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PHYLOGENY OF CYPERACEAE BASED ON DNA SEQUENCE DATA—A NEW *rbc*L ANALYSIS

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ABSTRACT

Since the Monocots II meeting in 1998, significant new data have been published that enhance our systematic knowledge of Cyperaceae. Phylogenetic studies in the family have also progressed steadily. For this study, a parsimony analysis was carried out using all *rbc*L sequences currently available for Cyperaceae, including data for two new genera. One of the four subfamilies (Caricoideae) and seven of the 14 tribes (Bisboeckelereae, Cariceae, Cryptangieae, Dulichieae, Eleocharideae, Sclerieae, Trilepideae) are monophyletic. Subfamily Mapanioideae and tribe Chrysitricheae are monophyletic if, as the evidence suggests, *Hellmuthia* is considered a member of Cypereae. Some other features of our analysis include: well-supported Trilepideae and Sclerieae–Bisboeckelereae clades; a possible close relationship between Cryptangieae and Schoeneae; polyphyletic tribes Schoeneae and Scirpeae; the occurrence of Cariceae within the Dulichieae–Scirpeae clade, and a strongly supported clade, representing *Cyperus* and allied genera in Cypereae, sister to a poorly supported *Ficinia–Hellmuthia–Isolepis–Scirpoides* clade. Such patterns are consistent with other studies based on DNA sequence data. One outcome may be that only two subfamilies, Mapanioideae and Cyperoideae, are recognized. Much further work is needed, with efforts carefully coordinated among researchers. The work should focus on obtaining morphological and molecular data for all genera in the family.

Key words: Cyperaceae, monocotyledons, phylogeny, *rbc*L, sequence.

INTRODUCTION

Cyperaceae comprise ca. 5000 species in ca. 102 genera, 14 tribes, and four subfamilies (Goetghebeur 1998). Since the Monocots II meeting in 1998, significant new data have been published that further enhance systematic knowledge of the family. New species have been described in various genera including *Carex* L. (Reznicek and González-Elizondo 1999; Naczi et al. 2001, 2002), *Hypolytrum* Rich. ex Pers. (Alves and Thomas 2002; Alves et al. 2002), *Isolepis* R. Br. (Muasya and Simpson 2002), *Oreobolopsis* T. Koyama & Guagl. (Dhooge and Goetghebeur 2002), and *Schoenoplectus* (Rchb.) Palla (Hayasaka 2003). New genera, such as *Capeobolus* J. Browning, *Cypringlea* M. T. Strong, *Khaosokia* D. A. Simpson, Chayam. & J. Parn., and *Zameioscirpus* Dhooge & Goetgh., have recently been discovered (Browning and Gordon-Gray 1999; Strong 2003; Dhooge et al. 2003; Simpson et al. 2005). Important floristic treatments have been published, including those for the *Flora of North America* (Flora of North America Editorial Committee 2002), *Flora of Pakistan* (Kukkonen 2001), *Flora of Thailand* (Simpson and Koyama 1998), and *Flora of the Venezuelan Guayana* (Kearns et al. 1998). Information has been gathered on the economic and ethnobotanical importance of Cyperaceae showing that ca. 10% of the family are used, particularly at local or regional levels in the tropics (Simpson and Inglis 2001). The first evolutionary dating evidence has also been presented indicating that the cyperoid clade had a west Gondwanan origin ca. 100–120 millions of years ago (mya), and that the split of Juncaceae and Cyperaceae occurred ca. 65–80 mya (Bremer 2002).

Phylogenetic studies in the family have progressed steadily since 1998. At the family level, suprageneric relationships have been evaluated using plastid *rbc*L (Muasya et al. 1998) and combined DNA and morphological studies (Muasya et al. 2000*a*; Nieuwborg et al. 2001). Studies within subfamilies have focused on Caricoideae (Starr et al. 1999, 2003, 2004, in press; Yen and Olmstead 2000;

Roalson et al. 2001), Cyperoideae (Muasya et al. 2000*b*, 2001, 2002; Zhang et al. 2004*a, b*) and Mapanioideae (Simpson et al. 2003). These studies have had minimal overlap of the taxa.

For this study we concentrated on a molecular analysis that encompassed the broadest possible spectrum of genera in Cyperaceae, including data for two new genera (*Khaosokia* and *Zameioscirpus*).

MATERIALS AND METHODS

Analyses included a total of 167 species of Cyperaceae, representing 66 genera from the 14 tribes, and four subgenera recognized by Goetghebeur (1998). Sequences of *rbc*L from published studies (Muasya et al. 2000*a, b,* 2001, 2002; Bremer 2002; Dhooge et al. 2003) were analyzed together with 12 newly sequenced taxa (Table 1). Total DNA was extracted from leaf and/or culm samples removed from herbarium specimens or material collected in the field (fresh and silica dried). DNA extraction, amplification, and sequencing were performed according to published procedures (e.g., Muasya et al. 2002). Data were easily aligned manually because no insertions/deletions occurred.

Heuristic analyses were carried out using PAUP* vers. 4.0 software (Swofford 2002) on a Macintosh G4. Searches were conducted using Fitch (1971) parsimony using equally weighted characters, TBR (tree-bisection-reconnection) branch-swapping, and random taxon additions (1000 replicates) with the MulTrees option in effect. Only ten trees were saved per replicate to avoid extreme swapping on suboptimal islands. Internal support for clades was estimated using 1000 bootstrap replicates (Felsenstein 1985), with simple taxon addition, TBR branch-swapping, and the MulTrees option in effect, holding ten trees per step. The following categories were used to describe levels of bootstrap support: weak = 50–74%, moderate = 75–84%, and strong = 85–100%.

RESULTS

A total of 1321 sites were included in the analysis of which 534 were variable and 318 were parsimony informative. Analysis resulted in 1370 equally parsimonious trees of 1720 steps, with consistency index (CI) = 0.42 and retention index (RI) = 0.76. One of these trees was randomly chosen and is shown in Fig. 1–3. Nodes not recovered in the strict consensus tree are indicated by arrows. Using *Philydrum* Banks ex Gaertn. (Philydraceae) and *Prionium* E. Mey. (Juncaceae) as outgroup taxa, Cyperaceae formed a monophyletic group with a bootstrap percentage (BP) of 100%.

Of the four subfamilies, only Caricoideae were monophyletic in the analysis. Seven of the 14 tribes (Bisboeckelereae, Cariceae, Cryptangieae, Dulichieae, Eleocharideae, Sclerieae, Trilepideae) were monophyletic. Abildgaardieae and Schoeneae 3 (Fig. 2) formed a polytomy in the consensus tree.

The analysis positions subfamily Mapanioideae (BP 100) as sister to the remainder of Cyperaceae (BP 79). Within Mapanioideae, Chrysitricheae are strongly supported (BP 97) but nested within Hypolytreae. Hypolytreae form a polytomy with *Hypolytrum* separate from the *Mapania* Aubl.–*Scirpodendron* Zipp. ex Kurz clade.

