

2 A systematic histological study of palm fruits. VIII. Subtribe
3 Dypsidinae (Arecaceae)

4 FREDERICK B. ESSIG

5 Institute for Systematic Botany, Department of Biology, SCA 110, University of South Florida,
6 4202 E. Fowler Ave., Tampa, FL 33620, USA; e-mail: essig@cas.usf.edu

8 **Abstract.** Analysis of the pericarp structure in the four genera of the palm subtribe
9 Dypsidinae reveals tissues similar to those in other taxa within the pseudomonome-
10 rous Indo-Pacific arecoid palms, but generally in unspecialized configurations consis-
11 tent with their presumed basal position within this group. Unique tissues within some
12 members of genus *Dypsis* include thin-walled, tannin-filled fibers around the vascular
13 bundles. Large-fruited members of the presumably related genera *Lemurophoenix*,
14 *Masoala*, and *Marojejya* show more distinctive arrangements of protective tissues and
15 are quite different from one another. Only *Marojejya* appears to be closely related to
16 *Dypsis*. *Lemurophoenix* and *Masoala*, by possession of both unsheathed vascular
17 bundles and bundles with heavy fibrous sheaths, show possible affinities with genera
18 well-removed from *Dypsis*.

19 **Key Words:** Dypsidinae, palms, Arecaceae, fruits, pericarp, histology.

22 The subtribe Dypsidinae (tribe Areceae, 48
23 subfamily Arecoideae) has been in consider- 49
24 able flux in recent years. In *Genera Palmarum* 50
25 (Uhl & Dransfield, 1987), it was considered 51
26 to consist of 6 genera (*Dypsis*, *Neodypsis*, 52
27 *Chrysallidocarpus*, *Neophloga*, *Vonitra*, and 53
28 *Phloga*), which recently have been considered 54
29 a single genus, *Dypsis* (Dransfield & Beentje, 55
30 1995). *Dypsis*, as currently recognized, con- 56
31 sists of approximately 140 diverse species 57
32 divided into 18 groups. Recently, the mono- 58
33 typic genera *Masoala* and *Lemurophoenix*, 59
34 plus *Marojejya* with 2 species, have been 60
35 moved into the subtribe based on results of 61
36 phylogenetic studies (Dransfield et al., 2005). 62
37 The subtribe is confined primarily to Mada- 63
38 gascar but with outliers in eastern Africa and 64
39 islands of the Indian Ocean.

40 The subtribe Areceae (sensu Dransfield et 66
41 al., 2005) consists of palms from the Indo- 67
42 Pacific region characterized by gynoecea that 68
43 are tricarpellate but unilocular by abortion of 69
44 two locules (pseudomonomerous), and uni- 70
45 ovulate. The Dypsidinae has been consid- 71
46 ered to represent an early branch of the 72
47 Areceae, in part because of the occasional

occurrence of trilocular (but functionally 48
uniovulate) gynoecea in some species (Uhl & 49
Dransfield, 1987). The sister group relation- 50
ship of Dypsidinae to the remaining pseudo- 51
monomerous palms is supported by Hahn 52
(2002a, b), but not clearly by Asmussen and 53
Chase (2001), Lewis and Doyle (2002), Loo et 54
al. (2006), or Norup et al. (2006). In these 55
studies, however, the major subdivisions of 56
this tribe are still highly unresolved, and so the 57
potential sister group relationship of the 58
Dypsidinae is not precluded. These analyses 59
are also not consistent with respect to the 60
monophyly of either *Dypsis* or Dypsidinae. 61

The analysis of Lewis and Doyle (2002) 62
suggests that *Masoala*, *Marojejya*, and 63
Lemurophoenix are nested within a para- 64
phyletic *Dypsis*. In the analysis of Asmussen 65
and Chase (2001), *Marojejya* and *Lemuro-* 66
phoenix fall out close to *Dypsis lutescens*, but 67
Masoala appears to be closely related to 68
Roscheria, the Arecinae, and other advanced 69
members of the tribe Areceae. In Loo et al. 70
(2006), members of the Dypsidinae fall into 71
different branches of a polytomy, with 72
Masoala in a clade with *Bentinckia* and 73

74 *Oncosperma*, & with *Lemurophoenix* & *Dyp-*
 75 *sis heterophylla* in a terminal polytomy with
 76 *Cyrtostachys*. *Marojejya* is unresolved within
 77 the bigger polytomy. Clearly the phylogenetic
 78 relationships of this group are not fully
 79 resolved.

80 The present study is the eighth in a series
 81 focusing on the comparative histology of the
 82 pericarp in the arecoid palms (Essig, 1977,
 83 1999, 2002; Essig & Young, 1979; Essig &
 84 Hernandez, 2002; Essig & Litten, 2004; Essig
 85 et al., 1999, 2001). This installment com-
 86 pletes the analysis of the tribe Areceae.

87 **Materials and methods**

88 The study employed standard histological
 89 techniques following the preceding papers in
 90 this series. Preserved fruits representing 42
 91 species in 13 of the 18 groups of *Dypsis*, plus
 92 several unnamed specimens, and one each of
 93 *Lemurophoenix*, *Masoala*, and *Marojejya*
 94 were obtained from herbaria (primarily Kew
 95 (K) in this instance) and prepared for section-
 96 ing by dehydrating in an ethanol/TBA
 97 sequence, embedding in paraplast and section-
 98 ing on a rotary microtome. Slides were
 99 stained with safranin and fast green. Quality
 100 of the slides varied with the quality of
 101 preservation, and some were fragmentary.
 102 Representative taxa were illustrated by semi-
 103 diagrammatic line drawings, and traced from
 104 digital photographs, which show the distribu-
 105 tion, size, and shape of various tissues, but
 106 not cellular detail. A few representative
 107 photographs of the unique features of this
 108 group are included.

