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Contribution to the revision of the genus *Sargassum* (Fucales, Phaeophyceae) in Madagascar using morphological and molecular data

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Abstract – The marine macroalgae of Madagascar have been poorly studied, probably due to difficulties in accessing most of the 4,828 kms of coastline spreading across more than 14º of latitude. Recent collecting trips in the southern and northern sections of the island provided large collections to contribute towards a better knowledge of the marine macrophyte diversity of Madagascar. The present study focuses on the brown macroalgal genus *Sargassum*. Based on morphological and molecular analyses of the nuclear ITS2, chloroplastic partial RuBisCO operon and mitochondrial cox3 and 23S, we delineated a total of 11 taxa including seven new records (*) for Madagascar and an unidentified taxon: *S. elegans**, *S. ilicifolium*, *S. ilicifolium* var. *acaraeocarpum**, *S. incisifolium, S.* cf. *latifolium, S. obovatum**, *S. polycystum, S. portierianum**, *S. robillardii**, *S. swartzii** and *S.* sp In addition, nine taxa listed in the literature were not found during these recent collecting trips, implying a possible full list of 20 *Sargassum* species for Madagascar. More collections are required for a comprehensive revision of the *Sargassum* diversity of the island, particularly along its west and east coasts.

Cox3 / diversity / Indian Ocean / ITS-2 / mt23S / phylogeny / RuBisCO / seaweeds / systematics

Résumé – Les macroalgues marines de Madagascar ont été peu étudiées, probablement due à la difficulté d'accès de la majorité des 4828 kms de côtes qui s'étendent sur plus de 14° de latitude. De récentes campagnes d'échantillonnage, menées dans les régions Sud et Nord de l'île, ont permis de constituer d'importantes collections dans le but de contribuer à la connaissance de la Flore marine de Madagascar. Notre étude s'est concentrée sur l'analyse du genre d'algues brunes *Sargassum*. L'analyse combinée de la morphologie et de quatre marqueurs moléculaires, (ITS2, opéron RuBisCO partiel, cox3 et mt23S), a permis l'identification de 11 taxons dont sept sont nouveaux pour Madagascar (*) et un reste sans nom: *S. elegans**, *S. ilicifolium*, *S. ilicifolium* var. *acaraeocarpum**, *S. incisifolium, S.* cf. *latifolium, S. obovatum**, *S. polycystum, S. portierianum**, *S. robillardii**, *S. swartzii** et *S.* sp.*. Neuf taxons supplémentaires sont recensés dans la littérature disponible pour Madagascar mais n'ont pas été re-collectés lors des campagnes d'échantillonnage récentes, en conséquence la liste complète des Sargasses de Madagascar compte un total de

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20 espèces. Des collections supplémentaires, en particulier le long des côtes Est et Ouest de Madagascar sont nécessaires afin de finaliser la réévaluation de la diversité du genre *Sargassum* à Madagascar.

Cox3 / diversité / Océan Indien / ITS-2 / mt23S / phylogénie / RuBisCO / algues marines / systématique

INTRODUCTION

Madagascar is the largest island state in the Indian Ocean. It spreads across 14º of latitude, with a coastline that is 4,828 kms long (http://world.bymap.org/Coastlines.html) and represents more than a third of the total length of the East African coast from the tip of Somalia down to the Cape of Good Hope. From a biogeographical perspective, Madagascar is a very interesting region in the Indian Ocean. To the west, the Mozambique Channel is characterised by strong currents and eddies that create turbulent and specific circulation patterns (Quartly & Srokosz, 2004; Halo *et al.*, 2014; Hancke *et al.*, 2014). These result in unique patterns of distribution and connectivity over the whole latitudinal gradient of the west of the island, and between adjacent coasts and islands (Forbes *et al.*, 1999; Gopal *et al.*, 2006; Braby, 2014; José *et al.*, 2014; Marsac *et al.*, 2014). A global study that selected the 200 World's ecosystems most important for conservation placed the 'Western Madagascar marine ecosystems' among the 23 "coral reef and associated marine ecosystem regions" chosen (Olson & Dinerstein, 1998). The Marine Ecosystems of the World system (MEOW: Spalding *et al.*, 2007) recognises two distinct marine ecoregions in Madagascar. Coasts in the northern Mozambique Channel (within the Western and Northern Madagascar Ecoregion) support a high diversity of corals (Obura 2012). On the other hand, in the southern Mozambique Channel (including southern Madagascar) there is higher productivity due to eddy-shelf interactions and upwelling from the South Madagascar Plateau, resulting in a transition to colder/higher nutrient fauna and habitats, and lower coral diversity (Obura, 2012).

