



Molecular phylogenetics and taxonomic revision of *Habenaria* section *Pentadactylae* (Orchidaceae, Orchidinae)

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As a step towards a revision of the sectional classification of Neotropical species of *Habenaria*, we focus here on section *Pentadactylae*. In its current delimitation, this is the largest of the 14 New World sections and embraces a group of 34 morphologically heterogeneous species. We expanded the sampling of Neotropical species currently placed in this section and performed Bayesian, maximum likelihood and parsimony analyses using nucleotide sequences from one nuclear (internal transcribed spacer, ITS) and three plastid (*matK*, *trnK* intron, *rps16-trnK*) DNA regions. In addition, morphological features of these species were reassessed. Based on our analyses, we propose that *Habenaria* section *Pentadactylae* should be recircumscribed to include only seven species: *H. pentadactyla* (the type species of the section), *H. dutrae*, *H. ekmaniana*, *H. exaltata*, *H. henscheniana*, *H. megapotamensis* and *H. montevidensis*. Thirty-two species previously assigned to the section grouped within unrelated clades and are therefore excluded from the section. There are no unambiguous morphological synapomorphies for the section, but the group can be confidently recircumscribed and identified on the basis of a combination of diagnostic morphological vegetative and floral characters. Morphological floral features in *Habenaria montevidensis* are distinct from those of other species in the section, probably as a result of a shift to diurnal pollinators. Following a taxonomic revision of the group, *H. crassipes* is placed under the synonymy of *H. exaltata* and neotypes are designated for *H. crassipes*, *H. montevidensis* and *H. recta* (= *H. ekmaniana*). All species in the section live in marshes or wet grasslands from northern Argentina to central Brazil; most species are concentrated in southern Brazil. Most species are probably rare, and five may be threatened according to the World Conservation Union (IUCN) criteria. © 2014 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2014, 175, 47–73.

ADDITIONAL KEYWORDS: Brazil – conservation – ITS – *matK/trnK* – Neotropics – phylogeny – *rps16-trnK* – sectional classification – taxonomy.

INTRODUCTION

Habenaria Willd. (Orchidaceae: Orchidinae) is a large genus of terrestrial orchids, currently estimated to comprise 881 species (Govaerts *et al.*, 2013). The

integrity of *Habenaria* as a genus has long been questioned. Rafinesque (1837) was the first to dismember the genus and, in the last decade, Szlachetko and co-workers (Szlachetko & Kras, 2006; Szlachetko, 2012) have undertaken a worldwide splitting of the genus. However, Szlachetko's research was based entirely on floral morphological characters and his

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Table 1. A comparison of the species assigned to *Habenaria* section *Pentadactylae* by different authors. Species sampled in the molecular phylogenetic analyses, including synonyms, are indicated by an asterisk

Kränzlin (1892)	Cogniaux (1893–1896)	Kränzlin (1901)	This work
<i>H. achnantha</i>	<i>H. achnantha</i>	<i>H. achnantha</i>	<i>H. dutrae</i> *
<i>H. aranifera</i> *	<i>H. alpestris</i> *	<i>H. alpestris</i> *	<i>H. ekmaniana</i> *
<i>H. armata</i> *	<i>H. aranifera</i> *	<i>H. aranifera</i> *	<i>H. exaltata</i> *
<i>H. conopodes</i>	<i>H. armata</i> *	<i>H. armata</i> *	<i>H. henscheniana</i> *
<i>H. corcovadensis</i> *	<i>H. caldensis</i> *	<i>H. caldensis</i> *	<i>H. megapotamensis</i> *
<i>H. culicina</i>	<i>H. candolleana</i>	<i>H. candolleana</i>	<i>H. montevidensis</i> *
<i>H. entomantha</i>	<i>H. confusa</i> *	<i>H. confusa</i> *	<i>H. pentadactyla</i> *
<i>H. epiphylla</i> *	<i>H. corcovadensis</i> *	<i>H. corcovadensis</i> *	
<i>H. gracilis</i>	<i>H. exaltata</i> *	<i>H. entomantha</i>	
<i>H. imbricata</i> *	<i>H. goyazensis</i> *	<i>H. exaltata</i> *	
<i>H. lactiflora</i>	<i>H. gracilis</i>	<i>H. goyazensis</i> *	
<i>H. lagunae-sanctae</i>	<i>H. graciliscapa</i> *	<i>H. gracilis</i>	
<i>H. leptoceras</i> *	<i>H. humilis</i> *	<i>H. graciliscapa</i> *	
<i>H. macilenta</i> *	<i>H. imbricata</i> *	<i>H. humilis</i> *	
<i>H. modestissima</i>	<i>H. janeirensis</i> *	<i>H. imbricata</i> *	
<i>H. moritzii</i> *	<i>H. lagunae-sanctae</i> *	<i>H. janeirensis</i> *	
<i>H. paivaeana</i>	<i>H. macilenta</i> *	<i>H. lactiflora</i>	
<i>H. pentadactyla</i> *	<i>H. modestissima</i>	<i>H. lagunae-sanctae</i> *	
<i>H. schomburgkii</i>	<i>H. moritzii</i> *	<i>H. macilenta</i> *	
<i>H. secunda</i> *	<i>H. muelleriana</i> *	<i>H. modestissima</i>	
<i>H. setacea</i> *	<i>H. pentadactyla</i> *	<i>H. moritzii</i> *	
<i>H. setifera</i> *	<i>H. riedelii</i> *	<i>H. paivaeana</i>	
<i>H. similima</i>	<i>H. rupicola</i> *	<i>H. pentadactyla</i> *	
<i>H. warmingii</i> *	<i>H. santensis</i>	<i>H. riedelii</i> *	
	<i>H. schenckii</i> *	<i>H. rupicola</i> *	
	<i>H. schomburgkii</i>	<i>H. santensis</i>	
	<i>H. secunda</i> *	<i>H. schenckii</i> *	
	<i>H. setacea</i> *	<i>H. schomburgkii</i>	
	<i>H. setifera</i> *	<i>H. secunda</i> *	
	<i>H. taubertiana</i>	<i>H. setacea</i> *	
	<i>H. ulaei</i>	<i>H. similima</i>	
	<i>H. warmingii</i> *	<i>H. taubertiana</i>	
		<i>H. ulaei</i>	
		<i>H. warmingii</i> *	

genera have not been accepted by most botanists. The geographical distribution of *Habenaria* includes tropical, subtropical and temperate regions of the Old and New Worlds (Pridgeon *et al.*, 2001; Batista *et al.*, 2011a). Its main centres of diversity are found in central and southern Africa, eastern Asia and Brazil (Kurzweil & Weber, 1992). The Brazilian flora is especially rich in *Habenaria* spp., and accounts for nearly one-quarter of all species known to belong to the genus (Hoehne, 1940; Pabst & Dungs, 1975; Batista *et al.*, 2011a, b). *Habenaria* spp. are characterized by frequently bifid petals, a tripartite lip, long rostellar arms, stalked stigmas and a well-developed nectariferous spur (Dressler, 1993; Pridgeon *et al.*, 2001). The flowers are also characterized by a deep division of the anther, which ultimately results in the formation

of two separate pollinaria in most species (Singer & Cocucci, 1997).

The only worldwide revisions of *Habenaria* were those of Kränzlin (1892, 1901), in which c. 427 species and 32 sections were recognized. Kränzlin's sectional classification was based on morphological characters (especially the degree of dissection of the petals and lip) and gynostemium structure (particularly the length of the stigmas). *Habenaria* section *Pentadactylae* Kraenzl (1892) was established in the first revision of the genus and included 24 species (Table 1). The diagnostic character for *H.* section *Pentadactylae* was the presence of labellum lobes similar in length to the anterior lobe of the petals (Kränzlin, 1892). Cogniaux (1893–1896), in his review of the genus in *Flora Brasiliensis*, followed, in general terms, the

sectional delimitation proposed by Kränzlin (1892), but included an additional 16 species and excluded eight species from the section (Table 1). Kränzlin (1901), in his second and final revision of the genus, attributed 34 species to the section (Table 1), making it the largest Neotropical section. However, examination of the species attributed by Kränzlin (1892, 1901) and Cogniaux (1893–1896) reveals that *H.* section *Pentadactylae* in its current delimitation comprises a highly heterogeneous assemblage of species, raising doubts about the monophyly of the sections and the consistency of the characters used for sectional delimitation. Recently, Batista *et al.* (2013) used sequence data from the nuclear internal transcribed spacer (ITS) region and part of the plastid *matK* gene to conduct a phylogenetic analysis of the New World species of the genus. This study revealed that the Neotropical species formed a monophyletic group, consisting of at least 21 well-supported subgroups, and that all Neotropical sections of the current sectional classification were paraphyletic or polyphyletic and will need extensive revision and recircumscription. The species currently placed in section *Pentadactylae* sampled for that study nested in several different and unrelated subgroups, or their placement was unresolved. It is important to stress, however, that this sampling (Batista *et al.*, 2013) lacked *H. pentadactyla* Lindl., the type species of the section; it was therefore not possible to ascertain which of the recovered clades should be considered as section *Pentadactylae* in its strictest sense.

In the present study, we have expanded the sampling of species currently placed in *H.* section *Pentadactylae*, including the type species of the section, and have used additional DNA regions (*matK-trnK*, *rps16-trnK*) to perform a molecular phylogenetic analysis focused on the section. Based on our phylogenetic analyses, we re-evaluated the morphological characters used to characterize the group and present a taxonomic revision of the section.

MATERIAL AND METHODS

TAXON SAMPLING FOR PHYLOGENETIC ANALYSES

Two datasets were used for the analyses. The first consisted of the combined ITS and partial *matK* DNA sequences of 207 terminals comprising 156 Neotropical *Habenaria* spp., corresponding to 52% of the total number of species known from the Neotropics (Batista *et al.*, 2011a, b), four African *Habenaria* spp. and *Gennaria diphylla* Parl., which was used as a functional outgroup. This dataset was basically the same as that used by us for a phylogenetic analysis of New World *Habenaria* (Batista *et al.*, 2013), but included some additional species (*H. pentadactyla*,

H. ekmaniana Kraenzl., *H. dutrae* Schltr., *H. megapotaensis* Hoehne) and excluded most of the Old World taxa. A second dataset consisted of a subset of the accessions used in the first analysis, but, in addition to the ITS region, also included the complete sequence of the *matK* gene, the *trnK* intron, downstream *matK* and the *rps16-trnK* intergenic spacer. This second dataset included 55 samples (43 species) of Neotropical *Habenaria* and the same Old World species as used in the first dataset (Table 2). The sequences from Old World taxa were obtained from GenBank and included only ITS and part of the *matK* gene. For these taxa, the remaining part of the *matK* gene, *trnK* intron and *rps16-trnK* intergenic spacer were coded as missing data. The sampling of Neotropical taxa included representatives of most Neotropical sections and taxa from all strongly supported terminal clades identified in our previous molecular analysis of Neotropical *Habenaria* (Batista *et al.*, 2013). Whenever possible, for species morphologically similar to *H. pentadactyla*, we sampled more than one population in order to evaluate possible intraspecific variation. Of the 40 taxa previously assigned to *H.* section *Pentadactylae* by Kränzlin (1892, 1901) and Cogniaux (1893–1896), 27 (67%) were sampled (Table 1).

MOLECULAR MARKERS

Nucleotide sequences from one nuclear genome region (ITS) and three plastid (*matK*, *trnK* intron and *rps16-trnK*) genome regions were used in the analyses. The nuclear region (nrITS) consisted of ITS1 and ITS2 and the intervening 5.8S gene of the nuclear ribosomal multigene family. Amplifications were made using the primers 17SE and 26SE (Sun *et al.*, 1994). The plastid DNA regions included the complete sequences of the *matK* gene and downstream contiguous *trnK* intron and the *rps16-trnK* intergenic spacer. The *matK* gene and *trnK* intron were amplified in two reactions: the amino-terminal part of the *matK* gene with primers-19F (Molvray, Kores & Chase, 2000) and *matk356R* (5'-AATCGCAACAAATGCAAA-3'), and the remaining part of the *matK* gene and complete downstream *trnK* intron with primers *matkF2* (5'-CTAATACCCCATCCCATCCAT-3') and 2R (Steele & Vilgalys, 1994). The *rps16-trnK* intergenic spacer was amplified with primers *rpS16x2F2* and *trnK* (UUU)x1 (Shaw *et al.*, 2007).

Genomic DNA was extracted from fresh or silica gel-dried material using the 2 × cetyltrimethylammonium bromide (CTAB) method adapted from Doyle & Doyle (1987). Polymerase chain reaction (PCR) amplifications were performed in an MJ96G Biocycler or Eppendorf Mastercycler thermal cycler. The general PCR system consisted of 2–3 µL genomic DNA (~20–

Table 2. Voucher information and GenBank accession numbers for samples in the internal transcribed spacer (ITS), *matK-trnK* and *rps16-trnK* dataset (Fig. 2). Voucher information and GenBank accession numbers for ITS and partial *matK* sequences of the larger dataset (Fig. 1) are the same as in Batista *et al.* (2013)