109 **Results**

110 Introductory information for each group, as
 111 well as distribution information, overall fruit
 112 measurements, notes on fruit color, and
 113 nature of the endosperm were largely taken
 114 from Dransfield and Beentje (1995).

115 *LEMUROPHOENIX*

116 Monotypic genus from northeastern
 117 Madagascar.

119 **Lemurophoenix halleuxii** J. Dransf. (*Dransfield*
 120 *55691*, K), northeastern Madagascar. Fruit 40
 121 mm in diameter, pericarp 8–10 m thick;

endosperm homogeneous to slightly ruminat. 122
 Outer surface irregular with obscure dark layer 123
 beneath, beneath that separated patches of 124
 brachysclereids; middle pericarp of scattered 125
 brachysclereids, short strands of tannin cells, 126
 occasional roundish vascular bundles with 127
 moderate fibrous sheath, many small naked 128
 vascular bundles in inner half; tannins and 129
 other distinctive tissues lacking in the inner- 130
 most pericarp; locular epidermis thick, of 131
 narrow macrosclereids. (Fig. 1A) 132

MAROJEJYA

A genus of 2 species form northeastern 134
 Madagascar. 135

Marojejya darianii J. Dransf. & N. Uhl 137
 (*Dransfield 6452*, K); northeastern Mada- 138
 gascar. Fruit 20 mm in diameter, pericarp 139

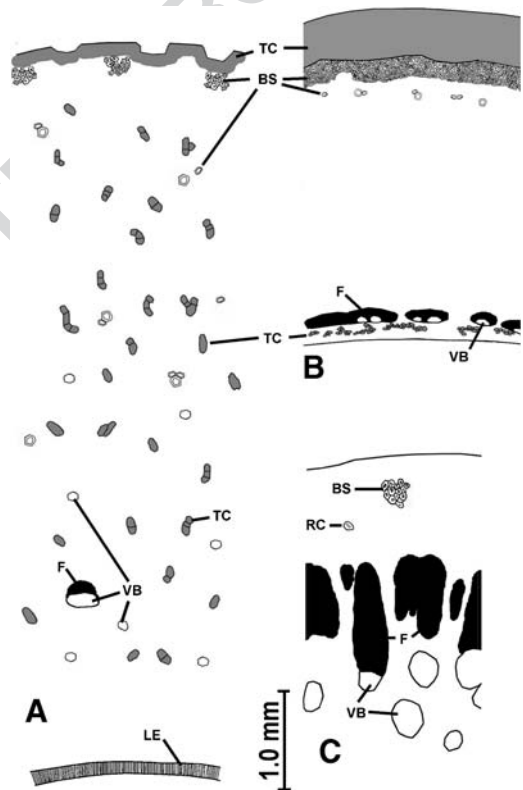


FIG. 1. A. *Lemurophoenix halleuxii* (from *Dransfield 55691*, K), B. *Marojejya darianii* (from *Dransfield 6452*, K), C. *Masoala madagascariensis* (from *Dransfield 6770*, K). LE Locular epidermis of macrosclereids, VB vascular bundle, F fibers, TC tannin-filled parenchyma cells, RC raphide cells, BS brachysclereids.

140	3 mm thick; endosperm homogeneous,	chysclereids irregularly distributed in clusters	189
141	but testa crenulate. Outer pericarp with	of various sizes or solitary, some in	190
142	thick band of continuous tannin/pigment	tight oblique clusters resembling short	191
143	filled cells, followed by thick mantle of	fibrous bundles, but lacking stegmata; vas-	192
144	brachysclereids, and a few larger, more	cular bundles discrete, flattened, rimmed	193
145	isolated brachysclereids close by; middle	with many stegmata. (Fig. 2A)	194
146	pericarp lacking distinctive tissues; dis-		
147	distinct endocarp of flattened fibrous vascular	Dypsis decaryi (Jum.) Beentje & J. Dransf.;	196
148	bundles; fibrous sheaths thick; a few	<i>Neodypsis decaryi</i> Jum. (<i>Read 827bis</i> _BH;	197
149	tannin cells to the interior; locular epider-	<i>Beentje & Andriampaniry 4614</i> , K); south-	198
150	mis lacking. (Fig. 1B)	ern Madagascar. Fruit 22.7 mm long,	199
		19.5 mm in diameter, bluish-white at	200
151	<i>MASOALA</i>	maturity; pericarp 1.9–2 mm thick. Epider-	201
152	A monotypic genus from northeastern	mis of squarish cells with convex external	202
153	Madagascar.	walls; outer pericarp with a discontinuous	203
		band of large tanniferous cells; brachy-	204
155	Masoala madagascariensis Jum. (<i>Dransfield</i>	sclereids in a continuous band, 2–4 cells	205
156	<i>6770</i> , K [immature]); northeastern Mada-	thick about 1/3 of the way into the	206
157	agascar. Fruit dimensions and color un-	mesocarp from the surface; middle to inner	207
158	known. Outer pericarp with scattered	pericarp of simple parenchyma tissue, with	208
159	large patches of brachysclereids and occa-	occasional scattered large raphide-bearing	209
160	sional small raphide cells; mid-region	cells; vascular strands oval, on the inner side	210
161	dominated by a layer of strongly radially	of thick, broad, flattened fibrous sheaths,	211
162	distended fibrous vascular bundles and	stegmata present; innermost pericarp with a	212
163	similarly-shaped purely fibrous; the imma-	thick band of small tanniferous cells.	213
164	ture interior with several series of vascular		
165	bundles without sheaths. (Fig. 1C)	Dypsis lastelliana (Baill.) Beentje & J.	215
		Dransf.; <i>Neodypsis lastelliana</i> Baill. (<i>Moore</i>	216
166	<i>DYPsis</i> GROUP 1	<i>9014</i> , BH); northern Madagascar. Fruit 18–	217
167	A large group of 23 species occurring in all	24 mm long, 12–17 mm in diameter, mature	218
168	parts of Madagascar, including species described	color unknown, pericarp 2.3–2.4 mm thick.	219
169	in both <i>Chrysalidocarpus</i> and <i>Neodypsis</i> ; endo-	Epidermis flat, pigmented; outer half of	220
170	sperm homogeneous or ruminat. Seven speci-	pericarp of parenchyma and scattered small	221
171	mens were examined, all with flattened, but	raphide-bearing cells; massive mantle of	222
172	discrete fibrovascular bundles; most with the	brachysclereids in mid-pericarp, inner peri-	223
173	outer 25–50% of the pericarp heavily tannini-	carp with frequent large raphide-bearing	224
174	ferous, and with scattered, sometimes bundle-	cells, vascular bundles with broad flattened,	225
175	like, patches of brachysclereids and enlarged	thick fibrous sheaths, fibers with thick walls;	226
176	raphide cells throughout the mesocarp.	thick band of very thin tanniferous cells	227
		adjacent to seed coat.	228
178	Dypsis ampasindavae Beentje; <i>Neodypsis</i>	Additional specimens examined briefly and	229
179	<i>loucoubensis</i> Jum. (<i>Beentje & Andriampaniry</i>	found to be generally similar to the above	230
180	<i>4701</i> , K); northwestern Madagascar. Fruit	(except as noted): Dypsis manajarensis	231
181	10–13 mm long, 7.5 mm in diameter,	(Jum. & H. Perrier) Beentje & J. Dransf.;	232
182	mature color unknown; pericarp 1.5–	<i>Chrysalidocarpus manajarensis</i> Jum. & H.	233
183	1.6 mm thick. Epidermis smooth, pig-	Perrier; <i>Chrysalidocarpus fibrosus</i> Jum.	234
184	mented; outer half of pericarp heavily	(<i>Beentje & Andriampaniry 4796</i> , K); Dypsis	235
185	tanniferous with some raphide cells;	ovobontsira Beentje (<i>Beentje et al. 4645</i> ,	236
186	inner half of the pericarp without tannins	K—outer pericarp essentially free of tannin;	237
187	but with scattered raphide cells, these	Dypsis prestonii Beentje (<i>Beentje 4672</i> , K);	238
188	largest in mid-pericarp, and abundant bra-	Dypsis tsaravoasira Beentje (<i>Baker et al.</i>	239
		<i>1017</i> , K).	240