The marine Flora of Madagascar is probably one of the poorest documented in the Western Indian Ocean. A search on Algaebase.org (Guiry & Guiry, 2014) returned a list of only 339 marine macrophytes which is considerably fewer than states with smaller coastlines in the region (e.g Seychelles: 431 spp., Mauritius: 435 spp., Tanzania: 506 spp., Kwazulu Natal, South Africa: 508 spp.; Bolton *et al.*, 2012; Guiry & Guiry, 2014). The low number of taxa recorded for Madagascar is most probably due to the inaccessibility of most of the island's coastline.

Few recent expeditions have aimed at making an inventory of marine macrophytes from various sections of the coastline. The largest collection was obtained in 2010 from the "Atimo Vatae" expedition to the south of the island. A second smaller expedition, focussed on marine macrophytes, was carried out in 2012 in the northern part of the island. Further specimens were obtained during sampling around Fort Dauphin in the south-east of Madagascar in 2013.

The present study focused on specimens of the brown algal genus *Sargassum* C. Agardh, that were collected during the expeditions mentioned above.

The genus *Sargassum* is ecologically significant in many regions of the world (Phillips, 1995), providing shelter and a nursery for numerous marine species, including commercial fish (Tanaka & Leite, 2003; Aburto-Oropeza *et al.*, 2007). However, it is taxonomically very complex and in great need of revision (Mattio & Payri, 2011). This is particularly true in the South-West Indian Ocean region where the genus has been reassessed only for the Mascarene Islands and South Africa (Mattio *et al.*, 2013, 2015). A number of studies have demonstrated the need for an integrated approach, combining morphological and molecular analyses for species identification in *Sargassum* (Mattio & Payri, 2010, 2011; Camacho *et al.*, 2015). Analyses using a range of molecular markers have not been able to separate closely related taxonomic units belonging to some of the sections of the genus (e.g. Mattio *et al.*, 2009; Cho *et al.*, 2012; Camacho *et al.*, 2015). The combination of the nuclear ITS2, chloroplastic partial RuBisCo and mitochondrial cox3 and 23S, however, remains the mostly widely used to-date and therefore provides the best comparative dataset (Mattio *et al.*, 2013).

The principal aim of this study was to assess the *Sargassum* diversity from recent field collections and contribute towards the revision of the 13 current *Sargassum* epithets recorded in the literature available for Madagascar. To do this we used a combined analysis of morphological characters and the four DNA markers listed above. We also compare the *Sargassum* flora of Madagascar with that of neighbouring regions in the southwest Indian Ocean, and discuss patterns in its biogeographical distribution.

MATERIALS AND METHODS

Study sites and specimen collection

The specimens used in this study were collected during three different sampling trips. The largest collection (a total of 24 *Sargassum* sampled from 12 localities) was obtained from the 2010 *Atimo Vatae* expedition to southern Madagascar, a joint initiative of the Muséum National d'Histoire Naturelle (MNHN, France) and Pro-Natura International (PNI). A second smaller expedition, focusing on marine macrophytes, was carried out in 2012 in the northern part of the island as part of a collaboration between L. Scott (ASCLME-IRD, South Africa), L. Mattio (UCT, South Africa) and F.X. Mayer (CetaMada, Madagascar). A total of 12 *Sargassum* samples were collected from eight sites spread between the Island of Sainte Marie in the north-east, Diego Suarez at the northern-most tip, and the island of Nosy Be, Marovasa Be and Majunga in the north-west. A third sampling trip in 2013 (K. Sink, SANBI, South Africa) provided seven more samples collected from five sites around Fort Dauphin, south-east Madagascar. Sampling localities are detailed in Table 1. All samples were pressed as herbarium voucher specimens (except as indicated in Table 1) and subsamples were preserved in silica gel for later molecular analyses (Chase & Hills, 1991).