Taxon	Voucher	Origin*	ITS	<i>matK-trnK</i>	<i>rps16-trnK</i>
<i>Gennaria diphylla</i> (Link) Parl.	GenBank	Africa	AY351380	AY368383	–
<i>Habenaria achalensis</i> Kraenzl.	Batista 2506 (BHCB)	Brazil, RS	HM777526	KJ021403	KJ021457
<i>Habenaria alpestris</i> Cogn.	Batista 1576 (BHCB)	Brazil, DF	HM777655	KJ021357	KJ021412
<i>Habenaria aranifera</i> Lindl.	Batista 2472 (BHCB)	Brazil, RS	HM777626	KJ021394	KJ021448
<i>Habenaria armata</i> Rchb.f.	Batista 1297 (CEN)	Brazil, DF	HM777677	KJ021367	KJ021422
<i>Habenaria ayangannensis</i> Renz	Batista 1919 (BHCB)	Brazil, MG	HM777706	KJ021360	KJ021415
<i>Habenaria balansae</i> Cogn.	Batista 2336 (BHCB)	Brazil, MG	HM777683	KJ021362	KJ021417
<i>Habenaria caldensis</i> Kraenzl.	Batista 250 (CEN)	Brazil, GO	HM777645	KJ021363	KJ021418
<i>Habenaria clavata</i> (Lindl.) Rchb.f.	GenBank	Africa	DQ522074	DQ522093	–
<i>Habenaria crucifera</i> Rchb.f. & Warm.	Batista 1826 (BHCB)	Brazil, MG	HM777574	KJ021356	KJ021411
<i>Habenaria dives</i> Rchb.f.	GenBank	Africa	DQ522075	DQ522095	–
<i>Habenaria dutrae</i> Schltr.	Pedron 3 (ICN)	Brazil, RS	KJ021339	KJ021387	KJ021441
<i>Habenaria edwallii</i> Cogn.	Batista 1717 (BHCB)	Brazil, MG	HM777564	KJ021402	KJ021456
<i>Habenaria ekmaniana</i> Kraenzl.	Radins s.n. (BHCB)	Argentina, Misiones	KJ021340	KJ021383	KJ021438
<i>Habenaria exaltata</i> Barb.Rodr.	Batista 2771 (BHCB)	Brazil, MG	HM777621	KJ021388	KJ021442
<i>Habenaria exaltata</i> Barb.Rodr.	Batista 2520 (BHCB)	Brazil, PR	KJ021341	KJ021389	KJ021443
<i>Habenaria exaltata</i> Barb.Rodr.	Pedron 6 (ICN)	Brazil, RS	KJ021342	KJ021390	KJ021444
<i>Habenaria glaucophylla</i> Barb.Rodr. var. <i>glaucophylla</i>	Batista 761 (CEN)	Brazil, DF	HM777631	KJ021373	KJ021428
<i>Habenaria hamata</i> Barb.Rodr.	Batista 1519 (CEN)	Brazil, DF	HM777586	KJ021371	KJ021426
<i>Habenaria henscheniana</i> Barb.Rodr.	Mota 1584 (BHCB)	Brazil, SC	HM777622	KJ021377	KJ021432
<i>Habenaria henscheniana</i> Barb.Rodr.	Batista 2802 (BHCB)	Brazil, MG	HM777623	KJ021375	KJ021430
<i>Habenaria henscheniana</i> Barb.Rodr.	Pedron 2 (ICN)	Brazil, RS	KJ021343	KJ021376	KJ021431
<i>Habenaria hexaptera</i> Lindl.	Batista 2399 (BHCB)	Brazil, MG	HM777538	KJ021366	KJ021421
<i>Habenaria humilis</i> Cogn.	Batista 1901 (BHCB)	Brazil, MG	HM777581	KJ021364	KJ021419
<i>Habenaria imbricata</i> Lindl.	Batista 1123 (CEN)	Brazil, DF	HM777648	KJ021368	KJ021423
<i>Habenaria johannensis</i> Barb.Rodr.	Mota 2777 (BHCB)	Brazil, MG	HM777609	KJ021398	KJ021452
<i>Habenaria leptoceras</i> Hook.	Batista 2658 (BHCB)	Brazil, RJ	HM777597	KJ021370	KJ021425
<i>Habenaria leucosantha</i> Barb.Rodr.	Batista 1604 (BHCB)	Brazil, DF	HM777568	KJ021406	KJ021460
<i>Habenaria lithophila</i> Schltr.	GenBank	Africa	DQ522077	DQ522098	–
<i>Habenaria macilenta</i> (Lindl.) Rchb.f.	Batista 2393 (BHCB)	Brazil, MG	HM777606	KJ021400	KJ021454
<i>Habenaria macronectar</i> (Vell.) Hoehne	Batista 2519 (BHCB)	Brazil, PR	HM777614	KJ021399	KJ021453
<i>Habenaria megapotamensis</i> Hoehne	Pedron 10 (ICN)	Brazil, RS	KJ021345	KJ021384	KJ021439
<i>Habenaria megapotamensis</i> Hoehne	Pedron 10 (ICN)	Brazil, RS	KJ021346	KJ021385	KJ021440
<i>Habenaria megapotamensis</i> Hoehne	Klein 32 (UPCB)	Brazil, RS	KJ021347	KJ021386	–
<i>Habenaria melanopoda</i> Hoehne & Schltr.	Batista 1832 (BHCB)	Brazil, MG	HM777689	KJ021361	KJ021416
<i>Habenaria montevidensis</i> Spreng.	Batista 2479 (BHCB)	Brazil, RS	HM777619	KJ021378	KJ021433
<i>Habenaria montevidensis</i> Spreng.	Pedron 9 (ICN)	Brazil, RS	KJ021344	KJ021379	KJ021434
<i>Habenaria mystacina</i> Lindl.	Batista 1812 (BHCB)	Brazil, MG	HM777728	KJ021353	KJ021408
<i>Habenaria</i> cf. <i>nuda</i> Lindl.	Batista 2869 (BHCB)	Brazil, MG	HM777718	KJ021354	KJ021409
<i>Habenaria paranaensis</i> Barb.Rodr.	Batista 2436 (BHCB)	Brazil, MG	HM777528	KJ021405	KJ021459
<i>Habenaria parviflora</i> Lindl.	Batista 1813 (BHCB)	Brazil, MG	HM777560	KJ021401	KJ021455
<i>Habenaria pentadactyla</i> Lindl.	Pedron 11 (ICN)	Brazil, RS	KJ021348	KJ021380	KJ021435
<i>Habenaria pentadactyla</i> Lindl.	Pedron 11 (ICN)	Brazil, RS	KJ021349	KJ021381	KJ021436
<i>Habenaria pentadactyla</i> Lindl.	Klein 150 (BHCB)	Brazil, RS	KJ021350	KJ021382	KJ021437
<i>Habenaria pratensis</i> (Salzm. ex Lindl.) Rchb.f.	Batista 2686 (BHCB)	Brazil, BA	HM777546	KJ021374	KJ021429
<i>Habenaria pungens</i> Cogn.	Batista 2095 (BHCB)	Brazil, GO	HM777570	KJ021355	KJ021410

Table 2. Continued

Taxon	Voucher	Origin*	ITS	<i>matK-trnK</i>	<i>rps16-trnK</i>
<i>Habenaria regnellii</i> Cogn.	<i>Batista 2801</i> (BHCB)	Brazil, MG	HM777603	KJ021391	KJ021445
<i>Habenaria regnellii</i> Cogn.	<i>Barfknecht s.n.</i> (BHCB)	Brazil, PR	HM777604	KJ021392	KJ021446
<i>Habenaria regnellii</i> Cogn.	<i>Batista 3053</i> (BHCB)	Brazil, DF	KJ021351	KJ021393	KJ021447
<i>Habenaria repens</i> Nutt.	<i>Batista 2522</i> (BHCB)	Brazil, PR	HM777627	KJ021395	KJ021449
<i>Habenaria rodeiensis</i> Barb.Rodr.	<i>Mota 2824</i> (BHCB)	Brazil, MG	HM777577	KJ021359	KJ021414
<i>Habenaria cf. rupicola</i> Barb.Rodr.	<i>Batista 2568</i> (BHCB)	Brazil, MG	HM777533	KJ021365	KJ021420
<i>Habenaria schenckii</i> Cogn.	<i>Batista 2882</i> (BHCB)	Brazil, BA	HM777580	KJ021372	KJ021427
<i>Habenaria secunda</i> Lindl.	<i>Batista 2640</i> (BHCB)	Brazil, RJ	HM777525	KJ021404	KJ021458
<i>Habenaria secundiflora</i> Barb.Rodr.	<i>Batista 2392</i> (BHCB)	Brazil, MG	HM777637	KJ021358	KJ021413
<i>Habenaria setacea</i> Lindl.	<i>Mota 3019</i> (BHCB)	Brazil, MG	HM777731	KJ021352	KJ021407
<i>Habenaria tridens</i> Lindl.	GenBank	Africa	DQ522080	DQ522101	–
<i>Habenaria trifida</i> Kunth	<i>Batista 1783</i> (BHCB)	Brazil, DF	HM777672	KJ021369	KJ021424
<i>Habenaria warmingii</i> Rchb.f. & Warm.	<i>Batista 2409</i> (BHCB)	Brazil, MG	HM777616	KJ021396	KJ021450
<i>Habenaria warmingii</i> Rchb.f. & Warm.	<i>Batista 2584</i> (BHCB)	Brazil, MG	HM777617	KJ021397	KJ021451

*Abbreviations for Brazilian states: BA, Bahia; DF, Distrito Federal; MG, Minas Gerais; GO, Goiás; PR, Paraná; RJ, Rio de Janeiro; RS, Rio Grande do Sul; SC, Santa Catarina.

Table 3. Data-matrix values and tree statistics for each of the parsimony analyses

Dataset	Terminals	Aligned length	Percentage of missing data	Potentially parsimony informative sites (%)	Trees	Consistency index (CI)	Retention index (RI)	Model
ITS + partial <i>matK</i>	207	1373	0.25	306 (22.3)	4350	0.63	0.85	–
ITS	60	742	0.16	139 (18.7)	1973	0.78	0.82	GTR + G
<i>matK</i>	60	1565	6.9	87 (5.6)	7863	0.81	0.91	GTR + I + G
<i>trnK</i> intron	60	251	10.8	16 (6.4)	9090	0.86	0.9	GTR + G
<i>matK-trnK</i>	60	1816	7.5	103 (5.7)	8410	0.8	0.9	–
<i>rps16-trnK</i>	60	947	10	68 (7.2)	6000	0.73	0.87	GTR + I + G
Plastid	60	2763	8.3	171 (7.3)	5360	0.76	0.88	–
Combined	60	3505	6.6	310 (8.8)	62	0.75	0.85	–

50 ng DNA), 1 × PCR Buffer (Phoneutria Biotecnologia, Belo Horizonte, Brazil), 1.5 mM MgCl₂, 200 μM deoxynucleoside triphosphates (dNTPs), 0.2 μM each primer, 1.5 U Taq DNA Polymerase (Phoneutria Biotecnologia) and water to a volume of 30 μL. Cycling conditions were as follows: an initial denaturation step at 94 °C for 4 min; 35 cycles each at 94 °C for 45 s, 58 °C for 45 s and 72 °C for 80 s; and a final extension step of 5 min at 72 °C. PCR products were purified by precipitation with polyethylene glycol and sequenced in a 3730XL genetic analyser by Macrogen Inc. (Seoul, South Korea). Sequencing primers were the same as those used in the amplifications. Bidirectional sequence reads were obtained for all of the DNA regions, and the resulting chromatograms were edited and assembled using Staden Package software

(Bonfield, Smith & Staden, 1995). The edited sequences were aligned with MUSCLE (Edgar, 2004), and the resulting alignment was manually adjusted using MEGA4 software (Tamura *et al.*, 2007). Taxa, voucher information and GenBank numbers are listed in Table 2. The percentages of missing data for each molecular marker are given in Table 3.

PHYLOGENETIC ANALYSES

The data were analysed by means of parsimony, maximum likelihood (ML) and Bayesian inference. Phylogenetic analyses using maximum parsimony (MP) were performed in PAUP version 4 (Swofford, 2002) with Fitch parsimony (equal weights, unordered characters; Fitch, 1971) as the optimality criterion.

Separate searches were initially performed on each dataset and the combined plastid sequences. No cases of strongly supported incongruence were detected (i.e. no conflicting groups among the two datasets obtaining strong internal support were observed). Therefore, a third search was performed with the combined nuclear and plastid datasets. Each search consisted of 1000 replicates of random taxon addition, with branch swapping using the tree bisection–reconnection (TBR) algorithm, saving ≤ 10 trees per replicate to avoid extensive swapping on suboptimal islands. Internal support was evaluated by character bootstrapping (Felsenstein, 1985) using 1000 replicates, simple addition and TBR branch swapping, saving ≤ 10 trees per replicate. For bootstrap support (BS) levels, we 50–70% as weak, 71–85% as moderate and $> 85\%$ as strong (Kress, Prince & Williams, 2002).

Bayesian analysis of individual and combined datasets was implemented in MrBayes v. 3.1.2 (Ronquist, Huelsenbeck & van der Mark, 2005), treating each DNA region (ITS, *matK*, *trnK* intron and *rps16–trnK*) as separate partitions. An evolutionary model for each DNA region was selected using the Akaike information criterion (AIC) in MrModeltest 2 (Nylander, 2004). Each analysis consisted of two independent runs with four chains for 5 000 000 generations, sampling one tree every 1000 generations. In the combined analysis, in order to improve swapping of chains, the temperature parameter for heating the chains was lowered to 0.01. Convergence between the runs was evaluated by the average standard deviation of split frequencies (< 0.01). After discarding the first 50% of the trees as burn-in, the remaining trees were used to assess topology and posterior probabilities (PPs) in a majority-rule consensus. PPs in Bayesian analysis are not equivalent to BS values, but are generally much higher (Erixon *et al.*, 2003). Therefore, we used criteria similar to a standard statistical test, considering groups with PPs > 0.95 as strongly supported, groups with PPs in the range 0.90–0.95 as moderately supported and groups with PPs < 0.90 as weakly supported.

The ML analysis was conducted with the program RAxML-HPC version 7.4.4 (Stamatakis, 2006) as implemented in the Cyberinfrastructure for Phylogenetic Research (CIPRES) Portal 2.0 (Miller, Pfeiffer & Schwartz, 2010). Analysis of 1000 rapid bootstrap replicates (Stamatakis, Hoover & Rougemont, 2008) was followed by a search for the tree that maximizes

the likelihood function, with the default value of 25 rate categories and the estimation of all free model parameters for four character partitions (*matK*, *trnK* intron downstream of *matK*, ITS region and *rps16–trnK* intergenic spacer). Both the bootstrap searches and the search for the ML tree used the GTRGAMMA model for nucleotides.

TAXONOMIC ANALYSES

Descriptions were based on pickled or herbarium material; however, live material was also extensively examined in the field. Floral details were examined under a stereoscopic microscope and measured with a digital paquimeter. Some gynostemium images were produced with a digital camera DFC295 coupled to a stereoscopic microscope (Leica M205C) and assembled using Leica Application Suite v. 3.8.0 software. Dried materials were rehydrated using concentrated ammonium hydroxide [35% (w/v) ammonia solution] as described by Toscano de Brito (1996). Data relating to flowering times, habitats and distribution were based on herbarium labels of collections or on field observations. Two hundred and thirteen sheets and digital images (photographs) were examined from the following herbaria: AMES, B, BHC, BM, BR, CESJ, CORD, G, HB, IAC, ICN, K, L, LP, M, MBM, MVFA, NY, OXF, P, PACA, PEL, R, RB, S, SI, SP, SPF, U, UB, UC, UPCB, UPS, US, W, Z and ZT. Descriptive terminology is based in Stearn (1992) and Simpson (2006).

RESULTS

PHYLOGENETIC ANALYSES

The matrix with the combined ITS and partial *matK* gene consisted of 1373 characters, 306 (22%) of which were potentially parsimony informative. Table 3 shows the data matrix values from the individual or combined datasets, with tree statistics and other parameters of the parsimony analyses. The Bayesian majority-rule consensus tree was overall congruent with the strict consensus tree of the combined parsimony analyses, but was more fully resolved and had stronger overall support. Therefore, this tree was chosen for presentation (Fig. 1). New World *Habenaria* spp. formed a well-supported monophyletic group (1.00 PP, 88% BS, Fig. 1) that was sister to the African *H. tridens* Lindl. (1.00 PP, 100% BS). Within the New World clade, several well-supported terminal

Figure 1. Bayesian tree of the combined internal transcribed spacer (ITS) and *matK* (partial) datasets. Numbers next to the nodes represent the posterior probabilities (PPs). Neotropical subgroups are numbered according to Batista *et al.* (2013). The generic name for all *Habenaria* spp. is abbreviated. Species in *H.* section *Pentadactylae* are shown in bold and indicated by an arrow. Subgroup 5 corresponds to *H.* section *Pentadactylae* as circumscribed in this work.



Figure 1. See caption on previous page.

subclades were formed (Fig. 1), corresponding to the subclades identified in our previous analyses (Batista *et al.*, 2013). Species currently assigned to *H.* section *Pentadactylae* by Kränzlin (1892, 1901) and Cogniaux (1893–1896) were dispersed in several subclades of the tree (Fig. 1), and the section in its current delimitation is therefore highly polyphyletic. However, in the Bayesian tree, *H. pentadactyla*, the type of the section, formed a subclade with *H. ekmaniana*, *H. montevidensis* Spreng., *H. henscheniana* Barb.Rodr., *H. megapotamensis*, *H. exaltata* Barb.Rodr. and *H. dutrae* (subclade 5), but support was low (0.70 PP) (Fig. 1). In the strict consensus tree of the parsimony analysis, this clade collapsed. Other relationships are similar to our previous results (Batista *et al.*, 2013).

To improve resolution and support of the analysis, we increased the number of molecular characters, including the complete sequence of the *matK* gene, the *trnK* intron downstream of *matK* and the *rps16-trnK* intergenic spacer, and used a subset of the previous sampling focused on the subclade containing *H. pentadactyla*. In all analyses of the combined matrices, *H. pentadactyla* formed a subclade (1.00 PP, 55% BS-MP, 71% BS-ML) with *H. ekmaniana*, *H. montevidensis* and *H. henscheniana*; this clade was sister, with strong to moderate support (0.97 PP, 71% BS-MP, 84% BS-ML), to a highly supported subclade (1.00 PP, 100% BS-MP, 100% BS-ML) formed by *H. megapotamensis*, *H. exaltata* and *H. dutrae* (Fig. 2). The clade containing *H. pentadactyla* was successively sister to a clade formed by *H. repens* Nutt. and the related species *H. aranifera* Lindl. and *H. warmingii* Rchb.f. & Warm. (0.96 PP, 54% BS-MP, 61% BS-ML), *H. regnellii* Cogn. (0.95 PP, 63% BS-MP, 82% BS-ML), the clade *H. johannensis* Barb.Rodr.–*H. macronectar* (Vell.) Hoehne (0.95 PP, 64% BS-MP, 75% BS-ML) and *H. macilentata* (Lindl.) Rchb.f. (1.00 PP, 87% BS-MP, 95% BS-ML) (Fig. 2).