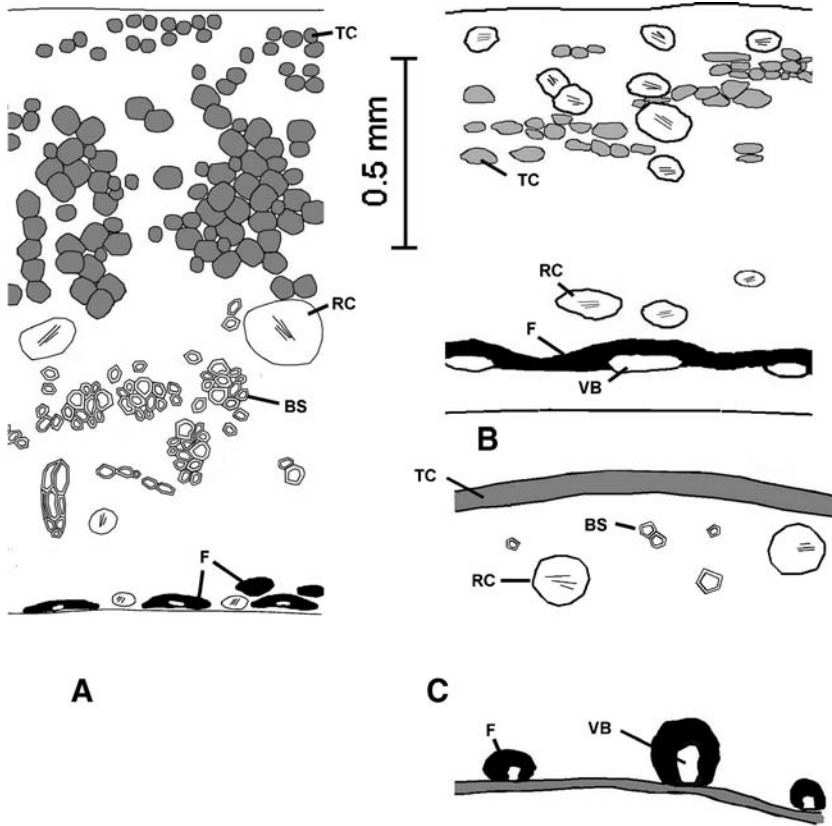


FIG. 2. A. *Dypsis ampasindavae*, group 1 (from Beentje & Andriampaniry 4701, K), B. *Dypsis andrianatonga*, group 3 (from Beentje et al. 4571, K), C. *Dypsis confusa*, group 9 (from Beentje et al. 4627, K). VB vascular bundle, F fibers, TC tannin-filled parenchyma cells, RC raphide cells, BS brachysclereids.

241 *DYPISIS* GROUP 2

242 This group consists of a single species
 243 originally placed in the genus *Chrysalidocarpus*
 244 and later in *Macrophloga*; seed with
 245 ruminant endosperm.

247 ***Dypsis decipiens*** (Becc.) Beentje & J.
 248 Dransf.; *Chrysalidocarpus decipiens*
 249 Becc., *Macrophloga decipiens* (Becc.)
 250 Becc. (Beentje & al. 4658, K); central
 251 Madagascar. Seed with homogeneous en-
 252 dosperm. Fruit 20–25 mm long, 20–22 mm
 253 in diameter, color at maturity unknown.
 254 The single specimen available for study
 255 was missing the entire outer pericarp. The
 256 endocarp consists of numerous discrete,
 257 overlapping, flattened fibrovascular bun-
 258 dles approximately 0.3–0.4 mm wide, with
 259 an underlying layer of tanniniferous cells.