Table 1. Specimens and sequences used in the present study with collection, publication and Genbank accession details. D, MADLYD, MADKS accessions are kept in the Herbarium of the Seaweed Unit at the University of Cape Town.
*Type localities are indicated in boldface.

Species	*Accessions*	*Collection details*	*ITS2*	*cox3*	*rbcLS*	*23S*
Sargassum subgenus Bactrophycus						
Sargassum confusum C. Agardh	GENT-HV2010	Japan – Dixon *et al.*, 2014; Mattio *et al.*, 2015	KF281943	KF281991	KF281801	KP720462
Sargassum coreanum J. Agardh	PF1452	South Korea – Cho *et al.*, 2012	JF931856	JF931753	JF931701	n.a.
Sargassum fusiforme (Harvey) Setchell	PF589	South Korea – Cho *et al.*, 2012	JF931859	JF931743	JF931691	n.a.
Sargassum hemiphyllum (Turner) C. Agardh	GENT-HV2007	Japan – Dixon *et al.*, 2014; Mattio *et al.*, 2015	KF281933	KF281985	KF281791	KP720463
Sargassum horneri (Turner) C. Agardh	IRD5219	Japan – Dixon *et al.*, 2014; Mattio *et al.*, 2015	KF281925	KF281979	KF281783	KP720464
Sargassum incisifolium (Turner) C. Agardh	BOL44346	South Africa, Cape Point ***Type locality*** – Dixon *et al.*, 2014; Mattio *et al.*, 2015	KF281919	KF281974	KF281777	KP720454
	BOL44347	South Africa – Dixon *et al.*, 2014; Mattio *et al.*, 2015	KF281920	KF281975	KF281778	KP720453
	MADKS12	Madagascar (SE), near Fort Dauphin – Jul. 2013, K. Sink	KP720360	KP720327	KP720395	KP720302
	PC0166486	Madagascar (SE), Partitioned BEAST Bayesian Inference consensus tree based on partitioned ITS2, cox3, partial RuBisCO and mt23S; posterior probabilities greater than 0.9 and ML bootstrap greater than 90% are displayed. Country abbreviations: Aus, Australia; C, Colombia; HI: Hawaii; FJ: Fiji; FP, French Polynesia; Kr, Korea; JP, Japan; MAD, Madagascar; MAUR, Mauritius; MAY, Mayotte; NL, Netherlands; NC, New Caledonia; NZ, New Zealand; RUN, Réunion; Va: Vanuatu; SA, South Africa; Kr, South Korea; TZ, Tanzania. Baie des Galions, Fort Dauphin – Dixon *et al.*, 2014; Mattio *et al.*, 2015	KF281917	KF281972	KF281775	KP720455

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*Type localities are indicated in boldface. *(continued)*

Species	*Accessions*	*Collection details*	*ITS2*	*cox3*	*rbcLS*	*23S*
Sargassum incisifolium (Turner) C. Agardh *(continued)*	PC0166775	Madagascar (SE),Partitioned BEAST Bayesian Inference consensus tree based on partitioned ITS2, cox3, partial RuBisCO and mt23S; posterior probabilities greater than 0.9 and ML bootstrap greater than 90% are displayed. Country abbreviations: Aus, Australia; C, Colombia; HI: Hawaii; FJ: Fiji; FP, French Polynesia; Kr, Korea; JP, Japan; MAD, Madagascar; MAUR, Mauritius; MAY, Mayotte; NL, Netherlands; NC, New Caledonia; NZ, New Zealand; RUN, Réunion; Va: Vanuatu; SA, South Africa; Kr, South Korea; TZ, Tanzania. Cap d'Ansirabe, Fort Dauphin – Dixon *et al.*, 2014; Mattio *et al.*, 2015	KF281918	KF281973	KF281776	KP720456
	PC0143112	Madagascar (SE), Baie des Galions – Mattio *et al.,* 2015	KP720520	n.a.	KP720551	KP720444
	PC0171790	Madagascar (SE), Baie des Galions – Mattio *et al.*, 2015	KP720521	KP720484	KP720552	KP720445
Sargassum lacerifolium (Turner) C. Agardh	PERTH08286566	Australia – Dixon *et al.*, 2014	JN243807	JN243780	JN243845	n.a.
Sargassum micracanthum (Kützing) Endlicher	GENT-HV1938	Japan – Dixon *et al.*, 2014; Mattio *et al.*, 2015	KF281928	KF281981	KF281786	KP720460
Sargassum muticum (Yendo) Fensholt	SGAD-NL (no voucher)	Netherlands – Dixon *et al.*, 2014; Mattio *et al.*, 2015	KF281922	KF281976	KF281780	KP720464
Sargassum nigrifolium Yendo	IRD5215	Japan – Dixon *et al.*, 2014; Mattio *et al.*, 2015	KF281924	KF281978	KF281782	KP720461
Sargassum ringgoldianum Harvey	GENT-HV1951	Japan – Dixon *et al.*, 2014; Mattio *et al.*, 2015	KF281929	KF281982	KF281787	KP720457
Sargassum sinclairii J.D. Hooker & Harvey	SGAD-1016	New Zealand ***Type locality*** – Dixon *et al.*, 2014; Draisma *et al.*, 2010	KF281916	KF281971	KF281774	FM958388