DISCUSSION

CIRCUMSCRIPTION OF *HABENARIA* SECTION *PENTADACTYLAE*

Our phylogenetic analyses confirm the monophyly of New World *Habenaria* and further indicate that the currently recognized sections are polyphyletic and require extensive revision and recircumscription

(Figs 1, 2). In particular, our findings clearly demonstrate that, in its current circumscription, *H.* section *Pentadactylae* is polyphyletic and needs to be re-evaluated (Figs 1, 2). Based on our phylogenetic analyses and re-evaluation of morphological characters, we propose that *H.* section *Pentadactylae* be recircumscribed to include *H. pentadactyla* (the type species of the section), *H. dutrae*, *H. ekmaniana*, *H. exaltata*, *H. henscheniana*, *H. megapotamensis* and *H. montevidensis*, and to exclude 32 species or names previously assigned to the section by Kränzlin (1892, 1901) and Cogniaux (1893–1896) (Table 1). Of the seven species included in our new circumscription, only *H. pentadactyla* and *H. exaltata* were previously assigned to the section (Table 1). *Habenaria henscheniana* was assigned by Cogniaux (1893–1896) and Kränzlin (1901) to *H.* section *Pratenses* Kraenzl.; *H. montevidensis* was placed in *H.* section *Quadratae* Kraenzl. by Kränzlin (1892) and transferred to *H.* section *Microstylinae* Kraenzl. by Cogniaux (1893–1896); *H. ekmaniana* was assigned by Kränzlin (1911) to *H.* section *Macroceratitae* Kraenzl., and *H. megapotamensis* and *H. dutrae* were described subsequently by Kränzlin (1901, 1911) and Cogniaux (1893–1896), and were not assigned any formal sectional classification. In our phylogenetic analyses, the support value for the clade was strong to moderate (0.97 PP, 71% BS-MP, 84% BS-ML, Fig. 2). Furthermore, six species in the clade (*H. dutrae*, *H. ekmaniana*, *H. exaltata*, *H. henscheniana*, *H. megapotamensis* and *H. pentadactyla*) share similar features with respect to morphology, type of habitat and geographical distribution, and form a consistent, homogeneous group (see the Taxonomic Treatment section and the respective descriptions). The inclusion of *H. montevidensis* in the new circumscription, and also in the subclade formed with *H. henscheniana* (1.00 PP, 61% BS-MP, 58% BS-ML, Fig. 2), was unexpected, because *H. montevidensis* has a distinct set of floral features shared with neither of the other members of *H.* section *Pentadactylae* nor with any other Neotropical *Habenaria* spp. (Figs 4F, 5G, 7D–F; see also the respective description in the Taxonomic Treatment section).

The circumscription of *H.* section *Pentadactylae* followed here, based on our molecular phylogenetic analysis, differs markedly from those of previous authors (Kränzlin, 1892, 1901; Cogniaux, 1893–1896;

Figure 2. Maximum likelihood (ML) tree of the combined nuclear (internal transcribed spacer, ITS) and plastid (*matK*, *trnK* intron, *rps16-trnK*) datasets. Numbers next to the nodes are bootstrap values from ML, posterior probabilities (PPs) from the Bayesian analysis and bootstrap values from the parsimony analysis (ML/PP/MP). Neotropical subgroups are numbered according to Batista *et al.* (2013). The generic name for all *Habenaria* spp. is abbreviated. Subgroup 5 corresponds to *H.* section *Pentadactylae* as circumscribed in this work.

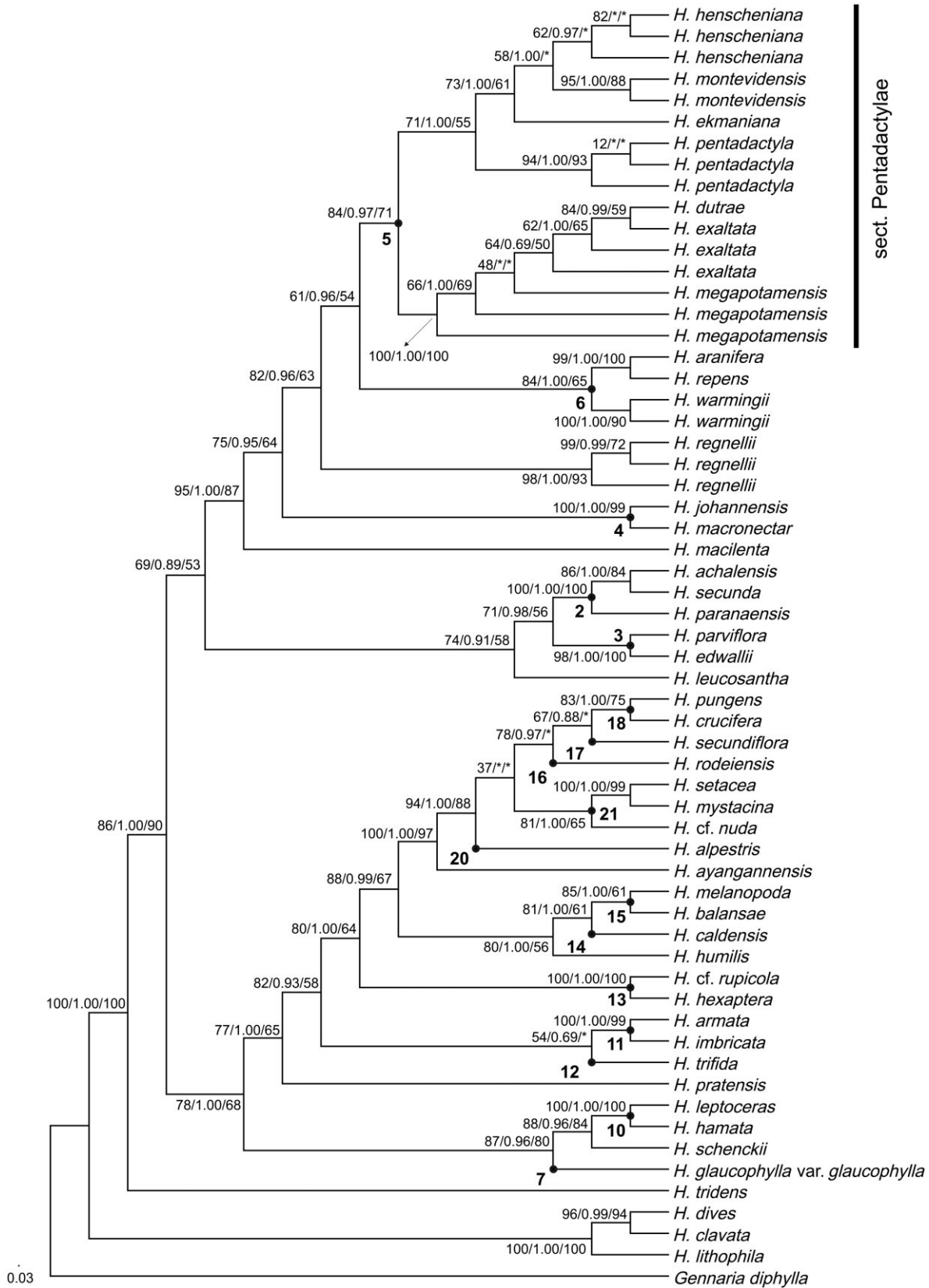


Figure 2. See caption on previous page.

Table 1). However, despite the different approaches, a re-analysis of the morphological characters used to characterize the sections and morphology of the species reveals a series of mistakes and misplacements. Kränzlin (1892) placed *H.* section *Pentadactylae* with *H.* sections *Medusaeformes* Kraenzl., *Dolichostachyae* Kraenzl., *Micranthae* Kraenzl. and *Pratenses*, in a group characterized by leafy stems, with the largest leaves concentrated at the base. However, several of the species he assigned to *H.* section *Pentadactylae* do not have these characters. *Habenaria culicina* Rchb.f. & Warm., *H. lagunae-sanctae* Kraenzl. (= *H. secundiflora* Barb.Rodr.) and *H. setacea* Lindl., for example, are characterized by leaves reduced and adpressed to the stem, and *H. achnantha* Rchb.f., *H. corcovadensis* Kraenzl. (= *H. rodeiensis* Barb.Rodr.), *H. paivaeana* Rchb.f., *H. schomburgkii* Lindl., *H. secunda*, *H. setifera* Lindl. (= *H. trifida* Kunth), *H. warmingii* and even *H. pentadactyla* have leaves distributed along the stem, with the largest leaves usually at the middle. Among the above-mentioned sections, the distinctive character for *H.* section *Pentadactylae* was the lip lobes being similar in length to the anterior lobe of the petals. However, in *H. epiphylla* Rchb.f. & Warm. (= *H. glaucophylla* Barb.Rodr.) and *H. leptoceras* Hook. (Table 1), the anterior lobe of the petals is much shorter than the lip lobes. Cogniaux (1893–1896) added a few characters in the characterization of *H.* section *Pentadactylae*, describing the anterior petal lobe as longer than the posterior one. However, similarly to Kränzlin, many of the species he added to the section do not display these characters. In *H. alpestris* Cogn., *H. exaltata* and *H. janeirensis* Kraenzl. (= *H. paranaensis* Barb.Rodr.), for example, the anterior lobe of the petals is shorter than the posterior lobe. Thus, most of the discrepancies between our results and the previous sectional treatments are not caused by the different datasets used in the analyses (morphology vs. DNA sequences) or the weight given to a particular character or combination of morphological characters, but by the poor morphological characterization and misplacement of most species by Kränzlin (1892, 1901) and Cogniaux (1893–1896).

Several species previously assigned to *H.* section *Pentadactylae* by Kränzlin (1892, 1901) and Cogniaux (1893–1896) and sampled in our phylogenetic analyses do not belong to the same clade as *H. pentadactyla* and are excluded from the section based on molecular analyses and differences in morphology (Fig. 1, Table 1). These species include *H. alpestris*, *H. araniifera*, *H. armata* Rchb.f., *H. caldensis* Kraenzl., *H. confusa* Cogn. (= *H. secundiflora*), *H. corcovadensis* (= *H. rodeiensis*), *H. culicina*, *H. epiphylla* (= *H. glaucophylla*), *H. goyazensis* Cogn., *H. graciliscapa* Barb.Rodr. (= *H. imbricata* Lindl.), *H. humilis* Cogn.,

H. imbricata, *H. janeirensis* (= *H. paranaensis*), *H. lagunae-sanctae* (= *H. secundiflora*), *H. leptoceras*, *H. macilenta*, *H. moritzii* Ridl. (= *H. armata* p.p.), *H. muelleriana* Cogn. (= *H. macilenta*), *H. riedelii* Cogn. (= *H. warmingii*), *H. rupicola* Barb.Rodr., *H. schenckii* Cogn., *H. secunda*, *H. setacea*, *H. setifera* (= *H. trifida*) and *H. warmingii*. Other species not sampled in our present phylogenetic analyses are excluded from the section based on morphological differences compared with the species in the clade formed by *H. pentadactyla* (Table 1). *Habenaria achnantha*, *H. modestissima* Rchb.f. and *H. taubertiana* Cogn. are similar and related to *H. repens* and *H. araniifera*. *Habenaria ulei* Cogn. is similar and closely related to *H. parviflora*. *Habenaria paivaeana* is similar to the species in the *H. secunda* clade (Fig. 1, Clade 2). *Habenaria santensis* Barb.Rodr. is an obscure taxon and similar to *H. rodeiensis* and *H. tamanduensis* Schltr. *Habenaria simillima* Rchb.f. is a synonym of *H. distans* Griseb., which is characterized by the two or three broadly lanceolate or oblong basal leaves. *Habenaria entomantha* (Lex.) Lindl. and *H. lactiflora* A.Rich. & Galeotti are Mexican taxa. Although not sampled in our molecular analyses in the ITS, *matK-trnK* and *rps16-trnK* dataset, these species are morphologically similar to other Mexican taxa that form a distinct, strongly supported clade (Fig. 1, Clade 9), which is related to the clades containing *H. leptoceras* (Fig. 1, Clade 10) and *H. distans* (Fig. 1, Clade 7). *Habenaria gracilis* Lindl. is an illegitimate name. It is morphologically similar to *H. repens* and *H. rupicola*, and apparently related to one of these species. The affinities of *H. candolleana* Cogn. are not clear, but the species is clearly distinct from those in *H.* section *Pentadactylae*. In flower morphology, *H. candolleana* is similar to *H. juruenensis* Hoehne, which forms a strongly supported clade with *H. rupicola* and *H. hexaptera* Lindl. (Fig. 1). Finally, the affinities of *H. schomburgkii* are also unclear; however, it is morphologically similar and apparently related to *H. repens*.

In his first description of *H.* section *Pentadactylae*, Kränzlin (1892) included one African species, *H. conopodes* Ridl., and 23 Neotropical species (Table 1). Sampling of African *Habenaria* in our previous phylogenetic analysis (Batista *et al.*, 2013) was low compared with the number of species and diversity of the genus found in Africa. Nevertheless, none of the African species sampled fell into the Neotropical clade, and DNA sequence differences between the African and Neotropical species were high (Batista *et al.*, 2013). Thus, we do not expect any other African taxa to fall eventually inside the Neotropical clade. In addition, examination of the type material of *H. conopodes* at K revealed that the viscidia are spaced apart and the stigma lobes lack the projection in the inner

margin that is found in most species of *H.* section *Pentadactylae*. Thus, the placement of this species in *H.* section *Pentadactylae* seems equivocal.

TAXONOMIC TREATMENT

HABENARIA SECTION PENTADACTYLAE KRAENZL.,
BOT. JAHRB. SYST. 16: 52. 1892.

Type species: Habenaria pentadactyla Lindl., Gen. Sp. Orchid. Pl. 307. 1835.

= *Rhinorchis* Szlach., Richardiana 13: 73. 2012. *pro parte*.

Description: Semi-aquatic herbs. Plants 12–149 cm high, including the inflorescence. Stem erect or sinuose. Leaves 5–18, spreading, largest at the lower half or centre of the stem, linear-lanceolate, ovate-lanceolate or lanceolate, 5–28 × 0.6–5.5 cm. Inflorescence 2.5–38.0 cm long, few- to many-flowered, lax to congested, spiral; bracts ovate or ovate-lanceolate, acuminate, 11–33 × 3–10 mm, generally shorter than the ovary. Flowers 3–110, small to medium sized; ovary parallel or spreading from the rachis, 13.2–27.0 mm; ovary arched, 11–19 mm, pedicel 1.5–9.8 mm. Sepals green, mucronate, margins smooth; dorsal sepal orbicular, elliptical or ovate, 3–7 × 2.7–6.6 mm; lateral sepals obliquely elliptical or elliptical, deflexed, reflexed, reclined or turned upward, 4.7–10.4 × 2.3–5.0 mm. Petals bipartite or simple, white, yellowish green, or base whitish turning greenish yellow towards the lobe apices; anterior lobe generally curved laterally and facing upward, linear-filiform, inserted at the base of the posterior lobe, 0.9–7.0 mm long, shorter, about the same length or longer than the posterior lobe, 7–10 × 5–9 mm, obtuse, free from dorsal sepal; posterior lobe oblong-falcate or falcate, 3.2–7.1 × 0.9–2.9 mm, acute or obtuse, connivent with the dorsal sepal or free from it but not spread. Lip tripartite, white, yellowish green, or base whitish turning green towards the lobe apices; undivided basal part 1.0–2.4 × 1.0–2.7 mm; lateral lobes pendent, straight, deflexed or reflexed, linear or slightly lanceolate, 3.0–10.5 mm long, filiform or up to 1.2 mm wide, shorter, about the same length or longer than the median lobe; median lobe linear or oblanceolate, straight, deflexed or reflexed, 3.5–8.3 × 0.6–2.5 mm; spur deflexed or reflexed, free or partially covered by the bracts, linear or slightly clavate, shorter to longer than the ovary, 11–78 mm long, mostly green. Gynostemium erect, 2.4–3.1 mm high; connective emarginate or obtuse, greenish or white; auricles fleshy, verrucose, whitish, 1.3–1.7 × 0.7–1.2 mm. Pollinaria two, separated, 1.7–4.0 mm long; viscidia exposed, spaced 0.6–2.5 mm apart. Stigma lobes two, closely parallel, 2.3–4.0 mm long; receptive surface whitish or green, concave or

convex, turned frontwards, thickened, inner margin with or without a protruding erect projection placed in front of the rostellum mid-lobe, which partially divides the spur entrance into two apertures. Rostellum greenish or white; mid-lobe triangular, fleshy, acute or subacute, erect, completely placed between or partially projected beyond the anther loci, 1.1–3.0 × 1.7–2.5 mm; side-lobes parallel throughout or convergent towards the apex, 1.1–2.0 mm long. Fruit a capsule full of minute, dust-like, seeds.