DYPISIS GROUP 3

A widespread group of 22 species occur-
 ring throughout Madagascar, on the island of
 Pemba off the coast of Tanzania, and in the
 Comoros Islands, including species formerly
 placed in *Chrysalidocarpus*, *Neodypsis* and
Phloga; considered closely related to group 1;
 endosperm homogeneous to ruminant. Seven
 species were examined; most with very
 broad, flat, more-or-less confluent fibrous
 bundle sheaths, but in this regard, *Dypsis*
lanceolata is anomalous with distinct, broad-
 ly ovate bundles.

Dypsis andrianatonga Beentje. (Beentje et
 al. 4571, K); northern Madagascar. Fruit
 9–20 mm long, 7–15 mm in diameter,
 color at maturity unknown; pericarp ca.
 1 mm thick. Epidermis flat, lightly pig-

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279	mented; outer pericarp with subepidermal	large raphide-bearing cells, sclereids ex-	330
280	layer of clear cells, scattered patches of	tremely rare; inner pericarp with 1–2 layers	331
281	tanniferous cells, and scattered large	of vascular bundles with roundish fibrous	332
282	raphide cells; middle pericarp with scat-	sheaths; fibers thick-walled, without tannin	333
283	tered small clusters of brachysclereids;	in lumen, with stegmata; innermost pericarp	334
284	inner pericarp without tannins, with scat-	densely tanniferous, partially enveloping	335
285	tered large raphide-bearing cells; vascular	the vascular bundles.	336
286	bundles with broad, flat, confluent fibrous		
287	sheaths. (Fig. 2B)		
289	Dypsis pembana (H. E. Moore) Beentje & J.	Additional specimens examined briefly and	337
290	Dransf.; <i>Chrysalidocarpus pembanus</i> H. E.	found to be generally similar to the above:	338
291	Moore. (Moore 9030, BH; Williams 177/	Dypsis scottiana (Becc.) Beentje & J. Dransf.	339
292	56-7, K); Tanzania: Pemban Island. Fruit	(Beentje & Andriampaniry 4608, K).	340
293	11.2 mm long, 5 mm in diameter, dark red		
294	at maturity; pericarp 0.7–0.9 mm thick	<i>DYPsis</i> GROUP 5	342
295	(specimens examined immature). Epidermis	No specimens available.	343
296	flat; outer pericarp with a thick subepidermal		
297	band of tanniferous cells; middle pericarp	<i>DYPsis</i> GROUP 6	344
298	with scattered tanniferous cells, occasional	No specimens available.	345
299	brachysclereids and large raphide/raphide-		
300	bearing cells; vascular bundles broadly ovate,	<i>DYPsis</i> GROUP 7	346
301	sometimes confluent; fibers with stegmata.	No specimens available.	347
303	Additional specimens examined briefly and		
304	found to be generally similar to the above,	<i>DYPsis</i> GROUP 8	349
305	(except as noted): D. lanceolata (Becc.)	Seven species formerly placed in <i>Neophloga</i>	350
306	Beentje & J. Dransf. (<i>Hull s.n.</i> , K)—fibrovas-	with yellow, orange or red fruits and homoge-	351
307	cular bundles broadly ovate, rather than broad	neous endosperm. Two species were examined,	352
308	and flat; Dypsis baronii (Becc.) Beentje &	both with flattened fibrous bundle sheaths.	353
309	Dransf. (Beentje 4412, K); Dypsis onilahane-		
310	sis (Jum. & H. Perrier) Beentje & J. Dransf.	Dypsis concinna Baker; <i>Neophloga concinna</i>	355
311	(Beentje & Andriampaniry 4586, K); Dypsis	(Baker) Becc. (Beentje et al. 4653, K);	356
312	rivularis (Jum. & H. Perrier) Beentje (<i>Du Puy</i>	central eastern Madagascar. Fruit length	357
313	<i>et al.</i> 176A, K); <i>Dypsis serpentina</i> Beentje	unknown, 6.1 mm in diameter, fruit red at	358
314	(Dransfield et al. 7502, K).	maturity; pericarp ca. 0.6 mm thick; epi-	359
315	<i>DYPsis</i> GROUP 4	dermis papillate, lightly pigmented; outer	360
316	Six species of eastern Madagascar formerly	pericarp with thick, discontinuous band of	361
317	placed in the genus <i>Neophloga</i> , with red fruits	tanniferous cells, with occasional large	362
318	and ruminant endosperm. Two species were	raphide-bearing cells; mid-pericarp with	363
319	examined, both with roundish vascular bundles.	additional series of large raphide-bearing	364
321	Dypsis macdonaldiana Beentje. (Beentje &	cells, sclereids lacking; inner pericarp with	365
322	<i>Andriampaniry</i> 4591, K); southeastern	a single layer of vascular bundles with	366
323	Madagascar. Fruit 7.4 long, 5.0 mm in	flattened fibrous sheaths, with small tanni-	367
324	diameter, red at maturity; pericarp ca.	niferous cells on both sides, fibers thick-	368
325	0.75 mm thick. Epidermis of squarish cells	walled, without internal tannin.	369
326	with convex outer walls; outer pericarp with		
327	thick band of tanniferous/pigmented tissue	Additional specimens examined briefly and	370
328	immediately below epidermis; middle to	found to be generally similar to the above: D.	371
329	outer pericarp of parenchyma with frequent	heterophylla Baker (Beentje & <i>Adriampaniry</i>	372
		4408, K).	373