The topology of the clade comprising the rest of Cyperaceae was well resolved in the individual trees, although a number of clades lacked BP >50. Many subclades within major clades were not recovered in the strict consensus tree. Strongly supported clades included those corresponding to Trilepideae (BP 100), Sclerieae–Bisboeckelereae (BP 98), and Rhynchosporeae (BP 99). Two large clades were resolved from taxa mainly assigned to Cypereae. One of these was strongly supported (BP 98) and comprised members *Cyperus* L. and allied genera (Fig. 3: Cypereae 2). The other was weakly supported (BP 62) and included *Hellmuthia* Steud. (Fig. 3: Chrysitricheae 2), together with species of *Isolepis, Ficinia* Schrad., and allied genera in Cypereae (Fig. 3: Cypereae 3).

DISCUSSION

Various DNA studies, based on multiple gene regions (e.g., Muasya et al. 1998, 2000*a*, 2001, 2002), are beginning to reveal a consistent pattern of higher-level relationships in Cyperaceae. The features of this pattern shown by our analysis include: a strongly supported clade representing Mapanioideae; strongly supported Trilepideae and Sclerieae–Bisboeckelereae clades; a possible close relationship between Cryptangieae and Schoeneae; polyphyletic tribes Schoeneae and Scirpeae; the occurrence of Cariceae within a Dulichieae–Scirpeae clade, and a strongly supported clade representing *Cyperus* and allied genera in Cypereae sister to a poorly to moderately supported *Ficinia–Hellmuthia–Isolepis–Scirpoides* Ség. clade.

Mapanioideae form a strongly supported group in our analysis, with an outlying member, *Hellmuthia,* placed as sister (BP 62) to the Cypereae 3 clade. A similar pattern has been observed in other morphological and DNA studies (e.g., Bruhl 1995; Muasya et al. 1998, 2000*a*, 2001; Simpson et al. 2003) in which *Hellmuthia* has been variously associated with *Desmoschoenus* Hook. f., *Ficinia, Isolepis,* and *Scirpoides. Hellmuthia* has been included in Chrysitricheae by Haines and Lye (1976) and Goetghebeur (1998) based on an interpretation of its floral morphology (the presence of two floral scales), which was regarded as homologous with that of other members of the tribe. However, in other characteristics the plant is morphologically similar to *Ficinia,* and is endemic to the sand dunes of the Western Cape of South Africa, an area that is the center of diversity for the *Ficinia–Isolepis* group. Given the weight of evidence now available, we consider that its position in Chrysitricheae cannot be maintained and propose its transfer to Cypereae. This would also make Mapanioideae and Chrysitricheae monophyletic. However, further work is needed to determine its precise relationships within Cypereae and to evaluate patterns of floral evolution.

Opinion has differed as to whether Mapanioideae comprises one or two tribes. Bruhl (1995), based on non-molecular data, favored the former (Hypolytreae), as Chrysitricheae were usually nested in other mapanioids in his analyses. However, recent studies (Simpson et al. 2003), with a more comprehensive sample that included both pollen and molecular data, supported the recognition of both Hypolytreae and Chrysitricheae. Hypolytreae have been shown to have pollen that is unlike that of other Cyperaceae (Simpson

Table 1. List of taxa sampled with vouchers and GenBank accession numbers.

Taxon	Voucher	GenBank accession numbers
I. CARICOIDEAE Pax		
Cariceae Kunth ex Dumort.		
Carex conferta A. Rich.	KENYA: *Muasya 1055* (K)	Y12999
C. echinochloe Kunze	KENYA: *Muasya 1051* (K)	Y12997
C. hostiana DC.	SWEDEN: cited in Chase et al. (1993)	L12672
C. monostachya A. Rich.	KENYA: *Muasya 1052* (K)	Y12998
Kobresia simpliciscula (Wahl.) Mack.	USA: Goodrich 19537 (WS)	U49232
Uncinia nemoralis K. L. Wilson	AUSTRALIA: *Wilson et al. 9533 (K)*	AY725956
II. CYPEROIDEAE Suess.		
Abildgaardieae Lye		
Abildgaardia ovata (Burm. f.) Kral	KENYA: *Muasya et al. 684* (EA, K)	Y12985
Bulbostylis atrosanguinea (Boeck.) C. B. Clarke	KENYA: *Muasya 1037* (EA, K)	Y12992
B. hispidula (Vahl) R. W. Haines	KENYA: *Muasya 1025* (EA, K)	Y12944
Fimbristylis complanata (Retz.) Link	KENYA: *Muasya 1029* (EA, K)	Y13009
F. dichotoma (L.) Vahl	KENYA: *Muasya 1006* (EA, K)	Y13008
Nemum spadiceum (Lam.) Desv. ex Ham.	WEST AFRICA: *Baldwin 9766* (K)	Y12945
Cypereae Dumort.		
Alinula paradoxa Goetgh. & Vorster	TANZANIA: *Faden et al. 96/29* (K)	AJ278290
Ascolepis capensis (Kunth) Ridl.	KENYA: *Muasya 1009* (EA, K)	Y13003
A. protea Welw.	CONGO: *Fay 2700* (K)	Y13002
Courtoisina assimilis (Steud.) Maquet	TANZANIA: *Faden et al. 96/119* (K)	AY40590
Cyperus compressus L.	THAILAND: *Muasya 1375* (K)	AF449506
C. congestus Vahl	AUSTRALIA: *Coveny et al. 17492* (K)	AF449507
C. cuspidatus Kunth	THAILAND: *Muasya 1374* (K)	AF449508
C. cyperoides (L.) Kuntze	THAILAND: *Muasya 1277* (K)	AF449509
C. dichroostachyus A. Rich.	KENYA: *Muasya 976* (EA, K)	Y12965
C. endlichii Kük.	KENYA: *Muasya 695* (K)	AF449510
C. involucratus Rottb.	MADAGASCAR: Kew Acc. 6136603 (K)	Y12967
C. kerstenii Boeck.	KENYA: *Muasya 984* (EA, K)	Y13018
C. laevigatus L.	KENYA: *Muasya 1041* (EA)	Y13017
C. longus L.	EUROPE: *Chase 2276* (K)	Y13015
C. meeboldii Kük.	KENYA: *Muasya 1255* (EA, K)	AF449511
C. papyrus L.	CHAD: *Hepper 4213* (K)	Y12966
C. plateilema (Steud.) Kük.	KENYA: *Muasya 969* (EA, K)	AF449512
C. pseudovestitus (C. B. Clarke) Kük.	KENYA: *Muasya 1268* (K)	AF449513
C. pulchellus R. Br.	THAILAND: *Muasya 1377* (K)	AY40591
C. pygmaeus Rottb.	KENYA: *Muasya 1133* (K)	AJ404698
C. rigidifolius Steud.	KENYA: *Muasya s. n.,* coll. 1995 (K)	Y13016
C. tenellus L. f.	SOUTH AFRICA: *Muasya 1151* (K)	AF449514
Desmoschoenus spiralis Hook. f.	NEW ZEALAND: *Ford 44/94* (NU)	AJ404701
Ficinia gracilis Schrad.	TANZANIA: *Grimshaw 93939* (K)	Y12963
F. nodosa (Rottb.) Goetgh., Muasya & D. A. Simpson	AUSTRALIA: *Stind 21216* (K)	Y12984
F. pinguior C. B. Clarke	SOUTH AFRICA: *Muasya 1183* (K)	AJ404703
F. striata (Thunb.) Kunth	SOUTH AFRICA: *Hanekon 1244* (K)	Y12964
F. tristachya (Rottb.) Nees	SOUTH AFRICA: *Muasya 1233* (K)	AJ404702
F. trollii (Kük.) Muasya & D. A. Simpson	ZIMBABWE: *Browning et al. 5970* (NU)	AJ404730
Isolepis antarctica (L.) Roem. & Schult.	SOUTH AFRICA: *Muasya 2247* (K)	AY725946
I. aucklandica Hook. f.	AUSTRALIA: *Wilson et al. 9462* (K)	AJ404704
I. bicolor Carmich.	TRISTAN DA CUNHA: *Richardson 105* (K)	AJ404705
I. cernua (Vahl) Roem. & Schult. var. *cernua*	BRITAIN: *Muasya 1058* (K)	Y13014
I. cernua (Vahl) Roem. & Schult. var. *meruensis* (Lye) Muasya	TANZANIA: *Muasya 1061* (K)	AJ404715
I. cernua (Vahl) Roem. & Schult. var. *platycarpa* (S. T. Blake) Muasya	AUSTRALIA: *Coveny et al. 17465* (K)	AJ404716
I. cernua (Vahl) Roem. & Schult. var. *setiformis* (Benth.) Muasya	SOUTH AFRICA: *Muasya 1194* (K)	AJ404725
I. costata A. Rich.	KENYA: *Muasya 1049* (EA, K)	Y12981
I. crassiuscula Hook. f.	AUSTRALIA: *Coveny et al. 17478* (K)	AJ404706