Distribution and conservation: One species, *H. ekmaniana*, ranges from central Brazil to northern Argentina; however, most species are concentrated in southern Brazil, with some also occurring in Paraguay and Uruguay (Fig. 3). The state of Rio Grande do Sul in southern Brazil, where all seven species occur, is particularly species rich and constitutes the centre of diversity of the section.

Habitat and ecology: Species in *H.* section *Pentadactylae* occur in swamps, wet grasslands, margins of streams or lakes or other types of humid habitat, at elevations ranging from sea level to 2000 m throughout the distribution range. Flowering occurs during the rainy season, from December to March. Some species from wet meadows, including *H. exaltata*, *H. henscheniana* and *H. megapotamensis*, are usually associated with species of *Eryngium* L. (Apiaceae).

Notes: With the partial exception of *H. montevidensis* (see Description), the species in section *Pentadactylae* form a morphologically uniform group. However, there are no unambiguous morphological synapomorphies for the section and it is characterized here by a combination of characters. The main vegetative features are the leafy and usually robust plants with spreading (patent) leaves. The well-developed leaves and leafy stem differentiate *H.* section *Pentadactylae* from species in *H.* section *Nudae* Cogn., which is characterized by the leaves reduced and adpressed to the stem. Most species in the section have greenish flowers, rostellar arms usually convergent toward the apices and short stigmatic lobes, which have a tooth-like process that partially divides the spur entrance into two apertures (Fig. 5A–F). However, similar stigmatic processes are also present in the unrelated *H. secunda* clade (Clade 2 in Batista *et al.*, 2013) and in at least one recently described, distantly related species, *H. psammophila* J.A.N.Bat., Bianch. & B.M.Carvalho in Batista *et al.* (2010) (placed near Clade 18 in Batista *et al.*, 2013). Nevertheless, all the above characters, as a whole, allow the diagnosis of the section, and they clearly separate *H.* section *Pentadactylae* from the species in the sister group of *H. repens* (Clade 6 in Batista *et al.*, 2013).

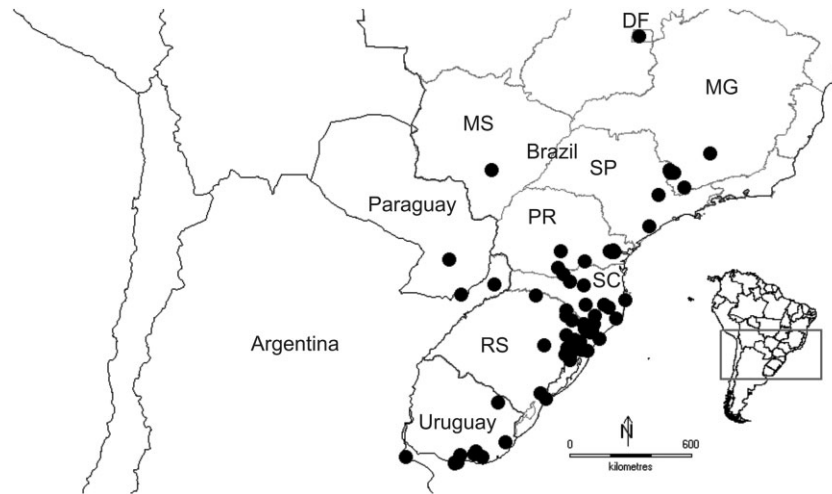


Figure 3. Distribution of *Habenaria* section *Pentadactylae*. Only one collection was plotted for each locality. Abbreviations for the Brazilian states: DF, Distrito Federal; MG, Minas Gerais; MS, Mato Grosso do Sul; PR, Paraná; RS, Rio Grande do Sul; SC, Santa Catarina; SP, São Paulo.

The type of *H.* section *Pentadactylae* was not indicated by Kränzlin (1892). According to article 22.6 of the *International Code of Nomenclature for algae, fungi and plants* (McNeill *et al.*, 2012): ‘When the epithet in the name of a subdivision of a genus is identical with or derived from the epithet in one of the originally included species names, the type of the higher-ranking name is the same as that of the species name, unless the original author of the higher-ranking name designated another type’. Therefore, the type of *H.* section *Pentadactylae* is *H. pentadactyla*.

Recently, Szlachetko (2012) proposed the segregation of a new genus (*Rhinorchis* Szlach.) from *Habenaria*. The presence of a rostellar median-lobe ‘similar to the horn of a rhino’ was proposed as the diagnostic feature for this newly proposed taxon. Two of the species placed under *Habenaria* section *Pentadactylae* here (*H. ekmaniana* and *H. megapotamensis*) were combined under this genus (Szlachetko, 2012). The diagnostic feature proposed by Szlachetko is inconsistent and absent in some newly combined taxa (see Fig. 5), and his newly proposed genus is highly polyphyletic as the species are distributed in several unrelated clades (see Batista *et al.*, 2013). We therefore consider *Rhinorchis* and combinations in that genus as synonyms.

1. *HABENARIA DUTRAE* SCHLTR., REPERT. SPEC.
NOV. REGNI VEG. BEIH. 35: 19. 1925.
(FIGS 4A, 5A, 6A, B)

Type: BRAZIL. Rio Grande do Sul: São Leopoldo, Fazenda dos Prazeres, ii.1904, *J. Dutra* 675 (holotype

B, destroyed; lectotype (designated by Batista *et al.*, 2011a): SP [38372]; islectotype: SI [39894]).

Synonym: *Habenaria schnittmeyeri* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 35: 23. 1925. *Habenaria schiedmeyeri* Schltr. ex Pabst, Sellowia 10: 127. 1959. Orthographical variant.

Type: BRAZIL. Rio Grande do Sul: São Leopoldo, i.1916, *M. Schiedmeyer s.n. ex Herb. Dutra* 995 (holotype B, destroyed; lectotype (designated by Batista *et al.*, 2011a): SP [40501, fragment]; islectotype: HB [1710, fragment]).

Description: Plants 38–95 cm, including the inflorescence. *Stem* erect. *Leaves* 9–15, ovate-lanceolate, 9.0–17.0 × 1.7–4.0 cm. *Inflorescence* many flowered, congested; bracts ovate-lanceolate, 13.0–22.0 × 4–7 mm, generally shorter than the ovary. *Flowers* 10–62; ovary parallel to the rachis or spreading from it, 13.0–14.0 mm, pedicel 2.4–4.0 mm. *Dorsal sepal* orbicular, 3.5–4.0 × 3.5–4.2 mm, margins revolute; lateral sepals obliquely elliptical, reflexed, 5.9–6.6 × 3.0–4.0 mm. *Petals* bipartite, base whitish, turning greenish yellow towards the lobe apices; anterior lobe curved laterally and facing upward, linear-filiform, inserted at the base of the posterior lobe, 5.0–5.9 mm long; posterior lobe falcate, 4.0–5.0 × 1.1–1.5 mm, acute, free from the dorsal sepal but not spread. *Lip* whitish at the base, turning green towards the lobe apices; undivided basal part 1.0–1.5 × 1.0–1.1 mm; lateral lobes pendent, straight or deflexed with apex facing upward, linear to slightly lanceolate, 6.2–7.4 × 0.9 mm; median lobe linear to oblanceolate, straight or deflexed, 5.3–6.6 × 1.0–

KEY TO THE SPECIES OF *HABENARIA* SECTION *PENTADACTYLAE*

- 1a. Dorsal sepal convex, reflexed; petals and lip completely white; petals entire, orbicular, unguiculate.....
.....*H. montevidensis*
- 1b. Dorsal sepal concave, not reflexed; petals and lip mostly green or greenish yellow; petals bipartite, not unguiculate..... 2
- 2a. Spur 11–20 mm long, slightly clavate, apex rounded..... 3
- 2b. Spur \geq 28 mm long, linear, not clavate, apex acute..... 6
- 3a. Anterior petal lobe and labellar lateral lobes shorter than the posterior petal lobe and median labellar lobe, respectively; rostellum mid-lobe projected beyond the anther loci.....*H. henscheniana*
- 3b. Anterior petal lobe and lateral lobes of labellum longer or similarly sized to the posterior petal lobe and median labellar lobe, respectively; rostellum mid-lobe not projected beyond the anther loci..... 4
- 4a. Anterior petal lobe and labellum lateral lobes longer than the posterior petal lobe and lip median lobe, respectively.....*H. dutrae*
- 4b. Anterior petal lobe and labellum lateral lobes similarly sized to the posterior petal lobe and lip median lobe, respectively..... 5
- 5a. Plants 84–152 cm tall; largest leaves ovate-lanceolate; lateral sepals deflexed.....*H. ekmaniana*
- 5b. Plants 12–45 cm tall; largest leaves linear-lanceolate; lateral sepals not deflexed.....*H. pentadactyla*
- 6a. Spur 28–35 mm long; anterior petal lobe shorter than the posterior.....*H. exaltata*
- 6b. Spur 57–78 mm long; petal lobes similarly sized.....*H. megapotamensis*

1.2 mm; spur deflexed or reflexed, free from the bracts, slightly clavate, about the same size as the pedicellate ovary, 14–17 mm long, green. *Gynostemium* 2.4 mm long; connective emarginate, greenish; auricles 1.5×1.2 mm. *Pollinaria* 2.6 mm long; viscidia spaced 0.8 mm apart. *Stigma* lobes 3.5 mm long; receptive surface whitish, convex, turned frontwards and to the sides, margins thickened, with a protruding, erect projection that partially divides the space between the stigma lobes and the entrance to the spur into two apertures. *Rostellum* greenish; mid-lobe acute, completely placed between the anther loci, 1.9×1.7 mm; side-lobes slightly convergent towards apices, 2 mm long.

Distribution and conservation status: Restricted to the eastern part of the state of Rio Grande do Sul in southern Brazil. The species is known from only eight collections in five localities. Two populations recently found by the authors are the only known extant populations of the species, after 51 years without records. Based on the World Conservation Union Red List Categories and Criteria (IUCN, 2001), *H. dutrae* can tentatively be classified as Endangered (EN: criteria B1ab(iii) + 2ab(iii); D).

Habitat and ecology: *Habenaria dutrae* is found in lowland swamps. Flowering occurs from January to February.

Etymology: Named after João Dutra, collector of the type material.

Illustrations: Hoehne (1940, plate 57, probably based on the type material, *Dutra* 675; plate 48, based on

the lectotype of *H. schnittmeyeri*), Pabst & Dungs (1977: 266, fig. 76, as *H. schiedmeyeri*, based on Hoehne, 1940, plate 48).

Additional specimens examined: BRAZIL. **Rio Grande do Sul:** Osório, Fazenda do Arroio, 4.i.1950, *Rambo s.n.* (PACA 45101); Porto Alegre, 12.ii.1960, *Orth* 1147 (HB); Porto Alegre, Morro da Glória, 20.i.1933, *Dutra s.n.* (SP 50513); Porto Alegre, Morro da Glória, 12 or 20.i.1933, *Orth* 579 (AMES, G, HB, K, PACA, S, SPF, US, W); Santo Antônio da Patrulha, 20.i.2011, *Pedron* 3 (ICN); Vacaria, 21.ii.2012, *Buzatto* 774 & *Nervo* (ICN).

Notes: *Habenaria dutrae* is similar to *H. ekmaniana* in terms of floral morphology (Fig. 6A–D). However, in *H. dutrae*, the lateral lobes of the lip are linear and longer than the median lobe, and the anterior lobe of the petals is longer than the posterior one (Fig. 4A), whereas, in *H. ekmaniana*, both petal and labellar lobes are similarly sized and the lip lobes are oblanceolate in shape (Fig. 4B).

2. *HABENARIA EKMANIANA* KRAENZL. KONGL. SVENSKA VETENSK. ACAD. HANDL., N.S. 46(10): 15. 1911. (FIGS 4B, 5B, 6C, D)

Type: ARGENTINA. Misiones: near La Granja, 17.xii.1907, *E.L. Ekman* 432 (holotype S [05–3163], isotypes AMES [69379], HBG [501061], S [R-2703; 05-3162], SI [63756, fragment]).

Synonyms: *Rhinorchis ekmaniana* (Kraenzl.) Szlach. Richardiana 13: 74. 2012.

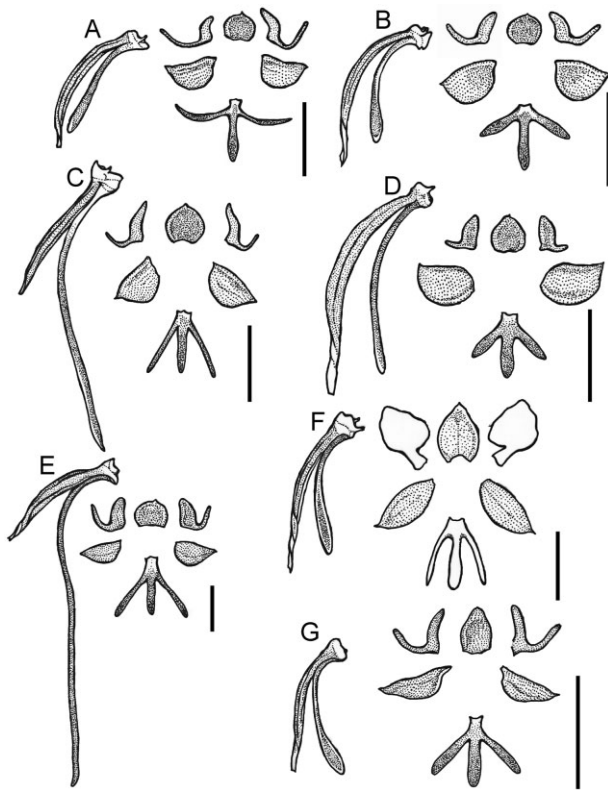


Figure 4. Floral morphology of *Habenaria* section *Pentadactylae*. Dissected perianth and lateral view of ovary, spur and gynostemium. A, *Habenaria dutrae* (Rambos n.s., PACA 45101). B, *Habenaria ekmaniana* (Radins s.n., BHCB). C, *Habenaria exaltata* (Batista 2798, BHCB). D, *Habenaria henscheniana* (Batista 2802, BHCB). E, *Habenaria megapotamensis* (Klein 145, BHCB). F, *Habenaria montevidensis* (Batista 2476, BHCB). G, *Habenaria pentadactyla* (Legrand 72, SP). Scales, 10 mm, in all cases.

Habenaria recta Schltr., Repert. Spec. Nov. Regni Veg. 16: 354. 1920.

Type: BRAZIL. Probably from São Paulo: C. Grossmann s.n. (holotype B, destroyed; no isotype located; neotype (designated here): Fl. Bras. (Hoehne) 12(1): t. 47. 1940 [illustration based on the holotype]).

Description: Plants 84–152 cm, including the inflorescence. Stem erect. Leaves 13–16, ovate-lanceolate, 13.0–26.0 × 2.7–5.5 cm. Inflorescence many flowered, congested; bracts ovate-lanceolate, 16–22 × 4–5 mm, generally shorter than the ovary. Flowers 11–97; ovary mostly parallel to the rachis, 11.4–20.0 mm, pedicel 3.4–7.0 mm. Dorsal sepal orbicular, 3.0–3.9 × 3.0–4.0 mm, margins revolute; lateral sepals obliquely elliptical, spreading (patent), 5.1–6.5 × 3.4–4.6 mm. Petals bipartite, base whitish, turning greenish yellow towards the lobe apices; anterior lobe curved laterally and facing upward, linear-filiform,

inserted at the base of the posterior lobe, 3.6–4.0 mm long; posterior lobe falcate, 3.6–4.9 × 1.2–1.5 mm, acute, free from the dorsal sepal but not spread. Lip whitish at the base, turning greenish yellow towards the lobe apices; undivided basal part 1.7–1.8 × 1.4–1.5 mm; lateral lobes pendent, linear to lanceolate, 4.4–5.4 × 1.0–1.3 mm; median lobe linear to oblanceolate, reflexed, 4.7–5.9 × 1.0–1.5 mm; spur reflexed, free or partially covered by the bracts, clavate, generally shorter than the ovary, 13–17 mm long, green. Gynostemium 2.3 mm long; connective emarginate, greenish; auricles 1.2 × 0.6 mm. Pollinaria 4 mm long; viscidia spaced 1.1–2.1 mm apart. Stigma lobes 2.7 mm long; receptive surface greenish, convex, turned frontwards, inner margins thickened, apices with a protruding, erect projection that partially divides the space between the stigma lobes into two apertures. Rostellum greenish, 2.7–2.9 mm long; mid-lobe acute, completely placed between the anther loci, 1.3 mm long, 1.8 mm tall; side-lobes parallel, 1.6 mm long.