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*Type localities are indicated in boldface. *(continued)*

Species	*Accessions*	*Collection details*	*ITS2*	*cox3*	*rbcLS*	*23S*
Sargassum subgenus Sargassum						
Sargassum aquifolium (Turner) C. Agardh	IRD1582	Fiji – Mattio *et al.*, 2009, 2013	EU833432	EU833406	EU833464	KF413722
	IRD1660	Solomon Is. – Mattio *et al.*, 2009, 2013	EU833447	EU833397	EU833462	KF413723
	IRD1681	Vanuatu – Mattio *et al.*, 2009, 2013	EU833456	EU833412	EU833476	KF413720
	sh01466	Hawaii – Mattio *et al.*, 2008, 2013	EU100796	EU100835	EU100821	KF413721
Sargassum carpophyllum J. Agardh	IRD1511	New Caledonia – Mattio *et al.*, 2008, 2013	EU100797	EU833415	EU100804	KF413725
Sargassum cymosum f. *borbonica* Grunow	ARV594/ BOL155928	Reunion Is., Sainte Rose ***Type locality*** – Mattio *et al.*, 2013	KF413691	n.a.	n.a.	KF413732
Sargassum elegans Suhr	PC0166774	Madagascar (SE), Baie des Galions near Fort Dauphin, May 2010, F. Rousseau	KP720378	KP720344	n.a.	KP720315
Sargassum ilicifolium (Turner) C. Agardh	IRD1589	Fiji – Mattio *et al.*, 2009, 2013	EU833439	n.a.	EU833470	KF413737
	IRD3931	New Caledonia – Mattio *et al.*, 2009, 2013	FJ170443	FJ170417	FJ170387	KF413736
	IRD#TZ0852	Tanzania – Mattio & Payri, 2010, Mattio *et al.*, 2013	HQ416061	HQ416133	HQ416022	KF413735
	MADLYD181	Madagascar (NE), Sainte Marie Island – May 2012, L. Mattio	KP720361	KP720334	KP720402	KP720307
Sargassum ilicifolium var. *acaraeocarpum* Grunow	GENT#TZ0047	Tanzania, Mbudya Island – H. Verbruggen	KP720370	KP720337	KP720405	n.a.
	GENT#TZ0631	Tanzania, Zanzibar, Nungwi ***Type locality*** – H. Verbruggen	KP720371	KP720338	n.a.	n.a.
	MADLYD038	Madagascar (N), Mer d'Emeraude, DiegoSuarez – May 2012, L. Mattio	KP720366	KP720332	KP720400	n.a.
	MADLYD137	Madagascar (NW), Majunga – May 2012, L. Mattio	KP720367	KP720333	KP720401	n.a.
	MADLYD180	Madagascar (NE), Sainte Marie Island – May 2012, L. Mattio	KP720365	KP720331	KP720399	KP720306