374	<i>DYPsis</i> GROUP 9	(<i>Dypsis forficifolia</i> Noronha ex Mart.); endosperm homogeneous.	421 422
375	A poorly defined group of three species;		
376	endosperm homogeneous.		
378	<i>Dypsis confusa</i> Beentje (<i>Beentje et al.</i> 4627, K); northeastern Madagascar. Fruit 8.4 mm long, 4.2 mm in diameter, orange to red at maturity; pericarp ca. 0.65 mm thick. Epidermis flat, pigmented; outer pericarp with a continuous subepidermal zone of tanniferous tissue, 5–6 cells thick; large raphide-bearing cells scattered through middle pericarp, sclereids lacking; vascular bundles in a single series in the inner pericarp, with thick fibrous sheaths, roundish in outline with unusual extensions radiating outward, fibers filled with tannin, with stegmata on some of the outer fibers; innermost pericarp consisting of a thin band of tanniferous cells. (Fig. 2C)	<i>Dypsis lantzeana</i> Baill. (<i>Beentje et al.</i> 4619, K); northeastern Madagascar. Fruit 10 mm long, 7 mm in diameter, cherry red to dark purple at maturity; pericarp ca. 0.9 mm thick. Outer pericarp with 2–3 layers of tanniferous cells, those immediately below the epidermis distinctly smaller and rounder, with large, scattered brachysclereids and occasional large raphide-bearing cell; inner pericarp with a single series of widely spaced vascular bundles with thick, terete fibrous sheaths, the fibers thin-walled with internal tannin, with a thin layer of flattened tanniferous cells between bundles and seed coat. (Fig. 3A)	424 425 426 427 428 429 430 431 432 433 434 435 436 437 438
389	Additional specimens examined briefly and found to be generally similar to the above:		
395	<i>Dypsis hiarakae</i> Beentje (<i>Beentje et al.</i> 4578, K).		
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399	<i>DYPsis</i> GROUP 10		439
400	No specimens available.	A group of three species of moderate-sized undergrowth palms, considered part of <i>Dypsis</i> sensu strictu, but at one time segregated as the genus <i>Adelodypsis</i> . Two specimens examined both with a highly unusual form of bundle-sheath, consisting of thin-walled fibers filled with tannin, and with radiating fibrous extensions from the sheath.	440 441 442 443 444 445 446 447
401	<i>DYPsis</i> GROUP 11		
402	A group of 17 species of small palms formerly placed in <i>Neophloga</i> ; endosperm homogeneous.	<i>Dypsis pinnatifrons</i> Mart. Eastern Madagascar (<i>Beentje & Andriampaniry</i> 4800, K). Fruit 14 mm long, 6.5 mm in diameter, green turning brownish at maturity; pericarp ca. 2 mm thick. Epidermis flat, unpigmented; outer pericarp with a loose aggregation of tanniferous cells, 4–5 cells thick; mid-pericarp with numerous scattered, large raphide-bearing cells; inner pericarp with a single series of vascular bundles with sheaths of very thin-walled fibers filled with tannin, and with radiating fibrous extensions, sheaths confluent with a thick band of tanniferous tissue, three to four cells thick. (Fig. 3B)	448 449 450 451 452 453 454 455 456 457 458 459 460 461 462
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405	<i>Dypsis catatiana</i> (Baill.) Beentje & J. Dransf. (<i>Beentje & Andriampaniry</i> 4669, K); eastern Madagascar. Fruit 10–15 mm long, 5–9.5 mm in diameter, deep, shiny red at maturity; pericarp ca. 1 mm thick; epidermis flat, darkly pigmented; outer pericarp with thick band densely tanniferous tissue immediately below the epidermis; middle to inner pericarp of parenchyma, without sclereids; inner pericarp with a single series of vascular bundles with roundish fibrous sheaths, fibers with thin walls and internal tannin, and a thin inner band of tanniferous cells.	Additional specimens examined briefly and found to be generally similar to the above: <i>Dypsis paludosa</i> J. Dransf. (<i>Dransfield</i> JD 6771, K).	463 464 465 466 467
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418	<i>DYPsis</i> GROUP 12	<i>DYPsis</i> GROUP 14	468
419	A group of 7 species of small undergrowth palms, including the type of the genus <i>Dypsis</i>	A single species of moderate-sized undergrowth palm; endosperm weakly ruminant.	469 470
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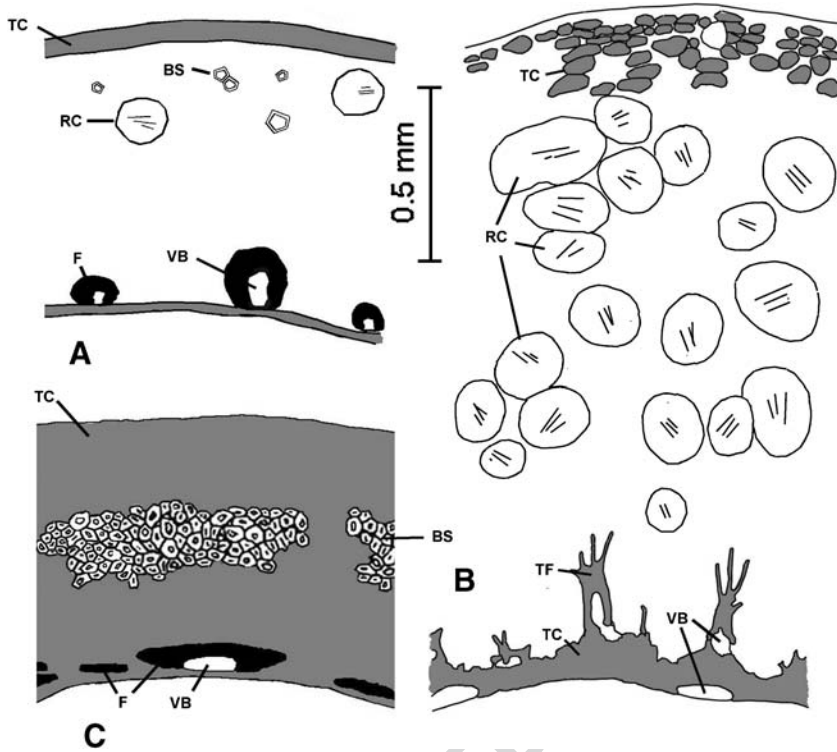


FIG. 3. **A.** *Dypsis lantzeana*, group 12 (from Beentje et al. 4619, K), **B.** *Dypsis pinnatifrons*, group 13 (from Beentje & Andriampaniry 4800, K), **C.** *Dypsis crinita*, group 16 (from Rafamantanait et al. 302, K).