Distribution and conservation status: *Habenaria ekmaniana* has the broadest distribution among the species in *H.* section *Pentadactylae*, ranging from central (Distrito Federal and Mato Grosso do Sul), south-eastern (Minas Gerais and São Paulo) and southern (Rio Grande do Sul) Brazil to northern Argentina (Misiones) and Paraguay. However, throughout its distribution range, the species is rare, and it is known from only nine collections in eight localities. There is only one recent record. Most of the collections are > 40 years old and from areas that are now highly modified by human activity; these populations are probably lost. In the Federal District of central Brazil, for example, there is only one record made in 1965. One of the authors has worked on a survey of Orchidaceae of Distrito Federal (Batista & Bianchetti, 2003) and has collected intensively there for > 20 years and has never found the species. Based on the World Conservation Union Red List Categories and Criteria (IUCN, 2001), *H. ekmaniana* can tentatively be classified as Endangered (EN: criterion C2a(i)).

Habitat and ecology: *Habenaria ekmaniana* is found in lowland or highland swamps. Flowering occurs from December to January.

Etymology: Named after Erik Leonard Ekman, collector of the type material.

Illustrations: Hoehne (1940, plate 56, based on the type material from S; plate 47, probably based on the holotype of *H. recta*), Insaurralde & Radins (2007: 80–81, colour photographs), Kränzlin (1911, plate 2,

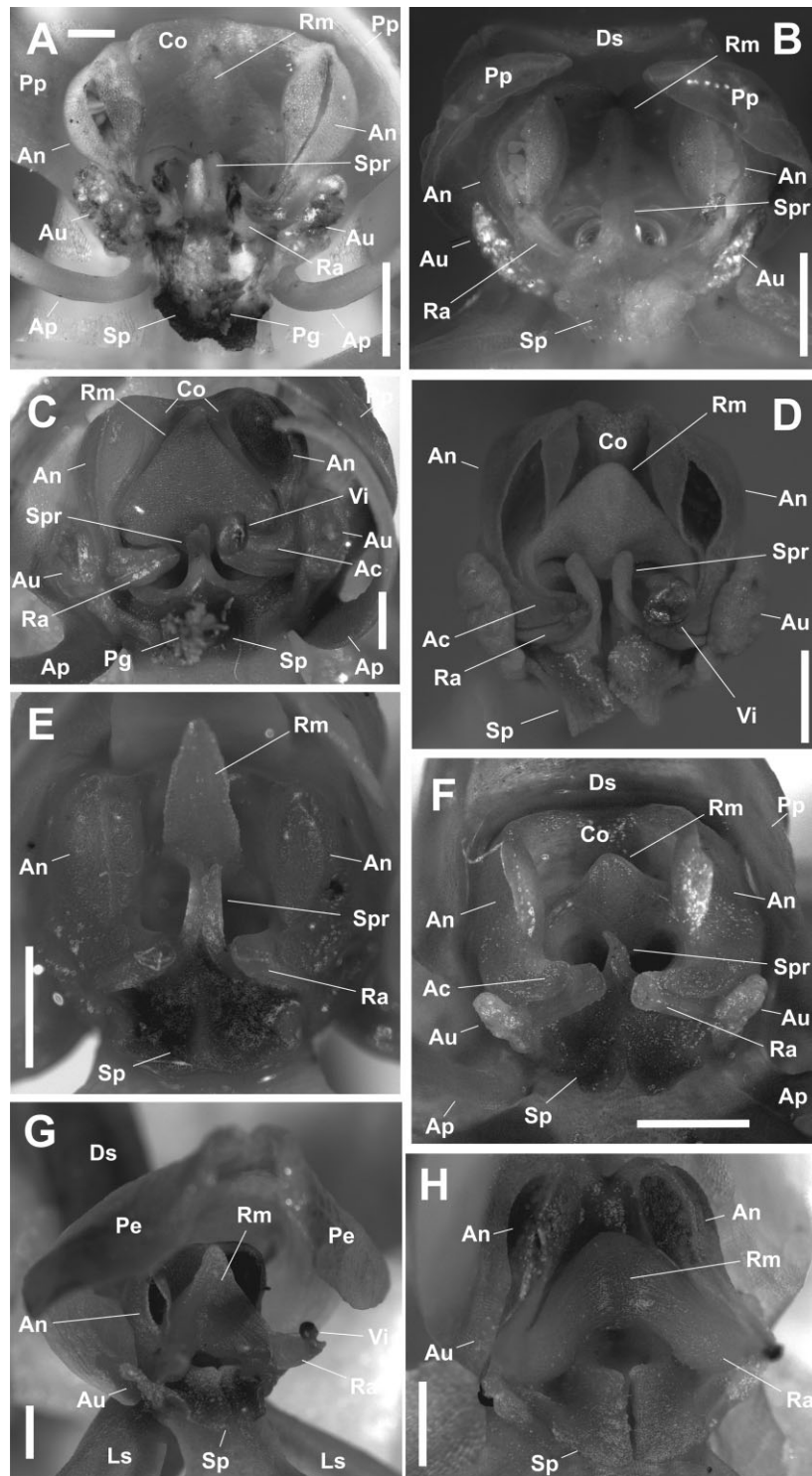


Figure 5. Gynostemium morphology in *Habenaria* section *Pentadactylae* and *H. leucosantha*. A, *Habenaria dutrae* (Pedron 3, ICN). B, *Habenaria ekmaniana* (Radins s.n., BHCB). C, *Habenaria megapotamensis* (Pedron 6, ICN). D, *Habenaria exaltata* (Pedron 10, ICN). E, *Habenaria henscheniana* (Pedron 2, ICN). F, *Habenaria pentadactyla* (Pedron 11, ICN). G, *Habenaria montevidensis* (Pedron 9, ICN). H, *Habenaria leucosantha* (Batista 1604, BHCB). Scale bars, 2 mm; Ac, anther canals; An, anther; Ap, anterior petal lobe; Au, auricles; Co, connective; Ds, dorsal sepal; Ls, lateral sepals; Pe, petal; Pg, pollen grains; Pp, posterior petal lobe; Ra, rostellum arms; Rm, rostellum mid-lobe; Sp, stigmatic processes; Spr, stigmatic projections; Vi, viscidium.

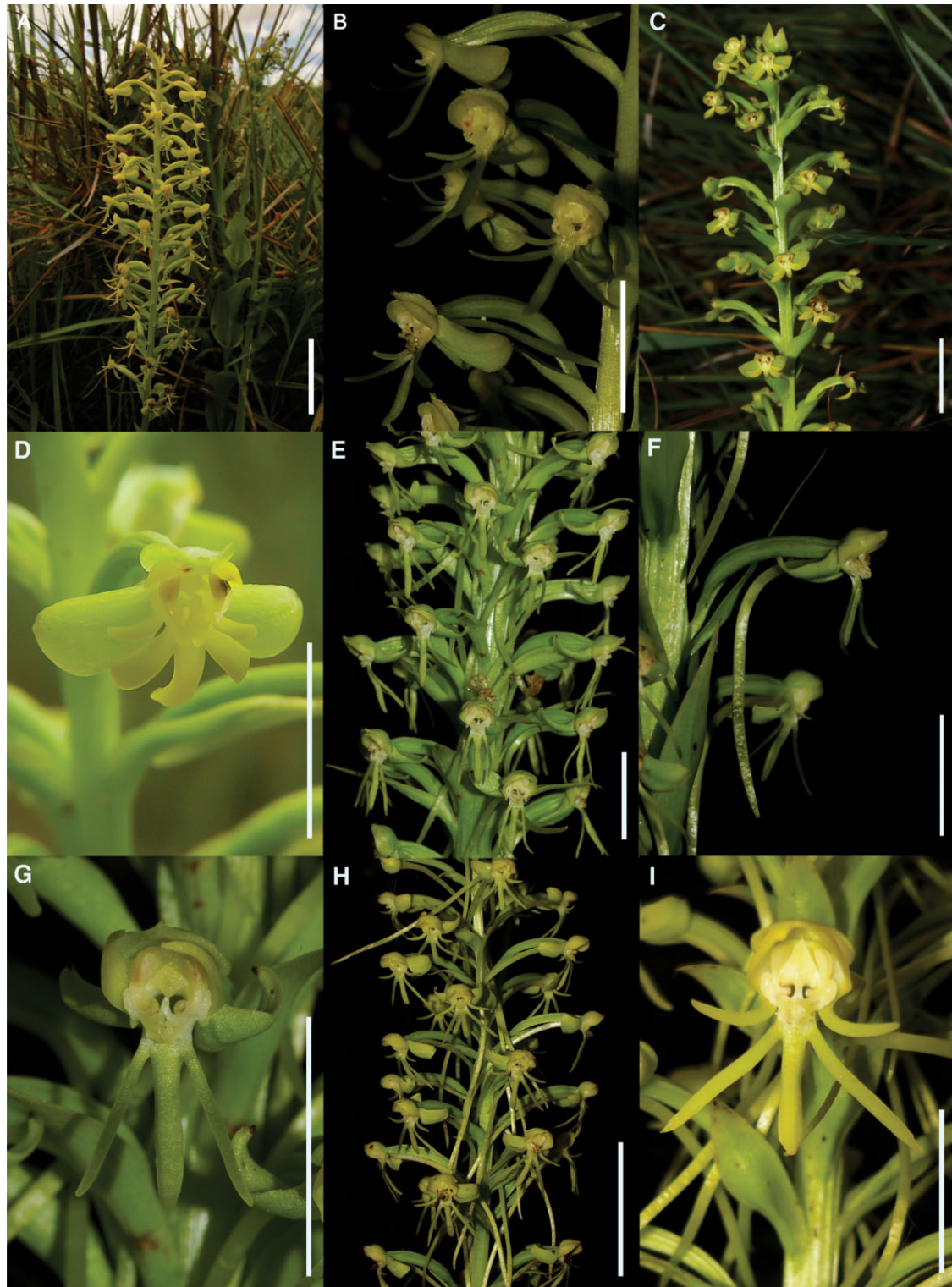


Figure 6. Inflorescence and floral morphology of *Habenaria* section *Pentadactylae*. *Habenaria dutrae*. A, Inflorescence. B, Flower (Santo Antônio da Patrulha, Rio Grande do Sul, Brazil, Pedron 3). *Habenaria ekmaniana*. C, Inflorescence. D, Flower (Posadas, Misiones, Argentina, Radins s.n.). *Habenaria exaltata*. E, Inflorescence. F, Flower, side view. G, Flower, close-up of front view (Piraquara, Paraná, Brazil, Batista 2520). *Habenaria megapotamensis*. H, Inflorescence. I, Flower (Cambará do Sul, Rio Grande do Sul, Brazil, Pedron 6). All photographs from the authors. Scale bars: A, C, H, 3 cm; B, D–G, I, 1 cm.

fig. 9, type illustration of *H. ekmaniana*, Pabst & Dungs (1975: 246, fig. 52, based on the type material, *Ekman 432*).

Additional specimens examined: ARGENTINA. **Misiones:** Posadas, xii.2010, *Radins s.n.* (BHCB). BRAZIL. **Distrito Federal:** Brasília, Zoobotânico, 20.xii.1965, *Heringer 10806* (HB, UB). **Mato Grosso do Sul:** Rio Brilhante, Fazenda Bela Vista, 20.i.1971, *Hatschbach 26125* (HB, MBM, S, UC, US). **Minas Gerais:** Bom Sucesso, 9.i.1950, *Krieger 15147* (BHCB, CESJ, HB). **Rio Grande do Sul:** Porto Alegre, i.1942, *Leite s.n.* (NY, SP 46558). **São Paulo:** Campinas, Fazenda Campo Grande, 18.xii.1938, *Guilherme s.n.* (IAC 3225, SP 40965). PARAGUAY. **Canindeyú:** In regione Yerbalium de Maracayú, 1898–1899, *Hassler 5610* (BM).

Notes: In terms of general floral morphology, *H. ekmaniana*, *H. henscheniana*, *H. dutrae* and *H. pentadactyla* are similar; in some instances, particularly with dried herbarium specimens, the species can be confused with each other. However, they can be distinguished by differences in the size of the petal lobes and in the size of the dorsal sepal relative to the lateral sepals. Distinctive features of *H. ekmaniana* are the anterior lobe of the petals and the lip lateral lobes about the same length as the posterior lobe and lip median lobe, respectively, and lateral sepals about twice the size of the dorsal sepal. A remarkable shared feature of *H. dutrae* and *H. ekmaniana* is the presence of large, broadly lanceolate to elliptical leaves, with the blades wide at the base, forming a bowl-like structure that retains and accumulates rain water. However, in comparison with *H. dutrae*, *H. ekmaniana* is generally a more robust species, with larger leaves.

The holotype of *H. recta* was not indicated. However, Grossman types were deposited at B, C and GOET. Schlechter's herbarium and types were mainly at B. Therefore, we assume that, if the type of *H. recta* was located at B, it was destroyed during World War II, because it is not cited in what remains of Schlechter's type collection in Berlin-Dahlem Herbarium (Butzin, 1978). No other duplicate of the type material has been located, even among the Berlin negatives at the Field Museum. Hoehne (1940, fig. 47) presented an illustration, based on the type material that he examined at the B herbarium before the material was lost. This is the only remaining element associated with the type, and therefore we designated it here as a neotype. In the protologue, Schlechter compared this species with *H. umbraticola* Barb.Rodr. and *H. nemorosa* Barb.Rodr.; however, these species have the anterior lobe of the petals either absent or reduced to a tooth-like projection, whereas, in

H. recta, the anterior lobe of the petals is about half the size of the posterior lobe. Based on the general similarity with *H. ekmaniana*, Batista *et al.* (2011a) considered *H. recta* to be a synonym of this species, and we follow this position here.

3. *HABENARIA EXALTATA* BARB.RODR., GEN. SP.
ORCHID. 1: 156. 1877. (FIGS 4C, 5D, 6E–G)

Type: BRAZIL. Minas Gerais: Capivary, 3.iii.1870, *A.F. Regnell ser. III 1689* (holotype not indicated; lectotype (designated by Batista *et al.*, 2011a): UPS [V-165856]; isolectotype: W-R [41328]).

Synonyms: *Habenaria henscheniana* Barb.Rodr. var. *densiflora* Cogn. Fl. Bras. (Martius) 3(4): 85. 1893.

Type: BRAZIL. Minas Gerais: Caldas, 5.iii.1876, *C.W.H. Mosén 4538* (holotype not indicated; lectotype (designated by Batista *et al.*, 2011a): S [07–7151]; isolectotypes: BR [889854 fragment, mixed with flowers of *H. henscheniana*], UPS [V-165880]).

Habenaria crassipes Schltr., Repert. Spec. Nov. Regni Veg. Beih. 35: 18. 1925. *syn. nov.*

Type: BRAZIL. Rio Grande do Sul: Venâncio Aires, near Tangerinas, 70 m, i.1924, *C. Jürgens 98* (holotype not indicated, probably B, destroyed; no isotype located; neotype (designated here): Fl. Bras. (Hoehne) 12(1): t. 49. 1940 [illustration based on the holotype]).

Habenaria sceptrum Schltr., Repert. Spec. Nov. Regni Veg. Beih. 16: 249. 1919.

Type: BRAZIL. Paraná: Pinhaes, 12.ii.1914, *P.K.H. Dusen 14498* (holotype not indicated; probably B, destroyed; lectotype (designated by Batista *et al.*, 2011a): S [R-2732]).