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Species	*Accessions*	*Collection details*	*ITS2*	*cox3*	*rbcLS*	*23S*
Sargassum ilicifolium var. *acaraeocarpum* Grunow *(continued)*	PC0165971	Madagascar (SE), Plage Monseigneur, Fort Dauphin – May 2010, F. Rousseau	KP720362	KP720328	KP720396	KP720303
	PC0165972	Madagascar (SE), Plage Monseigneur, Fort Dauphin – May 2010, F. Rousseau	KP720369	KP720336	KP720404	KP720309
	PC0166050	Madagascar (SE), Plage Monseigneur, Fort Dauphin – May 2010, F. Rousseau	KP720368	KP720335	KP720403	KP720308
	PC0166385	Madagascar (SE), Cap Ranavalona, Fort Dauphin – May 2010, F. Rousseau	KP720363	KP720329	KP720397	KP720304
	PC0171900	Madagascar (SW), Nosy Manitse – May 2010, E. Coppejans	KP720364	KP720330	KP720398	KP720305
Sargassum cf. *latifolium (*turner) C. Agardh	MADKS14	Madagascar (SE), near Fort Dauphin – Jul. 2013, K. Sink	KP720382	KP720350	KP720414	KP720321
	MADSK15	Madagascar (SE), near Fort Dauphin – Jul. 2013, K. Sink	KP720383	KP720351	KP720415	KP720322
	PC0142845	Madagascar (SE), Sainte Luce – Jun. 2010, L. LeGall	KP720381	KP720345	KP720410	KP720316
Sargassum obovatum Harvey	ARV141/IRD5184	Reunion Is. – Mattio *et al.*, 2013	KF413692	KF413710	n.a.	KF413745
	ARV461	Reunion Is. – Mattio *et al.*, 2013	KF413693	KF413709	n.a.	KF413744
	BOL44353	Mauritius, Cap Malheureux ***Type locality*** – Mattio *et al.*, 2013	KF413695	KF413714	KF413682	KF413743
	BOL44354	Mauritius – Mattio *et al.*, 2013	KF413694	KF413713	KF413681	KF413742
	PC0142969	Madagascar (SE), Roche Choumare, Jun. 2010 – L. LeGall	KP720380	KP720349	KP720413	KP720320
	PC0166578	Madagascar (SE), Nosy Lokaro – May 2010, F. Rousseau	KP720379	KP720347	KP720412	KP720318

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*Type localities are indicated in boldface. *(continued)*

Species	*Accessions*	*Collection details*	*ITS2*	*cox3*	*rbcLS*	*23S*
Sargassum obtusifolium J. Agardh	IRD1537	Hawaii ***Type locality*** – Mattio *et al.*, 2008	EU100794	EU100834	EU100820	n.a.
	UPF2651	French Polynesia – Mattio *et al.*, 2008	EU100785	EU100830	EU100819	n.a.
Sargassum pacificum Bory de Saint-Vincent	UPF2754	French Polynesia ***Type locality*** – Mattio *et al.*, 2008	EU100783	EU100824	EU100812	n.a.
Sargassum pfeifferae Grunow	ARV146/IRD5188	Reunion Is. – Mattio *et al.*, 2013	KF413699	n.a.	KF413686	KF413733
	BOL44355	Mauritius ***Type locality*** – Mattio *et al.*, 2013	KF413700	KF413716	KF413687	KF413734
Sargassum polycystum C. Agardh	ARV144/IRD5187	Reunion Is. - Mattio *et al.*, 2013	KF413701	KF413707	KF413688	KF413729
	BOL44349	Mauritius – Mattio *et al.*, 2013	KF413703	KF413717	KF413689	KF413746
	BOL44350	Mauritius – Mattio *et al.*, 2013	KF413702	KF413718	KF413690	KF413747
	GENT#TZ0049	Tanzania – Mattio & Payri, 2010	HQ416068	HQ416130	HQ416020	n.a.
	MADLYD035	Madagascar (N), Mer d'Emeraude, DiegoSuarez – May 2012, L. Mattio	KP720389	KP720356	KP720418	n.a.
	MADLYD105	Madagascar (NW), Plage de Sikona, Marovasa Be – May 2012, L. Mattio	KP720390	KP720357	KP720419	n.a.
	MADLYD125	Madagascar (NW), Baie de Moramba, Marovasa Be – May 2012, L. Mattio	KP720391	KP720358	KP720420	n.a.
	PC0166292	Madagascar (SE), NE of Evatra lighthouse, May 2010, F. Rousseau	KP720393	KP720359	KP720421	KP720326
	PC0171903	Madagascar (SW), Nosy Manitse – May 2010, E. Coppejans	KP720392	n.a.	n.a.	KP720325