Table 1. Continued.

Taxon	Voucher	GenBank accession numbers
I. diabolica (Steud.) Schrad.	SOUTH AFRICA: *Muasya 1163* (K)	AJ404707
I. digitata Nees ex Schrad.	SOUTH AFRICA: *Muasya 1230* (K)	AJ404708
I. fluitans (L.) R. Br.	KENYA: *Muasya 1057* (K)	Y12961
I. gaudichaudiana Kunth	AUSTRALIA: *Coveny et al. 17476* (K)	AJ404709
I. graminoides (R. W. Haines & Lye) Lye	KENYA: *Muasya 986* (EA, K)	Y12960
I. habra (Edgar) Soják	AUSTRALIA: *Coveny et al. 17477* (NSW)	AJ404710
I. humillima (Benth.) K. L. Wilson	AUSTRALIA: *Thomas et al. 622* (BRI)	AJ404728
I. hystrix (Thunb.) Nees	SOUTH AFRICA: *Muasya 1150* (K)	AJ404711
I. inundata R. Br.	AUSTRALIA: *Wilson et al. 9461* (NSW)	AJ404712
I. inyangensis Muasya & Goetgh.	ZIMBABWE: *Muasya et al. 2025* (K)	AJ297506
I. keniaensis Lye	KENYA: *Cabolt plant 'A'* (K)	Y12980
I. ludwigii (Steud.) Kunth	SOUTH AFRICA: *Muasya 1181* (K)	AJ404713
I. marginata (Thunb.) A. Dietr.	AUSTRALIA: *Coveny et al. 17452* (K)	AJ404714
I. montivaga (S. T. Blake) K. L. Wilson	AUSTRALIA: *Wilson et al. 9480* (K)	AJ297507
I. pellocolea B. L. Burtt	LESOTHO: *Gordon-Gray 49694* (NU)	AJ404729
I. producta (C. B. Clarke) K. L. Wilson	AUSTRALIA: *Wilson et al. 9510* (K)	AJ404717
I. prolifera (Rottb.) R. Br.	AUSTRALIA: *Coveny et al. 17487* (K)	AJ404718
I. rubicunda (Nees) Kunth	SOUTH AFRICA: *Muasya 1221* (K)	AJ404719
I. sepulcralis Steud.	AUSTRALIA: *Coveny et al. 17456* (K)	AJ404720
I. setacea (L.) R. Br.	KENYA: *Muasya 1059* (K)	Y12962
I. striata (Nees) Kunth	SOUTH AFRICA: *Muasya 1141* (K)	AJ404721
I. subtilissima Boeck.	AUSTRALIA: *Coveny et al. 17474* (K)	AJ297508
I. sulcata (Thouars) Carmich.	TRISTAN DA CUNHA: *Richardson 80* (K)	AJ404722
I. tenuissima (Nees) Kunth	SOUTH AFRICA: *Muasya 2369* (K)	AY725947
I. varians Steud.	CHILE: *Pisano 259* (K)	AJ404723
I. venustula Kunth	SOUTH AFRICA: *Muasya 1189* (K)	AJ404724
I. wakefieldiana (S. T. Blake) K. L. Wilson	AUSTRALIA: *Neish et al. 110* (K)	AJ404726
Kyllinga appendiculata K. Schum.	KENYA: *Muasya 991* (EA, K)	Y13007
K. brevifolia Rottb.	AUSTRALIA: *Coveny et al. 17459* (K)	AF449515
K. bulbosa P. Beauv.	KENYA: *Muasya 1020* (EA, K)	Y12979
Kyllingiella microcephala (Steud.) R. W. Haines & Lye	ZIMBABWE: *Muasya et al. 1118* (K)	AY040592
K. polyphylla (A. Rich.) Lye	TANZANIA: *Wingfield 497* (K)	Y13013
Lipocarpha hemisphaerica (Roth.) Goetgh.	THAILAND: *Muasya 1217* (K)	AF449516
L. microcephala (R. Br.) Kunth.	AUSTRALIA: *Wilson et al. 3383* (K)	Y12991
L. nana (A. Rich.) J. Raynal	KENYA: *Muasya 972* (EA, K)	Y12990
Oxycaryum cubensis (Poepp. & Kunth) Lye	ZAMBIA: *Richards 13318* (K)	Y13006
Pycreus flavescens (L.) Rchb.	KENYA: *Muasya 1022* (EA, K)	Y13005
P. mundtii Nees	THAILAND: *Muasya 1464* (K)	AF449517
P. nuerensis (Boeck.) S. S. Hooper	TANZANIA: *Muasya 940* (EA,K)	Y13004
Queenslandiella hyalina (Vahl) F. Ballard	KENYA: *Mwachala 296* (EA)	AY725953
Remirea maritima Aubl.	TANZANIA: *Faden et al. 96/48* (K)	AY040593
Scirpoides burkei (C. B. Clarke) Goetgh., Muasya & D. A. Simpson	SOUTH AFRICA: *Hargreaves 3361* (K)	Y13001
S. holoschoenus (L.) Soják	SOUTH AFRICA: *Acocks s. n.* (K)	Y12994
S. thunbergii (Schrad.) Soják	SOUTH AFRICA: *Muasya 1205* (K)	AJ404727
Sphaerocyperus erinaceus (Ridl.) Lye	TANZANIA: *Faden et al. 96/338* (K)	AJ404699
ELEOCHARIDEAE Goetgh.		
Eleocharis atropurpurea (Retz.) Presl	KENYA: *Muasya et al. 752* (EA, K)	Y13012
E. marginulata Steud.	KENYA: *Muasya 1039* (EA, K)	Y13011
E. pauciflora (Lightf.) Link.	USA: *Mastrogiuseppe 7461* (WS)	Y49229
DULICHIEAE Rchb. ex J. Schultze-Motel		
Blysmus compressus Panz.	AFGHANISTAN: *Dobson 221* (K)	AJ404700
Dulichium arundinaceum (L.) Britton	USA: *Goetghebeur 9914* (GENT)	AY725943
Khaosokia caricoides D. A. Simpson, Chayam. & J. Parn.	THAILAND: *Simpson et al. 1886* (K)	AY725948
FUIRENEAE Rchb. ex Fenzl		
Actinoscirpus grossus (L. f.) Goetgh. & D. A. Simpson	MALAYSIA: *Simpson 2660* (K)	Y12953