Description: Plants 38–149 cm, including the inflorescence. *Stem* erect. *Leaves* 9–17, lanceolate, 8.5–28 × 1.5–3.5 cm. *Inflorescence* many flowered, congested; bracts ovate-lanceolate, 12–26 × 3–6 mm, the lower longer, and upper with about the same length as the ovary. *Flowers* 17–110; ovary spreading from the rachis, 11–15 mm, pedicel 1.5–4.4 mm. *Dorsal sepal* slightly orbicular, 3.7–5.3 × 3.8–5.8 mm; lateral sepals obliquely elliptical, reflexed, 4.7–7.8 × 2.3–4.4 mm. *Petals* bipartite, base whitish, turning greenish yellow towards the lobe apices; anterior lobe curved laterally and facing upward, linear-filiform, inserted at the base of the posterior lobe, 1.2–4.4 mm long; posterior lobe oblong-falcate, 3.7–5.7 × 1.2–2.3 mm, acute, connivent with the dorsal sepal. *Lip* whitish at the base, turning green towards the lobe apices; undivided basal part 1.0–2.2 × 1.0–2.2 mm; lateral lobes pendent, deflexed or reflexed, linear-filiform, 4.6–8.6 mm long; median lobe linear to oblanceolate, deflexed or reflexed, 3.5–6.9 × 0.6–1.3 mm; spur reflexed, slightly or strongly arched,

free from the bracts, linear, longer than the ovary, 28–35 mm long, green. *Gynostemium* 2.6 mm long; connective emarginate, greenish; auricles 1.6 × 1.0 mm. *Pollinaria* 3.3 mm long; viscidia spaced 0.6 mm apart. *Stigma* lobes 3.2 mm long; receptive surface whitish, convex, turned frontwards and to the sides, margins thickened, with a protruding, erect projection that partially divides the space between the stigma lobes and the entrance to the spur into two apertures. *Rostellum* greenish; mid-lobe subacute, partially projected beyond the anther loci, 1.9 × 2.0 mm; side-lobes convergent towards apices, 1.8 mm long.

Distribution and conservation status: Distribution ranges from the southern part of the state of Minas Gerais, in south-eastern Brazil, to São Paulo, Paraná and Rio Grande do Sul, in southern Brazil, and Paraguay. Despite the broad distribution, *H. exaltata* is an occasional species throughout its distribution range. In Minas Gerais, it is known only from the vicinity of Poços de Caldas; there is only one record for São Paulo, three for Paraguay and none for Santa Catarina (which is within the species distribution range). The two populations with recent records from Minas Gerais are reduced to a few individuals, and threatened by reforestation with *Eucalyptus* L'Hér. and by urban expansion. Based on the World Conservation Union Red List Categories and Criteria (IUCN, 2001), *H. exaltata* can tentatively be classified as Vulnerable (VU: criterion B2ab(iii); D1).

Habitat and ecology: *Habenaria exaltata* is found in lowland and highland swamps. Flowering occurs from January to February. In most collections made by the authors, the species was found in wet meadows associated with *Eryngium* spp., usually growing at the base of the plants or between the leaves inside the dense rosettes.

Etymology: From the Latin *exaltatus* (raised high), probably referring to the size of the plants, which can reach up to 1.5 m in height and are usually prominent in relation to the surrounding vegetation.

Illustrations: Cogniaux (1893–1896, plate 18, fig. 2, reproduction of Barbosa Rodrigues' original illustration of *H. exaltata*), Hoehne (1940, plate 49, based on the holotype of *H. crassipes*; plate 58, as *H. sceptrum*), Pabst & Dungs (1975: 246, fig. 50, as *H. crassipes*, based on *Amadeus 37*; fig. 53, based on *Mosen 4538*, type material of *H. henscheniana* var. *densiflora*; fig. 58, as *H. sceptrum*), Barbosa Rodrigues (1996, vol. 1, t. 15B, reproduction of Barbosa Rodrigues' original illustration of *H. exaltata*).

Additional specimens examined: BRAZIL. **Minas Gerais:** Poços de Caldas, MG 877, between Esperança III and São Bento neighbourhoods, 1260 m, 3.ii.2009, *Batista et al.* 2798 (BHCB); Poços de Caldas, Morro do Ferro, 1378 m, 31.i.2009, *Batista et al.* 2771 (BHCB); Poços de Caldas, Morro do Ferro, 31.iii.1968, *Emmerich 3174* (HB, R). **Paraná:** Curitiba, 26.i.1904, *Dusen 3272* (R, SP, SPF); Curitiba, Rio Iguaçu, 3.ii.1967, *Hatschbach 15962* (HB, MBM); Guarapuava, posto agro-pecuário, 18.i.1968, *Hatschbach 18323* (MBM); Piraquara, Borda do Campo–Piraquara road, near Borda do Campo, 905 m, 4.ii.2008, *Batista et al.* 2520 (BHCB); Quatro Barras, 9.ii.1964, *Hatschbach 10946* (HB, L, MBM, U); São Mateus do Sul, Vila S'Ana, 8.ii.1966, *G. Hatschbach et al.* 13773 (MBM). **Rio Grande do Sul:** between Erval and Pedras Altas, 25.i.1966, *Trinta 1204* (HB, HBG, K, L, LP, M); Muitos Capões, 2.ii.2011, *Pedron 6* (ICN); Muitos Capões, Estação Ecológica de Aracuri, 13.i.1983, *Waechter 1976* (ICN). Muitos Capões, Estação Ecológica de Aracuri, 950 m, 26.i.1979, *Arzivenco 521* (ICN); Pelotas, Instituto Agrônomico do Sul, 31.i.1950, *Amadeu 37* (HB, ICN); São Francisco de Paula, estrada para Barragem do Blang, 22.ii.2012, *J. Klein 149* (BHCB); Viamão, Itapuã, 4.xii.1929, *Dutra 1074* (ICN, SI, SP). **São Paulo:** 84 km from São Paulo on the road São Paulo–Curitiba, 19.i.1952, *Pabst 1318* (B, HB, HBG, K, RB, S). PARAGUAY. **Guairá:** in regione collium, Cordillera de Villa-Rica, i.1905, *Hassler 8721* (BM); Villarrica, 10.i.1931, *Jorgensen 4648* (S, SI); Villarrica, i.1931, *Jorgensen 4646* (US).

Notes: Barbosa Rodrigues (1877, 1882) described several species based on material from Regnell and other collectors, and it is not always clear which material was used for his descriptions. It is generally accepted that Barbosa Rodrigues' herbarium was lost during a flood in the basement of his house, where the material was assumed to be deposited (Cribb & Toscano de Brito, 1996; Buzatto *et al.*, 2011, 2013). Currently, the herbarium of the Instituto de Botânica de São Paulo (SP) is the only herbarium in Brazil with some duplicates of Regnell Orchidaceae collections. Most of the Regnell collections are deposited at S or UPS. The only collection of the type material of *H. exaltata* is found in UPS, and because the holotype was not indicated, this material was designated as a lectotype by *Batista et al.* (2011a).

After its description, the identity of *H. exaltata* remained obscure for many years. Cogniaux (1893–1896), in *Flora Brasiliensis*, cited only the type material, whereas Hoehne (1940), in *Flora Brasiliensis*, cited an additional collection (*Lindman 2765*), which can be referred to *H. goyazensis*. Barbosa Rodrigues was a skilled illustrator, and his drawings have been

essential in clarifying the identity of several of the species he described. However, for *H. exaltata* and some other species, such as *H. henscheniana*, only a flower was sketched. This probably explains why the species was re-described as a variety of *H. henscheniana* by Cogniaux, and as *H. sceptrum* and *H. crassipes* by Schlechter. Examination of the type material of *H. henscheniana* var. *densiflora* and *H. sceptrum* has clearly shown that they can be referred to *H. exaltata*. The holotype of *H. crassipes*, located at B, was destroyed during World War II, and no isotypes have been located. However, a critical examination of the species protologue, together with Hoehne's illustration of *H. crassipes* (Hoehne, 1940; plate 49), which was based on the type material before it was lost, has shown that *H. crassipes* is inseparable from *H. exaltata*. The type material of *H. crassipes* is a robust specimen with a densely flowered inflorescence, but these are variable characters in *H. exaltata* and the flower details agree in all aspects with *H. exaltata*. Hoehne's illustration is the only extant material associated with the holotype of *H. crassipes*, and therefore we designate it here as a neotype.

Barbosa Rodrigues' original illustration of *H. exaltata* remained unpublished until it was reproduced by Sprunger (Barbosa Rodrigues, 1996). The illustration of *H. exaltata* in *Flora Brasiliica* (Hoehne, 1940; plate 68) is probably based on the material Lindman 2765 from S, because this is the only material of the species that Hoehne cited as being examined (Hoehne, 1940). We have examined this material (S10-20644 and S10-20645) and found that it is not *H. exaltata*, but can be referred to *H. goyazensis* Cogn.

Among the species in *H.* section *Pentadactylae*, distinctive features of *H. exaltata* are the long, linear spur, which is about twice the length of the ovary, and the anterior lobe of the petal shorter than the posterior lobe (Fig. 4C).

4. *HABENARIA HENSCHENIANA* BARB.RODR., GEN.

SP. ORCHID. 1: 157. 1877. (FIGS 4D, 5E, 7A–C)

Type: BRAZIL. Minas Gerais: Caldas, Rio Verde, 7.iii.1868, A.F. Regnell ser. III 999 (holotype not indicated; lectotype (designated by Batista *et al.*, 2011a): S [R-2711]; isolectotypes: BR [889854 fragment, mixed with flowers of *H. exaltata*], P [386905], S [05-3454; 07-7153], US [209488], W-R [41329]).

Description: Plants 21–118 cm tall, including the inflorescence. *Stem* erect. *Leaves* 5–16, lanceolate, 7.0–19.0 × 0.7–2.2 cm. *Inflorescence* few- to many-flowered, lax to congested; bracts ovate, 12–29 × 3–8 mm, generally shorter than the ovary. *Flowers* 7–51; ovary mostly parallel to the rachis, 11.2–17.0 mm long, pedicel 4.8–9.8 mm long. *Dorsal sepal* broadly

elliptical, 3.6–4.5 × 2.4–3.6 mm; lateral sepals obliquely elliptical, spreading (patent), 5.5–6.8 × 3.5–4.3 mm. *Petals* bipartite, base whitish, turning greenish yellow towards the lobe apices; anterior lobe curved laterally, linear-filiform, inserted at the base of the posterior lobe, 0.9–2.4 mm long; posterior lobe oblong-falcate, 3.3–3.9 × 1.4–2.0 mm, acute, connivent with the dorsal sepal. *Lip* whitish at the base, turning green towards the lobe apices; undivided basal part 1.0–2.0 × 1.1–2.0 mm; lateral lobes pendent, reflexed, linear, 3.0–4.4 × 1.0–1.2 mm; median lobe linear, reflexed, 3.7–4.8 × 1.2–1.6 mm; spur reflexed, arched downward, totally or partially covered by the bracts, slightly clavate to clavate, shorter than the ovary, 15–20 mm long, green. *Gynostemium* 2.6 mm long; connective emarginate, greenish; auricles 1.3 × 0.7 mm. *Pollinaria* 1.7 mm long; viscidia spaced 0.7 mm apart. *Stigma* lobes 2.3 mm long; receptive surface green, convex, turned frontwards, margins thickened, with a protruding, erect projection that partially divides the space between the stigma lobes and the entrance to the spur into two apertures. *Rostellum* greenish; mid-lobe acute, mostly projected beyond the anther loci, 1.1 × 2.5 mm; side-lobes convergent towards apices, 1.1 mm long.

Distribution and conservation status: Found only in south-eastern and southern Brazil in the states of Minas Gerais, Paraná, Santa Catarina and Rio Grande do Sul. The species is known from only 12 collections in nine localities. Most of the collections are from the 1950s and 1960s, and there are few recent records of the species. Based on the World Conservation Union Red List Categories and Criteria (IUCN, 2001), *H. henscheniana* can tentatively be classified as Endangered (EN: criterion C2a(i)).

Habitat and ecology: *Habenaria henscheniana* is found in highland swamps. Flowering occurs from January to February.

Etymology: Named in honour of Salomon Eberhard Henschen, a Swedish physician who worked with Anders Frederick Regnell and João Barbosa Rodrigues. Henschen, Regnell and other botanists made important contributions to the knowledge of Brazilian flora, especially the flora of Caldas, in the state of Minas Gerais, and their collections contributed through the monumental *Flora Brasiliensis*.

Illustrations: Hoehne (1940, plate 53, probably based on the type material from S), Pabst & Dungs (1975: 246, fig. 59, based on Becker 286), Barbosa Rodrigues (1996, vol. 1, t. 15C, reproduction of Barbosa Rodrigues' original illustration of *H. henscheniana*).

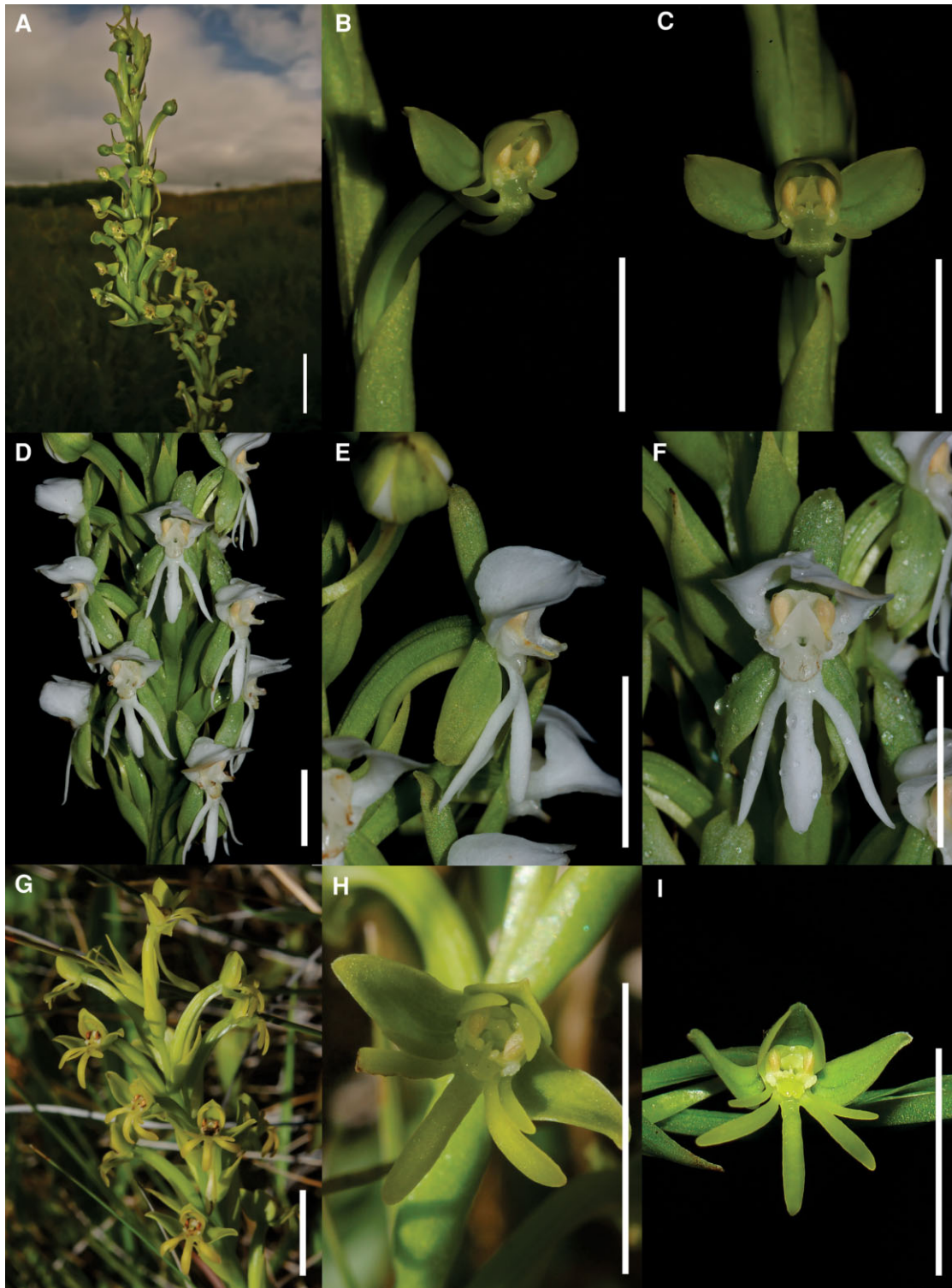


Figure 7. Inflorescence and floral morphology of *Habenaria* section *Pentadactylae*. *Habenaria henscheniana*. A, Inflorescence (São Francisco de Paula, Rio Grande do Sul, Brazil, *Pedron 2*). B, Flower, side view. C, Flower, front view (Poços de Caldas, Minas Gerais, Brazil, *Batista 2802*). *Habenaria montevidensis*. D, Inflorescence. E, Flower, side view. F, Flower, front view (Cambará do Sul, Rio Grande do Sul, Brazil, *Batista 2476*). *Habenaria pentadactyla*. G, Inflorescence. H, Flower, front view (Canelones, Uruguay, *González s.n.*). I, Flower, front view (São Francisco de Paula, Rio Grande do Sul, Brazil, *Pedron 11*). Photographs G and H from A. González; other photographs from the authors. Scale bars: A, 2 cm; B–I, 1 cm.