471 **Dypsis mirabilis** J. Dransf. (*Dransfield JD*
 472 *6771*, K); northeastern Madagascar. Fruits
 473 12 mm long, 7 mm in diameter, green (?)
 474 at maturity; pericarp 0.8–0.9 mm thick.
 475 Epidermis flat, unpigmented; outer peri-
 476 carp of 2–3 layers of unpigmented paren-
 477 chyma immediately below the epidermis,
 478 followed by a continuous band of tannini-
 479 ferous cells 2–4 layers thick; middle peri-
 480 carp with scattered, large brachysclereids
 481 and occasional large, raphide-bearing cells;
 482 inner pericarp with a single series of
 483 vascular bundles with thick, roundish
 484 fibrous sheaths, with thick-walled fibers
 485 lacking internal tannin, and a thick band of
 486 flat tanniniferous cells, ca. eight cells thick,
 487 to the interior.

488 **DYPISIS GROUP 15**

489 A group of 3 species of moderate under-
 490 growth palms; endosperm homogeneous or
 491 only slightly ruminant.

Dypsis fasciculata Jum. (*Beentje et al. 4636*, 492
 K); northeastern Madagascar. Fruit 493
 14 mm long, 7.5 mm in diameter, green 494
 (?) at maturity; pericarp 1.1–1.2 mm 495
 thick. Outer half of pericarp weakly 496
 tanniniferous, with scattered raphide-bear- 497
 ing cells; inner pericarp with a single 498
 series of vascular bundles similar to those 499
 of *D. pinnatifrons*, with thin-walled, tan- 500
 nin-filled fibers forming an irregular 501
 sheath with radiating extensions, and with 502
 a thin layer of tanniniferous cells to the 503
 interior. 504

DYPISIS GROUP 16

505 A group of 10 species of large to moderate 506
 palms, mostly from northeastern Madagascar, 507
 including the former genus *Vonitra*, and one 508
 species classified in the genus *Antongilia*, 509
 considered to be closely linked to groups 3 510
 and 7 by Dransfield and Beentje (1995); 511
 endosperm ruminant. 512

513	Dypsis crinita (Jum. & H. Perrier) Beentje &	564
514	J. Dransf.; <i>Vonitra crinita</i> Jum. & H.	565
515	Perrier; (<i>Rafamantanantsoa et al.</i> 55, K);	566
516	northern Madagascar. Fruit 20–24 mm	567
517	long, 17–18 mm in diameter, purple-black	568
518	at maturity. Pericarp 0.7 mm thick; epi-	569
519	dermis flat, pigmented; outer pericarp	570
520	densely tanniniferous/pigmented; middle	571
521	pericarp a massive, occasionally interrup-	572
522	ted, mantle of brachysclereids; inner peri-	573
523	carp densely tanniniferous with scattered	574
524	large raphide-bearing cells; vascular bun-	575
525	dles with broad, flat fibrous sheaths, the	
526	fibers thick-walled, sometimes with small	
527	tannin-filled lumens; an additional thin	
528	zone of tanniniferous cells adjacent to the	
529	seed coat. (Fig. 3C)	
531	Dypsis perrieri (Jum.) Beentje & J. Dransf.;	
532	<i>Antongilia perrieri</i> Jum. Northeastern	
533	Madagascar (<i>Dransfield et al.</i> 6749, K)	
534	Fruit 15–21 mm long, 12–16 mm in	
535	diameter, dull greenish-brown at maturity;	
536	pericarp ca. 2.5 mm thick. Epidermis flat,	
537	unpigmented; outer half of the pericarp	
538	with a thick band of unpigmented paren-	
539	chyma tissue, ca. 15 cells thick, followed	
540	by a massive mantle of tightly-packed	
541	brachysclereids, ca. 20 cells thick, raphi-	
542	de-bearing cells not evident; inner half of	
543	the pericarp with a thick region of unmod-	
544	ified parenchyma and ca. 3 layers of	
545	vascular bundles with thick, broad, fibrous	
546	sheaths, the fibers thick-walled and with-	
547	out interior tannin, tissue to the interior of	
548	the vascular bundles tanniniferous, a few	
549	layers thick.	
551	Additional specimens examined briefly and	
552	found to be generally similar to the above:	
553	Dypsis dransfieldii Beentje (<i>Dransfield et al.</i>	
554	6468, K); Dypsis fibrosa (Wright) Beentje &	
555	J. Dransf. (<i>Beentje</i> 4498, K); Dypsis moorei	
556	Beentje (<i>Moore</i> 9918, BH); Dypsis pusilla	
557	Beentje (<i>Beentje et al.</i> 4651, K).	
558	<i>DYPISIS</i> GROUP 17	
559	A single species previously segregated as	
560	the genus <i>Phloga</i> ; endosperm ruminant.	
562	Dypsis nodifera Mart.; <i>Phloga nodifera</i>	
563	(Mart.) Salomon. (<i>Henderson et al.</i> 759, K);	
	eastern Madagascar. Fruit 8–10 mm long, 5–	564
	8 mm in diameter, color when mature	565
	unknown, pericarp ca. 1 mm thick. Epider-	566
	mis flat; outer pericarp with a subepidermal	567
	layer of tanniniferous tissue 1–3 cells thick;	568
	middle pericarp of parenchyma tissue with	569
	scattered raphide-bearing cells and large	570
	brachysclereids; inner pericarp with a	571
	single series of vascular bundles with	572
	moderate, terete fibrous sheaths, fibers	573
	filled with tannin; a thick band of flat	574
	tanniniferous cells to the interior.	575
	<i>DYPISIS</i> GROUP 18	576
	A group of 18 species of small under-	577
	growth palms, including a group once segre-	578
	gated as the genus <i>Trichodypsis</i> ; endosperm	579
	homogeneous.	580
	Dypsis mocquersiana (Becc.) Becc.; <i>Tricho-</i>	582
	<i>dypsis mocquersiana</i> Becc. (<i>Dransfield</i>	583
	<i>et al.</i> 6368, K); northeastern Madagascar.	584
	Fruit 13 mm long, 5.5 mm in diameter,	585
	bright red at maturity, pericarp ca. 0.6 mm	586
	thick. Epidermis flat; outer pericarp with a	587
	continuous subepidermal layer of tanninifer-	588
	ous tissue ca. three cells thick; middle	589
	pericarp with scattered raphide-bearing	590
	cells, and no sclereids; inner pericarp with	591
	a single series of vascular bundles, but with	592
	alternating bundles somewhat displaced	593
	toward the center, with thick roundish	594
	fibrous sheaths, some of the outward-	595
	displaced bundles apparently with no	596
	mature vascular tissue within; fibers thick-	597
	walled without internal tannin; cells to the	598
	interior weakly tanniniferous, thin.	599
	Discussion	600
	In general, fruits in the Dypsidinae share	601
	the same set of tissues seen in other members	602
	of the Areceae, in similar varied patterns.	603
	These include fibrous vascular bundles, bra-	604
	chysclereids, tanniniferous cells, and raphide-	605
	bearing cells. All except <i>Lemurophoenix</i>	606
	(Fig. 1A), however, lack the sclerified, pali-	607
	sade-like locular epidermis characteristic of	608
	so many of the Areceae.	609
	There are some distinctive features, however,	610
	and some support for the Dypsidinae as the	611
	sister group to the remainder of the Areceae.	612