Table 1. Continued.

Taxon	Voucher	GenBank accession numbers
Bolboschoenus maritimus (L.) Palla	BOTSWANA: *Smith 2452* (K)	Y12996
B. nobilis (Ridl.) Goetgh. & D. A. Simpson	SOUTH AFRICA: *Leistner 144* (K)	Y12995
Fuirena Rottb. sp.	BRAZIL: *Thomas et al. 10404* (NY)	Y12970
F. ciliaris (L.) Roxb.	TANZANIA: *Muasya 951* (EA, K)	Y12971
F. welwitschii Ridl.	KENYA: *Muasya 1024* (EA, K)	Y12993
Schoenoplectus articulatus (L.) Palla	TANZANIA: *Muasya 947* (EA, K)	Y12987
S. junceus (Willd.) J. Raynal	KENYA: *Muasya et al. 775* (K)	Y12952
S. lacustris (L.) Palla	BRITAIN: *Muasya 1043* (EA, K)	Y12943
SCHOENEAE Dumort.		
Arthrostylis aphylla R. Br.	AUSTRALIA: *Wilson 8249* (NSW)	AY725939
Baumea rubiginosa (Spreng.) Boeck	AUSTRALIA: *Wilson et al. 9471* (K)	AY725940
Carpha alpina	Cited in Wardle et al. (2001)	AF307909
C. schoenoides	*Muasya s. n.* (K)	
C. glomerata (Thunb.) Nees.	SOUTH AFRICA: *Muasya 1176* (K)	AY725941
Caustis dioica R. Br.	AUSTRALIA: *Chase 2225* (K)	Y12976
Cladium P. Browne sp.	BRAZIL: *Mayo 259* (K)	Y12950
C. jamaicensis Crantz	BRAZIL: *Thomas et al. 10403* (NY)	Y12988
Evandra aristata R. Br.	AUSTRALIA: *Wilson et al. 8974* (NSW)	AY725944
Gahnia javanica Mor.	MALAYSIA: *Simpson 2657* (K)	Y12973
G. deusta (R. Br.) Benth.	AUSTRALIA: *Alcock 11198* (WS)	U49231
Gymnoschoenus sphaerocephalus (R. Br.) Hook. f.	AUSTRALIA: *Wilson et al. 9463* (K)	AY725945
Lepidosperma tortuosum F. Muell.	AUSTRALIA: *Coveny et al. 17470* (K)	AY725950
Mesomelaena pseudostygia (Kük.) K. L. Wilson	AUSTRALIA: *Chase 2226* (K)	Y12959
M. tetragona (R. Br.) Benth.	AUSTRALIA: *Chase 2227* (K)	Y12949
Neesenbeckia punctoria (Vahl) Levyns	SOUTH AFRICA: *Muasya 1214* (K)	AY725952
Oreobolus kuekenthalii Steenis	MALAYSIA: *Simpson 2659* (K)	Y12972
O. obtusangulus Gaudich.	CHILE: *Wardle et al.* CHR514085 (CHR)	AF307926
O. pectinatus Hook. f.	NEW ZEALAND: *Wardle et al.* CHR517321 (CHR)	AF307927
Pleurostachys Brongn. sp.	BRAZIL: *Kallunki et al. 513* (NY)	Y12989
Rhynchospora fascicularis (Michx.) Vahl.	USA: *Boufford 23053* (WS)	U49233
R. nervosa (Vahl.) Boeck.	BRAZIL: Kallunki et al. 512 (NY)	Y12977
Schoenus nigricans L.	ARABIA: *Edmondson 3382* (K)	Y12983
Tricostularia pauciflora (R. Br.) Benth.	AUSTRALIA: *Coveny et al. 17484* (K)	AY725954
SCIRPEAE Kunth ex Dumort.		
Eriophorum vaginatum L.	BRITISH ISLES: *Beyer et al. 2* (K)	Y12951
E. viridicarinatum (Engl.) Fern.	USA: *Boufford 23053* (WS)	U49230
Oreobolopsis inversa Dhooge & Goetgh.	ECUADOR: *Laegaard 21492* (GENT)	AJ811009
O. tepalifera T. Koyama & Guagl.	ECUADOR: *Laegaard 21493* (AAU, GENT, QCA)	AJ575932
Phylloscirpus acaulis (Phil.) Goetgh. & D. A. Simpson	ARGENTINA: *Ruthsatz 9341* (GENT)	AJ575926
P. boliviensis (Barros) Dhooge & Goetgh.	ECUADOR: *Laegaard 102805* (GENT)	AJ566081
P. deserticola (Phil.) Dhooge & Goetgh.	ECUADOR: *Laegaard et al. 21478* (GENT)	AJ704785
Scirpus polystachyus F. Muell.	AUSTRALIA: *Pullen 4091* (K)	Y12974
S. radicans Schkuhr	CZECH REPUBLIC: *Goetghebeur 9882* (GENT)	AJ811012
Trichophorum caespitosum (L.) Hartm.	BRITISH ISLES: *Nelmes 954* (K)	Y12969
T. clintonii Gray	CANADA: *Baldwin 4856* (K)	Y12982
T. rigidum (Boeck.) Goetgh., Muasya & D. A. Simpson subsp. *rigidum*	ARGENTINA: *Renvoize et al. 5021* (K)	AJ297509
T. rigidum (Boeck.) Goetgh., Muasya & D. A. Simpson subsp. *ecuadoriensis* Dhooge & Goetgh. (ined.)	ECUADOR: *Laegaard et al. 21574* (GENT)	AJ811008
T. subcapitatum (Thwaites & Hook.) D. A. Simpson	PAPUA NEW GUINEA: *Goetghebeur et al. 6581* (GENT)	AJ811006
Zameioscirpus atacamensis (Phil.) Dhooge & Goetgh.	BOLIVIA: *Ruthsatz 10328* (US)	AJ575929
Z. gaimardioides (E. Desv.) Dhooge & Goetgh.	ARGENTINA: *Ruthsatz 9676* (US)	AJ575938
Z. muticus Dhooge & Goetgh.	ARGENTINA: *Ruthsatz 9212* (GENT)	AJ575927
III. MAPANIOIDEAE C. B. Clarke		
CHRYSITRICHEAE Lestib. ex Fenzl		
Chorizandra cymbaria R. Br.	AUSTRALIA: *Saltzmann s. n.* (UPS)	AJ419940
C. enodis Nees	AUSTRALIA: *Clarke 2317* (S)	AJ419939

Table 1. Continued.