Additional specimens examined: BRAZIL. **Minas Gerais:** Poços de Caldas, MG 877, between Esperança III and São Bento neighbourhoods, 1.260 m, 3.ii.2009, *Batista et al.* 2802 (BHCB); Poços de Caldas, Morro do Ferro, 31.iii.1968, *Emmerich* 3176 (HB); Poços de Caldas, Morro do Ferro, 5.iii.1964, *Becker* 286 (HB). **Paraná:** Quatro Barras, Rio Taquari, 21.i.1975, *Hatschbach* 35770 (MBM, UC); Quatro Barras, Rio Taquari, 850 m, 9.i.1969, *Hatschbach* 20693 (HB, MBM, UPCB). **Rio Grande do Sul:** Bom Jesus, Aparados da Serra, 1100 m, 11.ii.1952, *Pabst* 1360 (HB, LP, MBM, PEL); Caxias do Sul, Vila Oliva, 3.i.1946, *Rambo* s.n. (PACA 30985); Osório, Fazenda do Arroio, 14.iv.1950, *Rambo* s.n. (PACA 46757); São Francisco de Paula, 21.i.2010, *Pedron* 2 (ICN). **Santa Catarina:** Lages, Santa Cecília, 21.i.1952, *Pabst* 1324 (HB); Urubici, Campo dos Padres, Fazenda Campo dos Padres, 1650 m, 25.i.1957, *Smith & Reitz* 10416 (HB, R, US); Urubici, Campo dos Padres, Serra Geral, próximo a nascente do rio Canoas, 1500 m, 19.ii.2008, *Mota et al.* 1584 (BHCB).

Notes: Similarly to *H. exaltata*, the holotype of *H. henscheniana* was not indicated, and a lectotype was designated by *Batista et al.* (2011a). The original illustration of the species remained unpublished until reproduced by Sprunger (Barbosa Rodrigues, 1996). There is some confusion regarding the data label of the type of *H. henscheniana*. The type and all duplicates are from Minas Gerais, Caldas, *Regnell* ser. III 999; however, the collection date and specific locality vary between 24.ii.1847, without specific locality (US, S [05-3454], P) and 7.iii.1868, Rio Verde (BR, S [R-2711], S [07-7153]). This is probably because, at that time, it was not unusual to use the same collection number for different collections of the same species. However, as both collection dates precede the species description and the species protologue includes data from both collections (near Rio Verde, February), we follow the position of *Batista et al.* (2011a) in the designation of the lectotype and consider the other *Regnell* ser. III 999 specimens as isolectotypes.

A distinctive feature of *H. henscheniana* among other species in *H.* section *Pentadactylae* is the position of the lateral sepals (Fig. 7A–C), which are spreading (patent) and stand wide open in front of the gynostemium. However, although this character is evident in live material, in herbarium specimens, the flowers are flattened and the lateral sepal appears appressed, resembling in this aspect *H. pentadactyla*. However, in this latter species, the whole plant and flowers are smaller.

5. *HABENARIA MEGAPOTAMENSIS* HOEHNE, ARQ. BOT. ESTADO SÃO PAULO N.S., F.M., 1: 41. 1939. (FIGS 4E, 5C, 6H, I)

Type: BRAZIL. Rio Grande do Sul: Taquara, Caracol, 13.i.1926, *J. Dutra* 873 (holotype: SP [29635]).

Synonym: *Rhinorchis megapotamensis* (Hoehne) Szlach. *Richardiana* 13: 77. 2012.

Description: Plants 78–122 cm tall, including the inflorescence. *Stem* erect. *Leaves* 11–18, ovate-lanceolate, 14.0–26.0 × 2.2–4.1 cm. *Inflorescence* many-flowered, congested; bracts ovate-lanceolate, 12–33 × 5–10 mm, generally shorter than the ovary. *Flowers* 16–74; ovary spreading from the rachis, 16–19 mm long, pedicel 6.4–8.0 mm. *Dorsal sepal* slightly orbicular, 5.4–7.0 × 5.5–6.6 mm; lateral sepals obliquely elliptical, reflexed, 7.7–10.0 × 4.0–5.0 mm. *Petals* bipartite, base whitish, turning greenish yellow towards the lobe apices; anterior lobe curved laterally and facing upward, linear-filiform, inserted at the base of the posterior lobe, 5.2–7.0 mm long; posterior lobe oblong-falcate, 5.5–7.1 × 1.8–2.9 mm, acute, connivent with the dorsal sepal. *Lip* whitish at the base, turning yellowish green towards the lobe apices; undivided basal part 1.7–1.8 × 1.8–2.3 mm; lateral lobes pendent, deflexed, linear, 8–10.5 × 0.7–1.0 mm; median lobe linear to oblanceolate, deflexed, 6.0–8.3 × 1.0–1.6 mm; spur reflexed, slightly or strongly arched, free from the bracts, linear, longer than the ovary, 57–78 mm long, green. *Gynostemium* 3.1 mm long; connective emarginate, greenish; auricles 1.7 × 1.2 mm. *Pollinaria* 3.3 mm long; viscidia spaced 0.7 mm apart. *Stigma* lobes 4 mm long; receptive surface whitish, convex, turned frontwards and to the sides, margins thickened, with a protruding, erect projection that partially divides the space between the stigma lobes and the entrance to the spur into two apertures. *Rostellum* greenish; mid-lobe subacute, partially projected beyond the anther loci, 3.0 × 2.5 mm; side-lobes convergent towards apices, 1.1 mm long.

Distribution and conservation status: *Habenaria megapotamensis* is restricted to southern Brazil, in the states of Paraná, Santa Catarina and Rio Grande do Sul. Most of the collections are from Rio Grande do Sul, where the species is common and several large populations are known. Based on the World Conservation Union Red List Categories and Criteria (IUCN, 2001), *H. megapotamensis* can tentatively be classified as Least Concern (LC).

Habitat and ecology: *Habenaria megapotamensis* is found in highland swamps. Flowering occurs from

January to March. *Habenaria megapotamensis* is pollinated by hawkmoths (Pedron *et al.*, 2012).

Etymology: From the Greek *mega* (large) and *potamos* (river or stream), probably referring to the state of Rio Grande do Sul. In southern Brazil, the state is commonly referred as Rio Grande, which means large river.

Illustrations: Hoehne (1939, plate 47, type illustration of *H. megapotamensis*), Hoehne (1940, reproduction of Hoehne, 1939), Pabst & Dungs (1975: 247, fig. 71, based on *Richter s.n.*), Pedron *et al.* (2012, fig. 1A and D, fig. 4A–B).

Additional specimens examined: BRAZIL. **Paraná**: Piraquara, road toward Borda do Campo, 17.ii.1953, *Hatschbach 3105* (HB, MBM, SI, Z). **Rio Grande do Sul**: Bom Jesus, Fazenda Bernardo Velho, 8.i.1947, *Rambo s.n.* (S 10-20641); Bom Jesus, Fazenda Caraúna, ii.1931, *Dutra 1092* (HB, ICN, SP); Bom Jesus, Fazenda do Cilho, 12.ii.2007, *Setubal et al. 848* (ICN); Cambará do Sul, 19.ii.2011, *Pedron 10* (ICN); Canela, Caracol road, 17.ii.1953, *Richter s.n.* (HB 2119); Canela, ii.1986, *Sobral & Silva 4984* (ICN, SP); Caxias do Sul: Vila Oliva, 8.ii.1955, *Rambo s.n.* (PACA 56756, S 10-20643); Jaquirana, 20.ii.1952, *Rambo s.n.* (HB 1730, PACA 52106, S 10-20642, US 00247310); São Francisco de Paula, 11.ii.2001, *Wasum 932* (US); São Francisco de Paula, 17.iii.2001, *Diesel s.n.* (US 00672816); São Francisco de Paula, estrada para Barragem do Blang, 8.ii.2012, *J. Klein 145* (BHCb); Vacaria, Fazenda da Ronda, 5.i.1947, *Rambo s.n.* (PACA 34841); Vacaria, s.d., *Dutra 1093* (ICN). **Santa Catarina**: Bom Retiro, 21.ii.2012, *Buzatto 772 & Nervo* (ICN); Caçador, 900–1000 m, 6.ii.1957, *Smith & Klein s.n.* (US 00247310).

Notes: *Habenaria megapotamensis* and *H. exaltata* are remarkably similar, and *H. megapotamensis* looks much like larger specimens of *H. exaltata*. Nevertheless, the two species are clearly distinct by the consistently larger flowers and longer spur of *H. megapotamensis*. Other differences are found in the relative sizes of the petal lobes. In *H. megapotamensis*, both petal lobes are similarly sized (c. 5.2–7.0 mm long) (Fig. 4E), whereas, in *H. exaltata*, the anterior lobe (1.2–4.4 mm long) is usually less than half the length of the posterior lobe (Fig. 4C).

6. *HABENARIA MONTEVIDENSIS* SPRENG., SYST. VEG. 3: 692. 1826. (FIGS 4F, 5G, 7D–F)

Type: URUGUAY. Montevideo, *F. Sello s.n.* (holotype: presumably B [probably destroyed], no isotype

located; neotype (designated here): BRAZIL, without locality, *F. Sello s.n.* (BM 32715); isoneotype: HBG [501305]).

Synonyms: *Habenaria arechavaletae* Kraenzl., Bot. Jahrb. Syst. 16(2): 185. 1892.

Type: URUGUAY. Sierra de Minas, ii.1874, *J.E. Gibert 1160* (holotype: B, destroyed; isotypes: BR [657428 fragment, mounted on the same sheet with *E.H.G.Ule 1904*], HB [966 fragment], MVM, ZT [14474]).

Habenaria arechavaletae Kraenzl. var. *elata* Cogn., Fl. Bras. (Martius) 3(4): 92. 1983.

Type: BRAZIL. Santa Catarina: Capivare, Serra Geral, ii.1891, *E.H.G.Ule 1904* (holotype: BR [657428]; isotypes HBG [500094; 501311], P [408631]).

Habenaria obovatipetala Schltr., Repert. Spec. Nov. Regni Veg. Beih. 35: 21. 1925. *Habenaria arechavaletae* Kraenzl. var. *obovatifetala* (Schltr.) Pabst (1954: 130).

Type: BRAZIL. Rio Grande do Sul, Caranna-Bom Jesus, 1000 m, i.1909, *J. Dutra 511* (holotype: B, destroyed; lectotype (designated by Batista *et al.*, 2011b): ICN [14511]; isolectotype: SI [39934]).

Description: Plants 21–79 cm, including the inflorescence. *Stem* erect to sinuose. *Leaves* 7–12, lanceolate, 6.0–16.0 × 1.0–2.5 cm. *Inflorescence* few- to many-flowered, congested; bracts ovate, 11–25 × 4–7 mm, generally shorter than the ovary. *Flowers* 3–31; ovary mostly parallel to the rachis, 12–15 mm long, pedicel 3–7 mm. *Dorsal sepal* ovate, 7.4–8.7 × 4.2–6.6 mm; lateral sepals elliptical, deflexed, 8.6–10.4 × 3.1–5.0 mm. *Petals* simple, white, obliquely orbicular, unguiculate, 7–10 × 5–9 mm, obtuse, free from dorsal sepal. *Lip* white, undivided basal part 1.4–2.4 × 1.3–2.7 mm; lateral lobes pendent, deflexed, linear, 7.3–9.4 × 0.8–1.0 mm; median lobe oblanceolate, deflexed, with apex slightly curved forwards, 6.4–7.8 × 1.8–2.5 mm; spur reflexed, arched downward, free or partially covered by the bracts, slightly clavate, about the same size as the ovary, 14–18 mm long; light green. *Gynostemium* 2.8 mm long; connective obtuse, white; auricles 1.7 × 1.2 mm. *Pollinaria* 3.8 mm long; viscidia spaced 2.5 mm apart. *Stigma* lobes 3.1 mm long; receptive surface white, concave, turned frontwards, with margins thickened; space between the stigma lobes elliptical. *Rostellum* white; mid-lobe acute, partially projected beyond the anther loci, 2.8 × 2.2 mm; side-lobes parallel throughout, 1.5 mm long.

Distribution and conservation status: Southern Brazil (Paraná, Santa Catarina, Rio Grande do Sul) and Uruguay. There is only one record of the species for the southern part of the state of Paraná, which marks

the northern limit of the species distribution. Otherwise, *H. montevidensis* is a common species throughout its distribution range and populations can be easily found. There is a single collection from the state of Rio de Janeiro [Alto Macaé, Nova Friburgo, 1892, *Glaziou s.n.* (BR)]. This record is far outside the known distribution range of the species; moreover, considering that many of the Glaziou collections have inaccurate or equivocal locality details (Wurdack, 1970), the record is doubtful. Based on the World Conservation Union Red List Categories and Criteria (IUCN, 2001), *H. montevidensis* can tentatively be classified as Least Concern.

Habitat and ecology: *Habenaria montevidensis* is found in lowland and highland swamps. Flowering occurs from January to March. *Habenaria montevidensis* is pollinated by butterflies (Pedron *et al.*, 2012). By contrast, other species in *H.* section *Pentadactylae* have floral syndromes associated with nocturnal moth pollination. One species with some superficial similarities to *H. montevidensis* is the unrelated *H. leucosantha* Barb.Rodr., which, in previous phylogenetic analyses, appeared as closely related to Clades 2 and 3 of Batista *et al.* (2013). Despite being unrelated, flower colour and gynostemium features in both species are quite similar (Fig. 5G, H), observations which suggest that *H. leucosantha* may also be pollinated by butterflies.

Etymology: Named after Montevideo in Uruguay, where the type material was collected.

Illustrations: Cogniaux (1893–1896, plate 15, fig. 2, as *H. arechavaletae*), Garay (1976: 117, reproduction of Reichenbach f. drawing from W-R 51316), Hoehne (1940, plate 32, fig. 2, as *H. arechavaletae*, probably based on the type material, *Gibert 1160*; plate 37, as *H. obovatipetala*), Pabst (1951, as *H. arechavaletae* and *H. obovatipetala*, plates 6–7), Pabst (1954, plates 1–3), Pabst (1956, reproduction of Pabst, 1954, plates 1–3), Pabst & Dungs (1975: 244, fig. 29, as *H. arechavaletae*, based on *Rambo s.n.* PACA 4829; 1977: 266, fig. 42b, as *H. obovatipetala*, based on Hoehne, 1940, table 37), Lombardo (1984, plate 148, fig. 2), Pedron *et al.* (2012, fig. 1A and E, fig. 4C–D).