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*Type localities are indicated in boldface. *(continued)*

Species	*Accessions*	*Collection details*	*ITS2*	*cox3*	*rbcLS*	*23S*
Sargassum polyphyllum J. Agardh	IRD1613	New Caledonia - Mattio *et al.*,Partitioned BEAST Bayesian Inference consensus tree based on partitioned ITS2, cox3, partial RuBisCO and mt23S; posterior probabilities greater than 0.9 and ML bootstrap greater than 90% are displayed. Country abbreviations: Aus, Australia; C, Colombia; HI: Hawaii; FJ: Fiji; FP, French Polynesia; Kr, Korea; JP, Japan; MAD, Madagascar; MAUR, Mauritius; MAY, Mayotte; NL, Netherlands; NC, New Caledonia; NZ, New Zealand; RUN, Réunion; Va: Vanuatu; SA, South Africa; Kr, South Korea; TZ, Tanzania. 2009, 2013	EU833424	EU833385	EU833458	KF413726
Sargassum portierianum Zanardini	ARV471	Reunion Is. – Mattio *et al.*, 2013	KF413705	n.a.	n.a.	KF413731
	BOL44348	Mauritius – Mattio *et al.*, 2013	KF413704	KF413715	KF413685	KF413730
	MADLYD124	Madagascar (NW), Baie de Moramba, Marovasa Be – May 2012, L. Mattio	KP720377	KP720341	KP720408	n.a.
Sargassum robillardii (Grunow) Mattio *et al.*	ARV034/IRD5189	Reunion Is. – Mattio & Payri 2010; Mattio *et al.*, 2013	HQ416073	n.a.	HQ416018	KF413738
	ARV143/IRD5186	Reunion Is. – Mattio *et al.*, 2013	KF413696	KF413708	KF413683	KF413739
	BOL44351	Mauritius ***Type locality*** – Mattio *et al.*, 2013	KF413698	KF413712	n.a.	KF413741
	BOL44352	Mauritius – Mattio *et al.*, 2013	KF413697	KF413711	KF413684	KF413740
	MADKS22	Madagascar (SE), near Fort Dauphin – Jul. 2013, K. Sink	KP720386	KP720353	KP720417	KP720324
	MADLYD004	Madagascar (N), Mer d'Emeraude, DiegoSuarez – May 2012, L. Mattio	KP720387	KP720354	n.a.	n.a.

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Species	*Accessions*	*Collection details*	*ITS2*	*cox3*	*rbcLS*	*23S*
Sargassum robillardii (Grunow) Mattio *et al.* *(continued)*	MADLYD106	Madagascar (NW), Plage de Sikona, Marovasa Be – May 2012, L. Mattio	KP720388	KP720355	n.a.	n.a.
	PC0166384	Madagascar (SE), Cap Ranavalona, Fort Dauphin – May 2010, F. Rousseau	KP720384	KP720346	KP720411	KP720317
	PC0166620	Madagascar, Flacourt, May 2010, F. Rousseau	KP720385	KP720348	n.a.	KP720319
Sargassum scabridum J.D. Hooker & Harvey	WELT-A028417	New Zealand ***Type locality*** – Mattio & Payri, 2009, 2013	FJ170456	FJ170423	FJ170393	KF413727
Sargassum spinuligerum Sonder	GENT#TZ0400	Tanzania – Mattio & Payri, 2010	HQ416072	HQ416131	HQ416019	n.a.
	IRD3978	New Caledonia – Mattio & Payri, 2009; Mattio & Payri, 2010	FJ170462	FJ170428	FJ170401	n.a.
Sargassum sp.	MADKS13	Madagascar (SE), near Fort Dauphin – Jul. 2013, K. Sink	KP720376	n.a.	KP720409	KP720314
	PC0165973	Madagascar (SE), Plage Monseigneur, Fort Dauphin – May 2010, F. Rousseau	KP720374	KP720342	n.a.	KP720312
	PC0166293	Madagascar (SE), NE of Evatra lighthouse, May 2010, F. Rousseau	KP720372	KP720339	KP720406	KP720310
	PC0166618	Madagascar (SE), Flacourt – May 2010, F. Rousseau	KP720375	KP720343	n.a.	KP720313
	PC0171786	Madagascar (SE), Baie des Galions near Fort Dauphin – May 2010, E. Coppejans	KP720373	KP720340	KP720407	KP720311
Sargassum schnetteri (Bula-Meyer) Camacho *et al.*	LAF06612	Colombia ***Type locality*** – Camacho *et al.*, 2015	KF437949	KF437931	KF437962	n.a.
	LAF04287A	Colombia ***Type locality*** – Camacho *et al.*, 2015	KF437950	KF437932	KF437963	n.a.