Taxon	Voucher	GenBank accession numbers
Chrysitrix capensis L.	SOUTH AFRICA: *Muasya 1242* (K)	AJ419938
Hellmuthia membranacea (Thunb.) R. W. Haines & Lye	SOUTH AFRICA: *Weerderman et al. 269* (K)	Y13000
Lepironia articulata (Retz.) Domin.	MALAYSIA: *Simpson 1236* (K)	Y12957
HYPOLYTREAE Presl ex Fenzl		
Hypolytrum bullatum C. B. Clarke	BRAZIL: *Thomas et al. 10318* (NY)	Y12956
H. nemorum (Vahl) Spreng.	MALAYSIA: *Simpson 1379* (K)	Y12958
Mapania cuspidata (Miq.) Uittien	BRUNEI: *Marsh 4* (K)	Y12955
M. meditensis D. A. Simpson	BRUNEI: *Simpson et al. 2515* (K)	Y12954
Scirpodendron bogneri S. S. Hooper	MALAYSIA: *Simpson 2650* (K)	Y12946
IV. SCLERIOIDEAE C. B. Clarke		
BISBOECKELEREAE Pax ex L. T. Eiten		
Becquerelia cymosa Brongn.	BRAZIL: *Thomas et al. 10284* (NY)	Y12948
Diplacrum africanum C. B. Clarke	TANZANIA: *Vollesen 3967* (K)	AY725942
CRYPTANGIEAE Benth.		
Lagenocarpus albo-niger (A. St.-Hil.) C. B. Clarke	BRAZIL: *Thomas 11111* (NY)	AY725949
SCLERIEAE Kunth ex Fenzl		
Scleria distans Poir.	KENYA: *Muasya 1023* (EA, K)	Y12968
S. foliosa A. Rich.	TANZANIA: *Muasya 939* (EA, K)	Y12986
S. terrestris (L.) Fassett	MALAYSIA: *Simpson 2658* (K)	Y12947
TRILEPIDEAE Goetgh.		
Coleochloa abyssinica (A. Rich.) Gilly	ETHIOPIA: *Vollesen 80/2* (K)	Y12975
Microdracoides squamosus Hua	CAMEROON: *Bonn s. n.,* Acc. 150 (K)	AY725951
Trilepis lhotzkiana Nees	BRAZIL: *Bonn s. n.* (K)	AY725955
Outgroups		
Prionium serratum Drège	SOUTH AFRICA: *Getliffe Norris s. n.* (NBG)	U49223
Philydrum lanuginosum Banks ex Gaertn.	CANADA: *Graham & Barrett 1* (TRT)	U41596

et al. 2003). Most Cyperaceae are wind pollinated, with thin-walled, pear-shaped (possibly aerodynamically shaped) pollen termed ‘‘pseudomonads,’’ which has a unique developmental pattern where three of the four nuclei produced by meiosis degenerate. In Hypolytreae, e.g., *Mapania tenuiscapa* C. B. Clarke, pollen is spheroidal with a thicker wall and appears to be monad. It is coated with lipid, suggesting this group is animal pollinated (Simpson et al. 2003). The relationships between genera within Hypolytreae are not so clear-cut and further work is needed.

The tribes in Sclerioideae are among the least studied of all Cyperaceae. Whereas most of the sclerioid tribes are well supported in our analysis, the relationships between them and with Schoeneae (Cyperoideae) are unresolved or received BP <50. Moreover, the single representative of Cryptangieae, *Lagenocarpus albo-niger,* in this analysis was unresolved within a grade comprising members of Schoeneae. This is the first time that a member of Cryptangieae has been sequenced and our data (cf. Bruhl 1995) indicate a closer relationship to Schoeneae than to the sclerioid tribes, although none of the clades in this part of the tree received BP >50. Cryptangieae have been included in Sclerioideae (Goetghebeur 1998) because of the presence of unisexual flowers; in Schoeneae all the flowers are bisexual. Historically, suprageneric groups in Cyperaceae have been recognized by the presence of either unisexual or bisexual flowers. However, such relationships are now open to question, as demonstrated by the close proximity Cariceae (unisexual flowers) to members of Scirpeae (bisexual flowers) in DNA sequencing studies (e.g., Muasya et al. 1998, 2000*a*; Simpson et al. 2003). Work is currently in progress on relationships within tribes Sclerieae and Bisboeckelereae (De Wilde, Simpson, Parnell, and Hodkinson pers. comm.), and within Schoeneae (Bruhl, Wilson, and Verboom pers. comm.), but there is a need for broader studies to resolve relationships between the sclerioid tribes and tribe Schoeneae.

Schoeneae (sensu Goetghebeur 1998) are the most diverse in terms of genera (29) in Cyperaceae, and are widely distributed, but with particular diversity in Australasia, southern Africa, and South America. Our analysis indicates they may not be monophyletic, with divisions into four major clades, one comprising *Cladium,* another *Carpha* Banks & Sol. ex R. Br., the third of *Rhynchospora* Vahl–*Pleurostachys,* and the fourth comprising the remaining genera in Schoeneae. The resolution of *Cladium* into a separate clade from other Schoeneae was also noted by Goetghebeur (1986), Bruhl (1995), and Muasya et al. (1998). Work by Zhang et al. (2004*a, b*) also indicates that *Carpha* forms a clade sister to other Schoeneae. Moreover, initial phylogenetic studies indicate that some widespread genera such as *Tetraria* P. Beauv. (not included in our analysis) are not monophyletic