Additional specimens examined: BRAZIL. **Paraná:** General Carneiro, Rio Iratim, 11.ii.1966, *Hatchbach 13708* (G, HBG, MBM). **Santa Catarina:** Bituruna, 9.ii.1948, *Mello-Filho 756* (R); Florianópolis, Trindade, 17.iii.1945, *Rohr s.n.* (PACA 28898); Santa Cecilia, 1000 m, 26.ii.1962, *Reitz & Klein 12529* (HB); Santa Cecilia, 100 km de Lages, on the road between Lages and Mafra, 21.i.1952, *Pabst 1326* (HB, RB); São Joaquim, Altos, 2.ii.1958, *Mattos 5107* (HB); São

Joaquim, Invernadinha, 20.i.1958, *Mattos 5003* (HB); São Joaquim, São Francisco Xavier, 1200 m, 4.ii.1963, *Reitz 6664* (HB, L, MBM, US); Urubici, 19.ii.2012, *C.R. Buzatto 761 & M.H. Nervo* (ICN). **Rio Grande do Sul:** Bom Jesus, 20.i.1958, *Camargo s.n.* (S 10-20600); Bom Jesus, Caraúna, *Dutra 1084* (ICN, SP); Bom Jesus, Lageadinho, 20.i.1958, *Camargo 3111* (PACA); Cambará do Sul, ~20.4 km NE from Cambará, on the road to São José dos Ausentes, 1038 m, 1.ii.2008, *Batista 2476* (BHCB); Cambará do Sul, ~27.8 km NE from Cambará, on the road to São José dos Ausentes, 1058 m, 1.ii.2008, *Batista 2479* (BHCB); Cambará do Sul, 900 m, ii.1948, *Rambo s.n.* (B, HB, PACA 36583, S 10-20605, SI); Canela, Caracol, 30.i.1934, *Dutra 1156* (ICN); Canela, Caracol, Tiririca stream, 27.i.1941, *Rambo s.n.* (PACA 11977); Canela, Passo do Inferno, 10.ii.1941, *Rambo s.n.* (HB, PACA 4829); Jaquirana, 20.ii.1952, *Rambo s.n.* (PACA 52057, S 10-20602); Santo Antônio da Patrulha, *Dutra 1183* (ICN); São Francisco de Paula, 1.ii.1936, *Rambo & Dutra 1541* (SP); São Francisco de Paula, 11.ii.2011, *Pedron 9* (ICN); São Francisco de Paula, Fazenda Englert, 1.ii.1936, *Buck s.n.* (B, PACA 1541); São Francisco de Paula, Morrinhos, 7.ii.1952, *Rambo s.n.* (HB, PACA 52110, S 10-20608, US 00247126); São José dos Ausentes, ~14.6 km NE from São José dos Ausentes, on the road to Silveira, 1185 m, 2.ii.2008, *Batista 2487* (BHCB); São José dos Ausentes, i.2002, *Sobral 9503* (RB); s.loc. s.d., *Gaudichaud 336* (BR). URUGUAY. **Cerro Largo:** Cerro de Las Cuentas, 23.ii.1938, *Rosengurt B2575* (HB, RB). **Lavalleja:** Cerro de Minas, 6.ii.1952, *Teague s.n.* (HB 1373, 1374, 1375, 1376). WITHOUT LOCALITY. Collector not indicated (W-R 51316).

Notes: We could not locate the holotype of *H. montevidensis* or any other specimen associated with the species protologue. As the Sello herbarium and types were deposited at B, these materials may have been destroyed during World War II. Garay (1976) recorded a voucher from Reichenbach Herbarium (W-R 51316), consisting of a specimen and a flower sketch drawn by Reichenbach, without locality and collector, and considered that it could be from Sello, because the Reichenbach herbarium contains a set of Sello's collections. Based on this information, Batista *et al.* (2011b) considered the material W-R 51316 as an isotype. However, there is no other evidence for this position. We know only two collections of *H. montevidensis* made by Sello, from Brazil, located at BM and HBG, and which are chosen here for typification of the species. Both are well preserved; however, the specimen at BM has more good flowers and is selected as the neotype.

For many years, the identity of *H. montevidensis* was obscure. The specific epithet was first used by

Sprengel (1826), and later by Lindley (1830–1840), but based on different types and species. Cogniaux (1893–1896), in *Flora Brasiliensis*, confused the two descriptions, using Sprengel's name with Lindley's description. Garay (1976) proposed the new name *H. uruguayensis* for *H. montevidensis* Lindl. (1835: 314), but the separation of this taxon from the widespread *H. parviflora* is not clear. Cogniaux's error was followed by all subsequent authors, who applied the name *H. montevidensis* Spreng. to *H. parviflora*.

There is some uncertainty regarding the data of the type of *H. arechavaletae*. In the protologue, Kränzlin (1892) recorded the type as Uruguay, Sierra de Minas, Arechavaleta 1160, whereas the type at ZT is labelled Montevideo, ii.1880. However, the material at MVM and the fragments at BR and HB are from *Gibert 1160*, Uruguay, Pagum, Minas, ii.1874. Arechavaleta original herbarium and types are at MVM, and therefore we follow the data of this herbarium. It is possible that, when duplicates from the Arechavaleta herbarium were distributed, the number 1160 was associated with Arechavaleta instead of Gibert.

Habenaria montevidensis is distinct from other species in *H.* section *Pentadactylae*, and also from all other Neotropical species, because of the reflexed, convex dorsal sepal and the entire, orbicular, unguiculate petals, which form a hood over the gynostemium (Fig. 7D–F). In addition, *H. montevidensis* is characterized by completely white petals and lip and absence of projection of the stigmatic processes (Figs 4F, 5G, 7D–F), the parallel rostellum arms and the well-spaced viscidia (Figs 5G, 7F). By contrast, in the other species of *H.* section *Pentadactylae*, flowers are greenish, petals are bipartite and the rostellum arms are confluent towards the apices, with the viscidia close to one another (Fig. 5A–F). The presence of a reflexed dorsal sepal is a widespread feature in the African species of *H.* section *Replicatae*, but is probably unique among Neotropical species. Pabst (1954, 1956), who collected and examined live material of *H. montevidensis*, was the first to draw attention to these characters.

7. *HABENARIA PENTADACTYLA* LINDL., GEN. SP.
ORCHID. PL. 307. 1835. (FIGS 4G, 5F, 7G–I)

Type: URUGUAY. Maldonado, Lagoa de los Patos, *J. Tweedie 543* (holotype: K [396199 mounted on the same sheet with *Gibert 892*]; isotype K-L).

Description: Plants 12–45 cm, including the inflorescence. *Stem* erect to sinuose. *Leaves* five to nine, linear-lanceolate, 5.0–13.0 × 0.6–1.1 cm. *Inflorescence* few- to many-flowered, lax to congested; bracts ovate-lanceolate, 12–25 × 4–5 mm, generally shorter than ovary. *Flowers* 3–17; ovary mostly parallel to the

rachis, 14–16 mm long, pedicel 3–6 mm. *Dorsal sepal* ovate to elliptical, 3.5–4.2 × 2.7–3.2 mm; lateral sepals obliquely elliptical, turned upward, 5.3–6.6 × 2.4–3.1 mm. *Petals* bipartite, yellowish green; anterior lobe curved laterally and facing upward, linear-filiform, inserted at the base of the posterior segment, 4.0–4.3 mm long; posterior lobe falcate, 3.2–4.2 × 1.0–1.2 mm, acute, connivent with the dorsal sepal. *Lip* whitish green at the base, turning yellowish green towards the lobe apices; undivided basal part 1.0–1.2 × 1.1–1.5 mm; lateral lobes pendent, straight or slightly deflexed, linear, 4.1–5.5 × 1.1 mm; median lobe linear, straight or deflexed, 3.7–5.4 × 0.8–1.1 mm; spur deflexed or reflexed, arched downward, free or partially covered by the bracts, clavate, about the same size as the ovary, 11–15 mm long, green. *Gynostemium* 2.0–2.1 mm long; connective slightly emarginate, whitish; auricles 0.85 × 0.60 mm. *Pollinaria* 1.7–1.8 mm long; viscidia spaced 0.3–0.4 mm apart. *Stigma* lobes 2.4 mm long; receptive surface greenish, slightly convex, turned upwards, inner margins thickened, with a protruding, erect projection that partially divides the space between the stigma lobes and the entrance to the spur into two apertures. *Rostellum* whitish, 1.9 mm long; mid-lobe obtuse, completely placed between the anther loci, 1.3–1.4 mm long, 1.3 mm tall; side-lobes convergent towards the apices, 0.6–0.7 mm long.

Distribution and conservation status: Restricted to Rio Grande do Sul, in southern Brazil, Uruguay and part of eastern Argentina, mainly in the coastal region. *Habenaria pentadactyla* is apparently a rare species, and most records are from the 1960s. The small and slender plants, with greenish flowers, are difficult to locate among the surrounding herbaceous vegetation, and this may account, at least in part, for the small number of collections. Many of these collections were made in areas that are now inhabited by humans, and the populations of the species are probably declining; however, a more accurate study is required to verify this. Based on the World Conservation Union Red List Categories and Criteria (IUCN, 2001), *H. pentadactyla* can tentatively be classified as Endangered (EN: criterion C2a(i)).

Habitat and ecology: *Habenaria pentadactyla* is found in sandy lowlands and highland swamps. Flowering occurs from December to March.

Etymology: From the Greek *penta* (five) and *dactylos* (finger), probably referring to the set formed by the three lobes of the lip, and the anterior lobe of each petal.

Illustrations: Hoehne (1940, plate 121, fig. 2), Pabst & Dungs (1975: 256, fig. 164, based on *Rosengurt B2611*), Lombardo (1984, plate 149, fig. 1).

Additional specimens examined: ARGENTINA. **Buenos Aires:** Buenos Aires, *Tweedie 183* (OXF). BRAZIL. **Rio Grande do Sul:** Osório, Fazenda do Arroxo, 6.iii.1950, *Pabst 561* (HB); Rio Grande, Quinta, 28.i.1950, *Bento 4* (HB, ICN); São Francisco de Paula, 19.ii.2011, *Pedron 11* (ICN); São Francisco de Paula, estrada entre Barragem do Blang e Divisa, 22.ii.2012, *J. Klein 150* (BHCB); Torres, Faxinal, 31.iii.1978, *Waechter 781* (ICN); Viamão, Itapuã, 5.x.1929, *Dutra 1077* (ICN, SI, SP). URUGUAY. **Canelones:** Arroio Sarandy, Rio de la Plata, Costa Azul, 3.ii.1942, *Augusto s.n.* (ICN 20356); Balneario Guazuvirá Nuevo, 11.ii.2012, *González s.n.* (MVFA); Carrasco, 4.iii.2011, *González s.n.* (MVFA); Colinas de Solymar, 12.ii.2012, *González s.n.* (MVFA). **Maldonado:** Maldonado, 3.ii.1916, *Herter 1198* (SP); Maldonado, i.1869, *Gibert 892* (K 396200, W); Piriapolis, 29.iii.1911, *Osten 5515* (SI); 28.i.1912, *Osten 5775* (CORD, SI). **Montevideo:** Montevideo, Carrasco, 11.iii.1932, *Osten 2247* (S); Montevideo, Carrasco, 27.ii.1914, *Berro 7269* (HB); Montevideo, Carrasco, 28.ii.1875, *C. Fruchart s.n.* (P 408881, P 408882, P 408883, SI); Montevideo, Carrasco, iv.1913, *Berro 6788* (HB); Montevideo, Carrasco, *Legrand 72* (SP); Montevideo, Carrasco, iii.1870, *Gibert 892* (BR, K 396198, W). **Rocha:** Laguna Negra, Angostura, 20.iii.1938, *Rosengurt B2611* (HB, ICN, RB).

Notes: Distinctive from other species in *H.* section *Pentadactylae*, plants of *H. pentadactyla* are smaller, have few flowers and the lateral sepals are turned upward (Fig. 7G–I). Although live material of *H. pentadactyla* is characteristic, dried specimens can be confused with other species, particularly with small specimens of *H. henscheniana*. A diagnostic character is the length and proportion of the petal lobes. In *H. pentadactyla*, the anterior petal lobe is 4.0–4.3 mm long and about the same size as the posterior lobe (Fig. 4G). In *H. henscheniana*, the anterior lobe is 0.9–2.4 mm long, and less than or about half the length of the posterior lobe (Fig. 4I). One specimen at ICN (*Sobral 2103*) has intermediate characters between *H. pentadactyla* and *H. henscheniana*, and may represent a hybrid between the two species.

In the protologue, Lindley recorded the type material from Bonaria, which refers to the city of Buenos Aires in Argentina. However, in Tweedie's collection, the material is recorded from Maldonado, which is located in Uruguay.

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APPENDIX 1. EXSICCATAE

Amadeu 37 (3), Arzivenco, L. 521 (3), Augusto s.n. [ICN 20355] (7), s.n. [ICN 20356] (7), Batista, J.A.N. *et al.* 2476 (6), 2479 (6), 2487 (6), 2520 (3), 2771 (3), 2798 (3), 2802 (4), Becker, J. 286 (4), Bento 4 (7), Berro, M.B. 6788 (7), 7269 (7), Buck, P. s.n. [PACA 1541] (6), Buzatto, C.R. 772 (5), 774 (1), Camargo, O.R. 3111 (6), s.n. [S 10-20600] (6), Diesel s.n. [US 00672816] (5), Dusen, P.K.H. 14498 (3), Dutra, J. 511 (6), 675 (1), 873 (5), 1074 (3), 1077 (7), 1084 (6), 1092 (5), 1156 (6), 1183 (6), s.n. [SP 50513] (1), Ekman, E.L. 432 (2), Emmerich, M. 3174 (3), 3176 (4), Fruchart, C. s.n. (7), Gaudichaud, C. 336 (6), Gibert, J.E. 892 (7), 1160 (6), González, A. s.n. (7), s.n. (7), s.n. (7), Grossmann, C. s.n. (2), Guilherme, s.n. [SP 40965] (2), Hassler, E. 5610 (2), 8721 (3), Hatschbach, G. *et al.* 10946 (3), 13708 (6), 13773 (3), 15962 (3), 18323 (3), 20693 (4), 26125 (2), 35770 (4), 3105 (5), Heringer, E.P. 10806 (2), Herter, W.G. 1198 (7), Jorgensen, P. 4646 (3), 4648 (3), Jürgens, C. 98 (3), Klein, J. 145 (5), Krieger, L. 15147 (2), Legrand, D. 72 (7), Leite, E. s.n. [SP 46558] (2), Mattos, J. 5107 (6), 5003 (6), Mello-Filho, L.E. 756 (6), Mosén, C.W.H. 4538 (3), Mota, N.F.O. *et al.* 1584 (4), Orth, C. 579 (1), 1147 (1), Osten, C. 2247 (7), 5515 (7), 5775 (7), Pabst, G.F.J. 561 (7), 1318 (3), 1324 (4), 1326 (6), 1360 (4), Pedron, M. 2 (4), 3 (1), 6 (3), 9 (6), 10 (5), 11 (7), Radins, J. s.n. (2), Rambo, B. s.n. [PACA 4829] (6), s.n. [PACA 11977] (6), s.n. [PACA 30985] (4), s.n. [PACA 34841] (5), s.n. [PACA 36583] (6), s.n. [PACA 45101] (1), s.n. [PACA 46757] (4), s.n. [PACA 52057] (6), s.n. [PACA 52106] (5), s.n. [PACA 52110] (6), s.n. [PACA 56756] (5), s.n. [S 10-20641] (5), Rambo, B. & Dutra, J. 1541 (6), Regnell, A.F. ser. III 999 (4), ser. III 1689 (3), Reitz, R. 6664 (6), Reitz, R. & Klein, R.M. 12529 (6), Richter, E. s.n. [HB 2119] (5), Rohr, A. s.n. [PACA 28898] (6), Rosengurtt, B. B2611 (7), B2575 (6), Schiedmeyer, M. s.n. ex Herb. Dutra 995 (1), Sello, F. s.n. [BM 32715, HBG 501305] (6), Setubal *et al.* 848 (5), Smith, L. & Klein, R.M. s.n. [US 00247310] (5), Smith, L. & Reitz, R. 10416 (4), Sobral, M. 9503 (6), Sobral, M. & Silva, R. 4984 (5), Teague, G.W. s.n. [HB 1373, 1374, 1375, 1376] (6), Trinta, Z.A. 1204 (3), Tweedie, J. 183 (7), 543 (7), Ule, E.H.G. 1904 (6), Waechter, J.L. 1976 (3), 781 (7), Wasum 932 (5).