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*Type localities are indicated in boldface. *(continued)*

Species	*Accessions*	*Collection details*	*ITS2*	*cox3*	*rbcLS*	*23S*
Sargassum swartzii C. Agardh	IRD1532	New Caledonia – Mattio *et al.*, 2008, 2013	EU882254	KF413706	EU100807	n.a.
	IRD3912	New Caledonia – Mattio *et al.*, 2010	EU882255	n.a.	EU882264	n.a.
	PC0166773	Madagascar (SE), Baie des Galions near Fort Dauphin – May 2010, F. Rousseau	KP720394	KP720352	KP720416	KP720323
Sargassum turbinarioides Grunow	IRD1604	New Caledonia ***Type locality*** – Mattio *et al.*, 2009, 2013	EU882256	EU882245	EU882265	KF413724
Outgroup						
Turbinaria decurrens Bory de Saint-Vincent	IRD5237	Mayotte, Dzaoudzi Is., North reef – Jun. 2010, L. Mattio	KP720530	KP720494	n.a.	KP720459
Turbinaria ornata (Turner) J. Agardh	D1599	South Africa, KwaZulu-Natal (northern), Bhanga Nek – Oct. 2013, L. Mattio, R. Anderson, J.J. Bolton	KP720529	KP720493	KP720559	KP720452
	IRD5193	Reunion Is., St Gilles – Mar. 2010, M. Zubia	KP720528	KP720492	KP720558	KP720458

Morphological analyses

Morphological analyses were performed on dried specimens and/or photographs of fresh specimens. All morphological features were thoroughly examined, including holdfasts, axes, leaves (or fronds), vesicles and receptacles (Yoshida, 1983; Mattio & Payri, 2011). Groups of specimens representing a morphological continuum were considered as a single morphotaxon as previously described by Mattio *et al.* (2013).

DNA processing and phylogenetic analyses

Silica gel samples were processed partly at the Central Analytical Facility, DNA sequencer, Stellenbosch University (South Africa) and partly in the systematics laboratory in the Department of Biological Sciences, University of Cape Town (South Africa) The nuclear ITS-2 (Internal Transcribed Spacer 2), chloroplastic partial RuBisCO operon, mitochondrial cox3 (Cytochrome c Oxydase subunit 3) and mt23S (mitochondrial ribosomal DNA 23S subunit) regions were PCR amplified using primers listed in Mattio *et al.* (2013). Purification and sequencing of all PCR products was done at the Central Analytical Facility using the NucleoFast membrane (Machery-Nagel, Düren, Germany) on a Freedom Evo robot (Tecan Group Ltd., Männedorf, Switzerland) followed by the BigDye Terminator v3.1 sequencing kit (Life Technologies, Johannesburg, South Africa).

Nuclear ITS-2 sequences were aligned manually using the BioEdit sequence alignment editor (Hall, 1999), following the method of Stiger *et al.* (2003). Partial RuBisCO operon, cox3 and mt23S sequences were aligned by eye with no ambiguities. Sequences for as many subgenera and sections of the genus *Sargassum* as possible, emphasising those present in the South Western Indian Ocean, were selected from those previously published (Table 1) and included in the alignments. The best-fit models for each individual alignment were estimated with FindModel (available online at http://www.hiv.lanl.gov) based on AIC values, as follows: ITS2 and cox3: General Time Reversible plus Gamma, partial RuBisCO operon: Hasegawa-Kishino-Yano plus Gamma, and mt23S: Tamura-Nei plus Gamma. Bayesian Inference and Maximum Likelihood were applied to a partitioned (ITS-2 + cox3 + partial RuBisCO operon + mt23S) dataset using BEAST v.1.8.0 (Drummond & Rambaut, 2007) and RAxML-HPC v.8. (Stamatakis, 2014) through the online CIPRES Science Gateway (Miller *et al.*, 2010, 2011). BEAST analyses used estimated base frequencies, 4 categories to model among-site rate heterogeneity, a relaxed lognormal molecular clock, a coalescent tree prior with a randomly generated starting tree, and were run for 50 million generations. Every 5,000th tree was sampled, outputs were analysed in Tracer v1.6.0 (Rambault *et al.*, 2014) and the consensus tree created in TreeAnnotator, with 10% of the trees discarded as burn-in. RAxML analyses used a GTRCAT model and 1,000 bootstrap replications. Trees were visualised in FigTree v1.3.1 (Drummond & Rambaut, 2007) and rooted with three sequences of species of the closely related genus *Turbinaria* (Mattio *et al.*, 2009).