613 According to Rudall et al. (2003), the species of
 614 *Dypsis* are variable with respect to the degree
 615 to which their ovaries are pseudomonomerous.
 616 Some have trilocular ovaries with an ovule in
 617 each locule, though no cases have been cited of
 618 more than one fertile ovule. As the single
 619 fertile ovule enlarges, the ovary bulges outward
 620 from the axis, with the stigma remaining close
 621 to the base on the opposite side, resulting in the
 622 lateral to basal stigmatic residues characteristic
 623 of mature fruits in this group. The fruits of
 624 triovulate genera, such as *Orania*, behave the
 625 same way when only one locule is fertilized.
 626 Fruits with basal to lateral stigmatic residues
 627 are found in genera amongst other subtribes of
 628 the Areceae (*Bentinckia*, *Iguanura*, *Basselinia*,
 629 *Deckenia*, and all members of the Clinosper-
 630 matinae and *Verschaffeltiinae*), but the trend,
 631 and most common condition is toward apical
 632 stigmatic residues resulting from more-or-less
 633 equal growth of the fertilized and non-fertilized
 634 sides of the ovary.

635 Another apparent archaic feature in the
 636 pericarp of the *Dypsidinae* is the presence of
 637 only one system of vascular and fibrous
 638 bundles. While there may be a mixture of
 639 naked and fibrous vascular strands, some-
 640 times with some intermixed purely fibrous
 641 bundles, none in this group has a separate
 642 series of fibrous bundles in the outer pericarp,
 643 as is found in the *Ptychospermatinae*, *Car-*
 644 *poxylinidae*, *Archontophoenicinae*, *Basselini-*
 645 *dae*, and others. Similar simple bundle
 646 systems are found in other genera scattered
 647 throughout the Areceae (e.g., *Bentinckia*,
 648 *Iguanura*, *Nephrosperma*, *Cyrtostachys*, and
 649 *Linospadix*).

650 In *Dypsis*, fruits lack the thickened locular
 651 epidermis that is so common among the
 652 Areceae. In this character, the genus may or
 653 may not also be archaic. Similar locular
 654 epidermises have been seen in a number of
 655 other groups, such as the *Phytelephantoideae*
 656 *Ceroxyloideae*, *Geonomeae* and *Caryoteae*
 657 (Essig, 1999), though these have not been
 658 carefully analyzed to see if they are homolo-
 659 gous. Also, some other Areceae lack a locular
 660 epidermis (*Cyrtostachydinae*, and many other
 661 individual genera). *Lemurophoenix*, if truly
 662 part of the *Dypsidinae*, is an exception with a
 663 well-developed locular epidermis. The fruits of
 664 *Lemurophoenix* are quite large, with an excep-
 665 tionally thick pericarp of 8–10 mm. Larger
 666 fruits in general are more amply endowed with
 667 protective tissues.

668 Species, rather than groups, within *Dypsis*
 669 can be distinguished by the relative amounts
 670 of tanniferous tissue, raphide-bearing cells,
 671 and brachysclereids, while the shape of the
 672 fibrous bundle sheaths may have more signif-
 673 icance (Table I). Most have fibrous vascular
 674 bundles that are round or radially distended in
 675 outline (Figs. 2A and 3A, B), but groups 1, 3,
 676 8, 16 have markedly flattened bundles
 677 (Figs. 2A, B and 3C). Two unusual special-
 678 izations are found in some of the groups of
 679 *Dypsis*. One is a modification of the fibrous
 680 bundle sheaths in which the fibers are thin-
 681 walled and filled with tannin (Figs. 2C, 3B,
 682 and 4A). This is found in groups 9, 11, 12, 13,
 683 15, 16, 17, and possibly others for which
 684 inadequate material were available. Tannin-
 685 filled fibers likely represent a synapomorphy
 686 defining a clade including these groups. I have