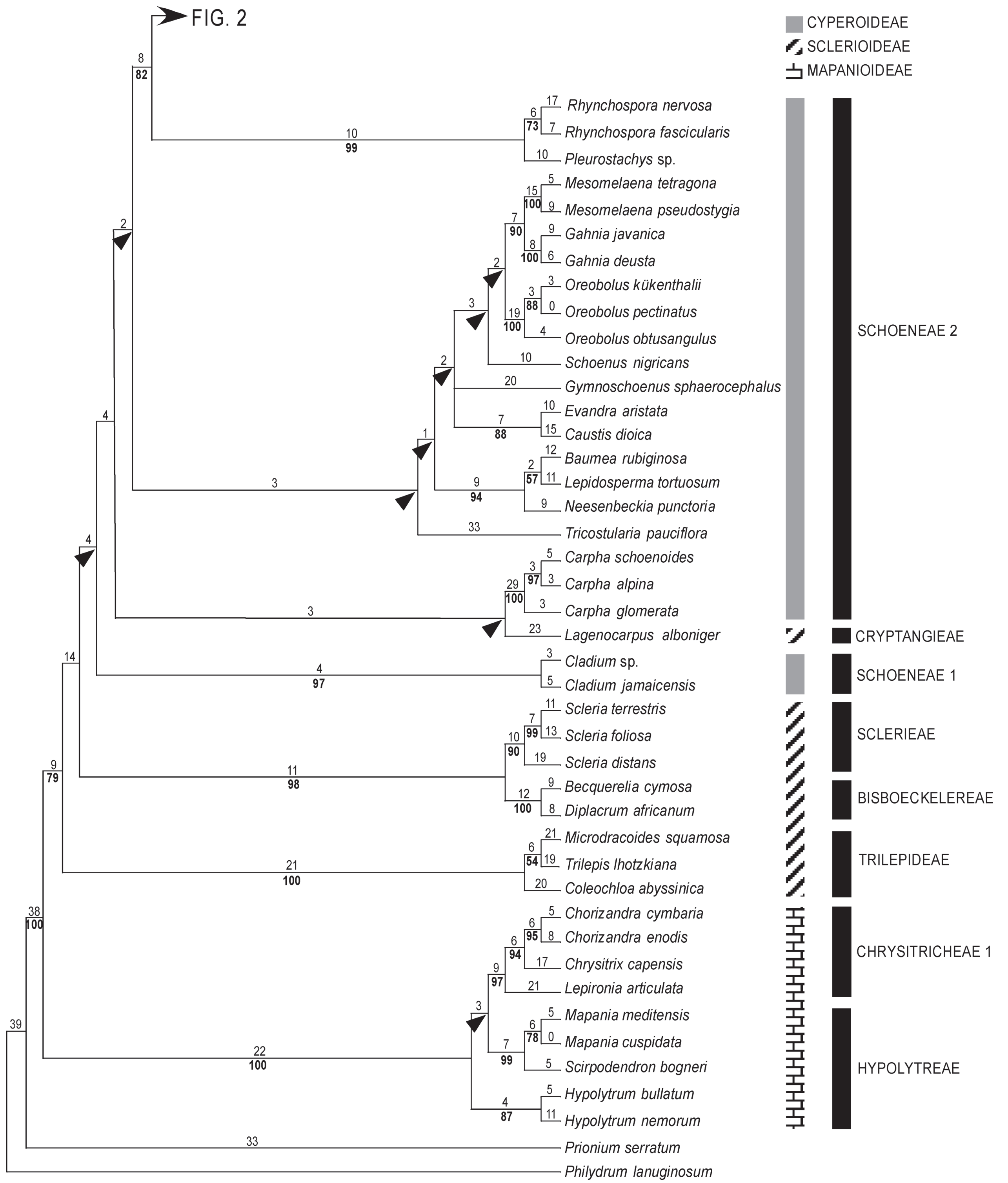

Fig. 1.—A part of one of the 1370 most-parsimonious trees based on *rbc*L data. The arrows mark clades not recovered in the strict consensus tree. Branch lengths (ACCTRAN optimization) are given above each branch and bootstrap percentages are given below.

(Verboom unpubl. data). Overall, the circumscription of Schoeneae is still far from being clear.

As in previous studies Scirpeae are polyphyletic with members dispersed throughout the tree. This result reflects the difficulties presented by the tribe at a morphological level with a lack of non-ambiguous synapomorphies to group genera. Bruhl (1995) observed Scirpeae to be paraphyletic in his morphological analyses. Cariceae are embedded within a clade comprising Dulichieae and some members of Scirpeae. Cariceae have been shown in other DNA studies to be closely related to Scirpeae and Dulichieae (e.g., Muasya et al. 1998, 2000*b*). Muasya et al. (1998) were cautious about

