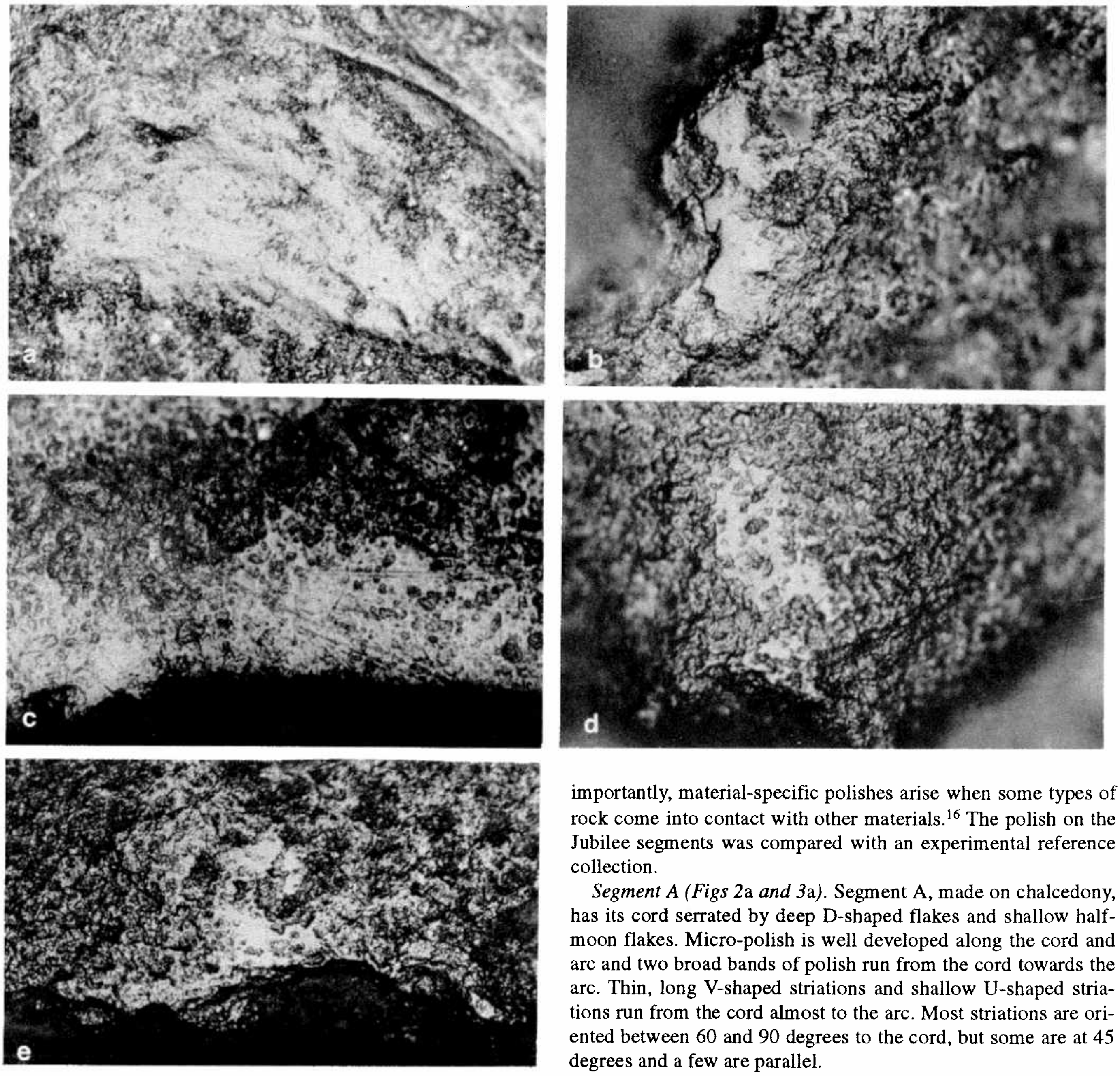

Fig. 3. *a*, Segment A. Polish on flake ripples near the cutting edge. 200 ×; *b*, segment D. Patches of well-developed polish along the arc near the tip. 200 ×; *c*, segment E. Well-developed polish and striations parallel and at 30–45° to the cord. 200 ×; *d*, segment F. Patches of well-developed polish along the arc. 200 ×; *e*, segment G. Well-developed band of polish along the cord. 100 ×.

none of the segments had traces of mastic. Thirty-five of the segments were manufactured on quartz, which is not particularly suitable for microwear studies because polish, being light reflective, is difficult to see on transparent surfaces.[15] There are, however, 29 chert, jaspilite, chalcedony and hornfels specimens and these were submitted to microwear analysis. Only seven of this sample show traces of polish; these segments vary in size and shape and the position of the polish is also variable (Fig. 2).

The Jubilee segments were soaked for 5 min, first, in a 10% HCl solution and, then, in a 10% KOH solution. Finally, the tools were examined under an incident-light microscope using magnifications of .between 50 and 400. The position and appearance of wear traces were examined because the direction of striations can sometimes indicate the direction in which a tool was used. More importantly, material-specific polishes arise when some types of rock come into contact with other materials.[16] The polish on the Jubilee segments was compared with an experimental reference collection.

Segment A (Figs 2a *and* 3a*).* Segment A, made on chalcedony, has its cord serrated by deep D-shaped flakes and shallow half-moon flakes. Micro-polish is well developed along the cord and arc and two broad bands of polish run from the cord towards the arc. Thin, long V-shaped striations and shallow U-shaped striations run from the cord almost to the arc. Most striations are oriented between 60 and 90 degrees to the cord, but some are at 45 degrees and a few are parallel.

Segment B (Fig. 2b*).* This small, triangular, chalcedony segment has a cord that is notched by a deep D-shaped flake. Shallow half-moon flakes are visible along the cord. Micro-polish is well developed along the cord, notch and at the tips and adjoining arc. Thin, long V-shaped striations concentrated at the point area run both parallel and at different angles to the cord.

Segment C (Fig. 2c*).* This segment, made on hornfels, has well-developed micro-polish on the higher areas of the micro-topography, such as the flake ridges and ripples, but is best developed at the points and along the arc.

Segment D (Figs 2d *and* 3b*).* Like the previous specimen, this hornfels segment has micro-polish on the higher areas of the micro-topography. Only a few short striations are, however, visible.

Segment E (Figs 2e *and* 3c*).* The micro-polish is well developed along the cord of this chalcedony segment, but wear is concentrated at the tips and arc. The striations are short and shallow and run parallel to the cord.

Segment F (Figs 2f *and* 3d*).* This large chalcedony segment has micro-polish along the cord and short, fine striations run both parallel and at various angles to the cord. The remainder of the tool has a shiny surface that cannot be attributed to any particular