TABLE I
 CHARACTERS OF POTENTIALLY DIAGNOSTIC VALUE WITHIN THE DYPSIDINAE

t1.1	Character	Groups/Genera
t1.2	Fibrovascular bundles strongly flattened, often confluent	<i>Dypsis</i> groups 1, 3 (exc. <i>D. lanceolata</i>), 8, 16, <i>Marojejya</i>
t1.3	Fibers of bundle sheath tannin-filled	<i>Dypsis</i> groups 9, 11, 12, 13, 15, 16, 17
t1.4	Bundle sheaths with radial extensions	<i>Dypsis</i> groups 9, 13, 15
t1.5	Bundle sheaths and fibrous bundles strongly radially distended	<i>Masaola</i>
t1.6	Vascular bundles widely dispersed in the pericarp, many without fibrous sheaths	<i>Lemurophoenix</i>
t1.7	Locular epidermis composed of macrosclereids	<i>Lemurophoenix</i>
t1.8	Brachysclereids numerous in mid to outer pericarp	<i>Dypsis</i> groups 1, 3, 12, 14, 16, 17, <i>Lemurophoenix</i> , <i>Marojejya</i> , <i>Masaola</i>

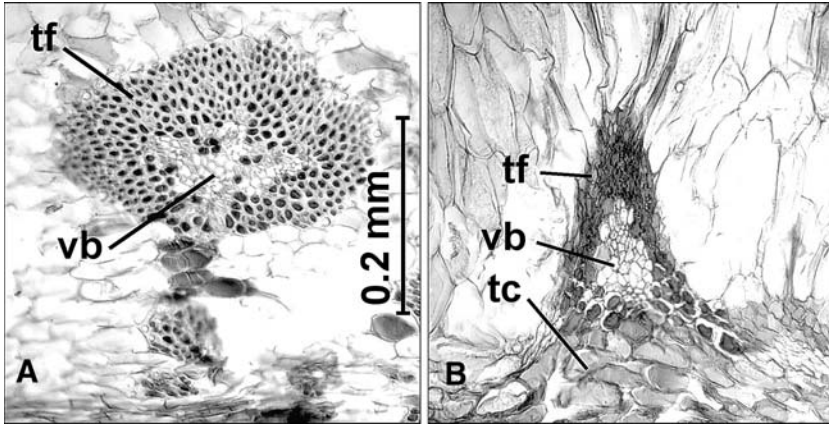


FIG. 4. Photomicrographs of the peculiar, tannin-filled fibers found around the vascular bundles in several species, note also the finger-like extensions in *D. pinnatifrons*; A. *D. catatiana* (from Beentje & Andriampaniry 4669, K), B. *D. pinnatifrons* (from Beentje & Andriampaniry 4800, K).

687 seen similar tannin-filled fibers elsewhere only
 688 in the peripheral cells of the fibrous bundles of
 689 *Alsmithia*, but there is no other reason to
 690 suggest a connection with that genus. A
 691 second modification, found as a subset of this
 692 group, consists of odd radial extensions of the
 693 fibrous bundle sheaths (Figs. 2C, 3B and 4B).
 694 This character is found so far in groups 9, 13,
 695 and 15. This is such a distinctive and unusual
 696 character that it is highly likely a synapomor-
 697 phy uniting these groups.

698 With respect to the other 3 genera, pericarp
 699 characters may shed some light on their
 700 unresolved relationships. Aside from the
 701 anomalous presence of a thickened locular
 702 epidermis, *Lemurophoenix* bears some resem-
 703 blance to *Masoala* (which might of course
 704 develop a locular epidermis as it matures),
 705 particularly in the occurrence of unsheathed
 706 vascular strands in addition to some with
 707 fibrous sheaths. In this regard, however, it
 708 shows little resemblance to any species of
 709 *Dypsis*, which all have thick fibrous sheaths
 710 around all of their vascular bundles. *Masoala*
 711 (Fig. 1C) is highly distinct, however, in that
 712 the fibrous sheaths of its outer band of
 713 vascular bundles are massive and radially
 714 distended, with some purely fibrous bundles
 715 intermixed, while fibrous sheaths are few and
 716 relatively thin in *Lemurophoenix*. Pericarp
 717 anatomy therefore is not supportive of a
 718 relationship between *Lemurophoenix* and/or
 719 *Masoala* with any members of *Dypsis* that
 720 have been seen.

Looking outside of the *Dypsidinae*, the
 pericarp anatomy of *Masoala* finds its
 greatest similarity with members of the
Oncospermatinae, and with the unplaced
 genera *Heterospatha* and *Bentinckia*, in
 which fruits have an outer series of thick
 fibrous vascular bundles and/or purely fi-
 brous bundles, and inner unsheathed vascu-
 lar bundles. This suggested link of *Masoala*
 with *Oncospermatinae* supports the relation-
 ship suggested by the recent phylogenetic
 studies of Loo et al. (2006) and Norup et al.

Marojejya (Fig. 1B) has the most *Dypsis*-
 like fruit, with flattened fibrous bundle
 sheaths, a thick layer of tanniferous tissue
 below the epidermis, and a dense mantle of
 brachysclereids below that. It shows affinities
 with *Dypsis* groups 1, 3, 8, and 16. Interest-
 ingly, *Marojejya* was resolved as sister to *D.*
lutescens (group 3) in one phylogenetic
 analysis (Asmussen & Chase, 2001), and
 with *D. heterophylla* (group 8) in another
 phylogenetic analysis (Loo et al., 2006).
 Pericarp data therefore support the inclusion
 of *Marojejya* in *Dypsis*.

This study, though very cursory and with a
 limited sample of species, reaffirms the value
 of anatomical data, which may both challenge
 and confirm conclusions derived from other
 sorts of data. Anatomical studies of the palms
 should continue and should be considered
 seriously in future revisionary and phyloge-
 netic studies.

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771 noncoding plastid DNA in palm systematics. *Ameri-*
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