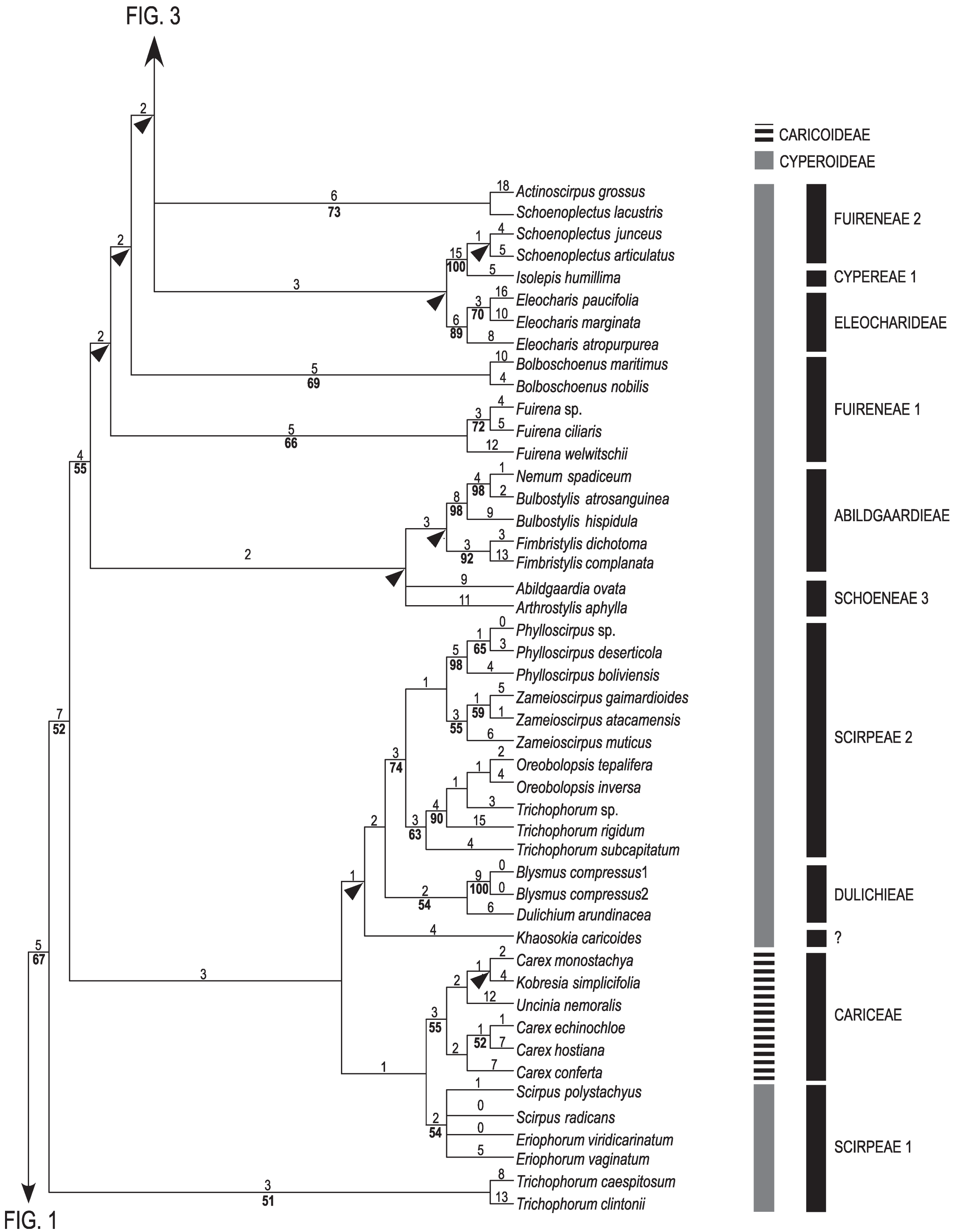

Fig. 2.—A part of one of the 1370 trees recovered from the analysis. The arrow marks the clade not recovered in the strict consensus tree. Branch lengths (ACCTRAN optimization) are given above each line and bootstrap percentages are given below.

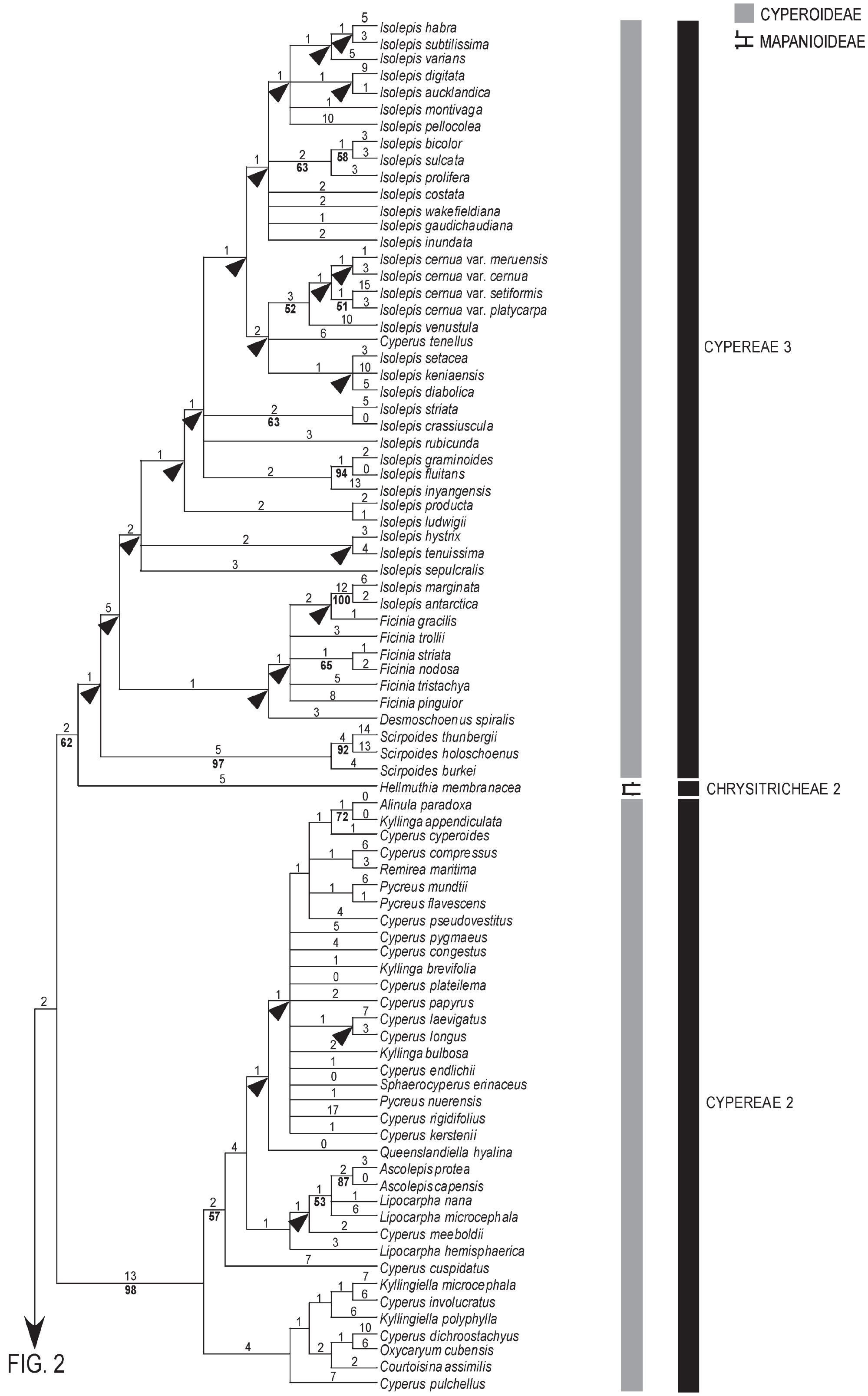

Fig. 3.—A part of one of the 1370 trees recovered from the analysis. The arrow marks the clade not recovered in the strict consensus tree. Branch lengths (ACCTRAN optimization) are given above each line and bootstrap percentages are given below.

accepting this relationship given that other authors had suggested links between Cariceae and Sclerieae (Goetghebeur 1986; Bruhl 1995). Cariceae have the presence of the utricle, a unique character, and unisexual flowers. However, they have been observed to share fungal parasites with some Scirpeae (Kukkonen and Timonen 1979). Molecular evidence from different DNA data sources (*rbc*L: Muasya et al. 1998, 2000*a*; ITS and *trn*T–L–F: Roalson et al. 2001; *trn*L–F and *rps*16: Simpson et al. 2003) indicates that a Cariceae–Dulichieae–Scirpeae relationship is probable, although there is still no fine-scale clarity and it does seem that too many tribes are currently recommended (cf. Bruhl 1995).

Trichophorum Pers. occurs in two different clades in our analysis. This ties in with morphological evidence that *Trichophorum* may not be monophyletic, as most of the northern temperate taxa (e.g., *T. caespitosum* (L.) Hartm.) have well-developed perianth bristles whereas the Andean taxa (e.g., *T. rigidum* (Boeck.) Goetgh., Muasya & D. A. Simpson) lack such a perianth. Phylogenetic studies in the group are currently in progress (Dhooge and Goetghebeur pers. comm.).

Two of the new genera that have recently come to light are resolved into the Cariceae–Dulichieae–Scirpeae clade. *Zameioscirpus* Dhooge & Goetgh. includes diminutive scirpoid taxa from the Andes previously placed in *Scirpus* L. and *Carex* (Dhooge et al. 2003). *Khaosokia,* a new genus from Southeast Asia (Simpson et al., 2005), is endemic to limestone cliffs in peninsular Thailand. It has male and female inflorescences, narrowly cylindric spikelets, and both sexes have well-developed perianth bristles. Superficially, *Khaosokia* resembles *Dulichium* Pers., but it lacks the specialization of the inflorescence seen in *Dulichium* (e.g., rachilla internodes breaking into one-flowered sections). It also has a resemblance to *Carex indica* L., but the female partial inflorescences do not have utricles. *Khaosokia* is uncertainly placed in the Cariceae–Dulichieae–Scirpeae clade (BP < 50), but its precise relationships have yet to be determined. *Cypringlea* was recently described for taxa endemic to Mexico, with rudimentary perianth bristles and a *Carex*-type embryo that were previously assigned to *Scirpus* sensu L. (Strong 2003). Although the genus needs to be sampled for DNA, it is also likely to be positioned within this clade. One eventual outcome may be to recognize the whole clade as a single tribe, but, as yet, support for the clade is weak (BP <50).

Abildgaardieae formed a polytomy in the consensus tree, although there was strong support for clades comprising *Bulbostylis* Kunth–*Nemum* Desv. (BP 98), and *Fimbristylis* Vahl (BP 92). Studies using the *trn*L–F region and a larger number of taxa (Ghamkhar, Bruhl, and Wilson unpubl. data) also demonstrate separate clades for *Bulbostylis* and *Fimbristylis.* The position of *Arthrostylis* R. Br. is unresolved in our analysis, although it does occur in the same polytomy as Abildgaardieae. Goetghebeur (1998) placed the four genera of Arthrostylideae (*Actinoschoenus* Benth., *Arthrostylis, Trachystylis* S. T. Blake, and *Trichoschoenus* J. Raynal) in Schoeneae, although, unlike many members of Schoeneae, they lack a perianth. Bruhl (1995) indicated support for a close relationship between Arthrostylideae and Abildgaardieae, based on phylogenetic analyses of morphological data. However, Ghamkhar, Bruhl, and Wilson (unpubl. data) also found *Arthrostylis* placed within in a well-resolved Abildgaardieae using *trn*L–F. Therefore, the recognition of tribe Arthrostylideae, as has been proposed by some authors (e.g., Goetghebeur 1986; Bruhl 1995), or the placement of *Arthrostylis* and related genera in Schoeneae (Goetghebeur 1998) may be inappropriate.

Eleocharideae are strongly supported in our analysis (BP 89), but are unresolved. Together with the *Fuirena, Bolboschoenus* Palla, and *Actinoscirpus* (Ohwi) R. W. Haines & Lye–*Schoenoplectus lacustris* clades they form a polytomy in the strict consensus tree. This pattern has been observed in other recent studies utilizing combined *rbc*L and *trn*L–F data (e.g., Muasya et al. 2001). Roalson and Friar (2000), working with ITS, indicated that *Eleocharis* R. Br. was not closely related to the large North American members of *Schoenoplectus.* Therefore, the relationships of *Eleocharis* to *Bolboschoenus, Schoenoplectus,* and *Fuirena* are not yet resolved and need further investigation.

Young et al. (2002) also observed that *Schoenoplectus* was represented by two monophyletic clades based on combined ITS and *trn*L–F data, one of which was sister to *Actinoscirpus grossus* (L. f.) Goetgh. & D. A. Simpson. This pattern is also indicated by our analysis, in which the perennial, temperate species, *S. lacustris,* is sister to *Actinoscirpus* whereas annual, tropical taxa (*S. articulatus* and *S. junceus*) form a separate clade. Recently, Lye (2003) described a new genus, *Schoenoplectiella* Lye, based mainly on the *rbc*L data presented in Muasya et al. (1998, 2000*b*), to segregate all the annual taxa previously part of *Schoenoplectus.*

The placement of *Isolepis humillima* in a clade away from other members of *Isolepis* was first indicated by Muasya et al. (2001) whose analysis resolved it in a clade sister to *Eleocharis marginulata* Steud. Our study refines their observations by including more taxa, and strongly supports a relationship with *Schoenoplectus.* Muasya and Simpson (2002) noted that the morphology of this plant was atypical of *Isolepis* in having *Cyperus*-like characters, including presence of several inflorescence bracts and Kranz anatomy. More work is needed to determine its precise relationships.

Two further large clades in our analysis comprise a strongly supported clade representing *Cyperus* and allied genera in Cypereae (Fig. 3: Cypereae 2) that is sister to a poorly to moderately supported *Ficinia–Hellmuthia–Isolepis–Scirpoides* clade (Fig. 3: Cypereae 3–Chrysitricheae 2). This pattern has been recovered in other analyses involving these taxa using combined *rbc*L and *trn*L–F (Muasya et al. 2001), or *rbc*L, *trn*L–F, and *rps*16 intron data (Muasya et al. 2002). A consistent feature observed is the occurrence of two subclades in the Cypereae 2 clade that represent taxa with C_3 (*Cyperus pulchellus–Kyllingiella microcephala*) and C_4 (*Alinula paradoxa–Queenslandiella hyalina*) anatomy. In the Cypereae 3 clade, a subclade comprising *Ficinia* is present although unsupported. Muasya et al. (2001) also recovered *Ficinia* as a moderately supported clade. As a result, *Isolepis trollii* (Kük.) Lye and *I. nodosa* (Rottb.) R. Br. were transferred to *Ficinia,* a move that was also supported by morphological evidence, including robust perennial habit, and the presence of a hypogynous disk in *F. nodosa* (Muasya et al. 2000*c*). In addition, the presence of a fimbriate anther connective tip has been observed in these taxa (Muasya unpubl. data), a feature that is also characteristic of *Ficina.* The positions of *Desmoschoenus* and *I. marginata–I. antarctica* need further investigation. Molecular and morphological studies of *Ficinia* are currently in progress (Muasya pers. comm.).

One outcome of our work is that subfamily delimitation may need to be reconsidered, with only two subfamilies recognized, namely Mapanioideae and Cyperoideae (cf. Bruhl 1995). Mapanioideae have a distinct suite of morphological characters that, in combination with forming a monophyletic clade sister to the rest of Cyperaceae, sets them apart from the rest of the family. The other subfamilies are not monophyletic (Cyperoideae and Sclerioideae) or are embedded within a larger clade (Caricoideae). Tribal delimitation may also need to be reassessed. For example, with Cariceae and Dulichieae embedded in the clade with select taxa of Scirpeae, the recognition of three tribes may be unjustified. Moreover, Scirpeae themselves are problematic by forming several clades in the DNA phylogeny.

Despite significant advances in our understanding of Cyperaceae, it is evident that much further work is needed. Future efforts should be carefully coordinated among researchers and should center on obtaining data for all genera in the family, including better infrageneric sampling and DNA sequences from regions in addition to *rbc*L. However, an equally important goal should be the attempt to better integrate both morphological and molecular data in our analyses.

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