Species identification and taxonomic revision

For the preliminary identification of morphotaxa we used literature that lists or describes *Sargassum* species in Madagascar and the South West Indian

Ocean region (Bory de Saint-Vincent, 1828; Suhr, 1840; Kützing, 1860, 1861; Martens, 1866; Grunow, 1868, 1915, 1916; Bornet, 1885; Hariot, 1902; Stephenson *et al.*, 1937; Papenfuss, 1940, 1952; Stephenson, 1944, 1948; Isaac, 1957; Isaac & Chamberlain, 1958; Price *et al.*, 1978; Seagrief, 1984; Bolton & Stegenga, 1987, 1990; Rabesandratana, 1988, 1996; Farrell, Critchley & Aken, 1993; Silva, Basson & Moe, 1996; Stegenga *et al.*, 1997; De Clerck *et al.*, 2005; Oliveira *et al.*, 2005; Mattio *et al.*, 2013, 2015), studies describing within-taxon morphological variation (Mattio *et al.*, 2008, 2009, 2010; Mattio & Payri, 2009), and historical diagnoses of various species for the genus (e.g. C. Agardh, 1820, 1824; J. Agardh 1848, 1889). Phylogenetic trees were then used to test the grouping of specimens based on morphological analysis, as well as a tool to help with identification when sequences clustered with published, reliably identified specimens, or sequences obtained from type localities. Although the genetic markers used here have proven useful to confirm most species as distinct in previous studies (Mattio & Payri, 2010; Cho *et al.*, 2012), we were aware that they might not always discriminate between closely related species; in all such instances it was decided that morphological characters were to be considered as diagnostic. Finally, species names were confirmed by comparison with our collection of scans and photographs of type specimens.

RESULTS

Phylogenetic analyses

A total of 38, 36, 29 and 40 new sequences were obtained for ITS-2 (335-460 bp), cox3 (434 bp), the partial RuBisCO operon (593-607 bp) and the mt23S (401-414 bp) respectively and included in the alignment (available upon request to the first author). GenBank accessions are given in Table 1. A number of sequences representing the various subgenera and sections of *Sargassum* were selected from among those previously published and available on GenBank. The final dataset comprised 2078 bp-long concatenated sequences (including gaps) for a total of 89 *Sargassum* specimens.

The tree resulting from the partitioned BEAST analysis is presented in Fig. 1, support for nodes are displayed for posterior probabilities (PP) above 0.90 and bootstrap support (BS) above 90% obtained from the ML analysis. Results displayed, within the genus *Sargassum*, two main fully supported clades (PP = 1, BS = 100%) representing both subgenera.

Bactrophycus and *Sargassum*. The first was further divided into one fully supported clade (PP = 1, BS = 100%) representing the *S.* sect. *Halochloa* and the second, moderately supported (PP = 0.87, BS = 99%), the three other sections of *S.* subgenus *Bactrophycus* (*S.* sect. *Hizikia*, *Spongocarpus* and *Teretia*). Three sequences newly obtained from Malagasy specimens clustered with two sequences of *S. incisifolium* (Turner) C. Agardh from South Africa and two from Madagascar in a fully supported group within the *S.* sect. *Halochloa* clade. The *S.* sect. *Halochloa* clade further included Genbank sequences from Japan and Australasia, while the other clades of *S.* subgenus *Bactrophycus* were represented by East Asiatic and European Genbank sequences (Fig. 1, Table 1). The *S.* subgenus *Sargassum* clade was further divided into six fully supported subclades representing

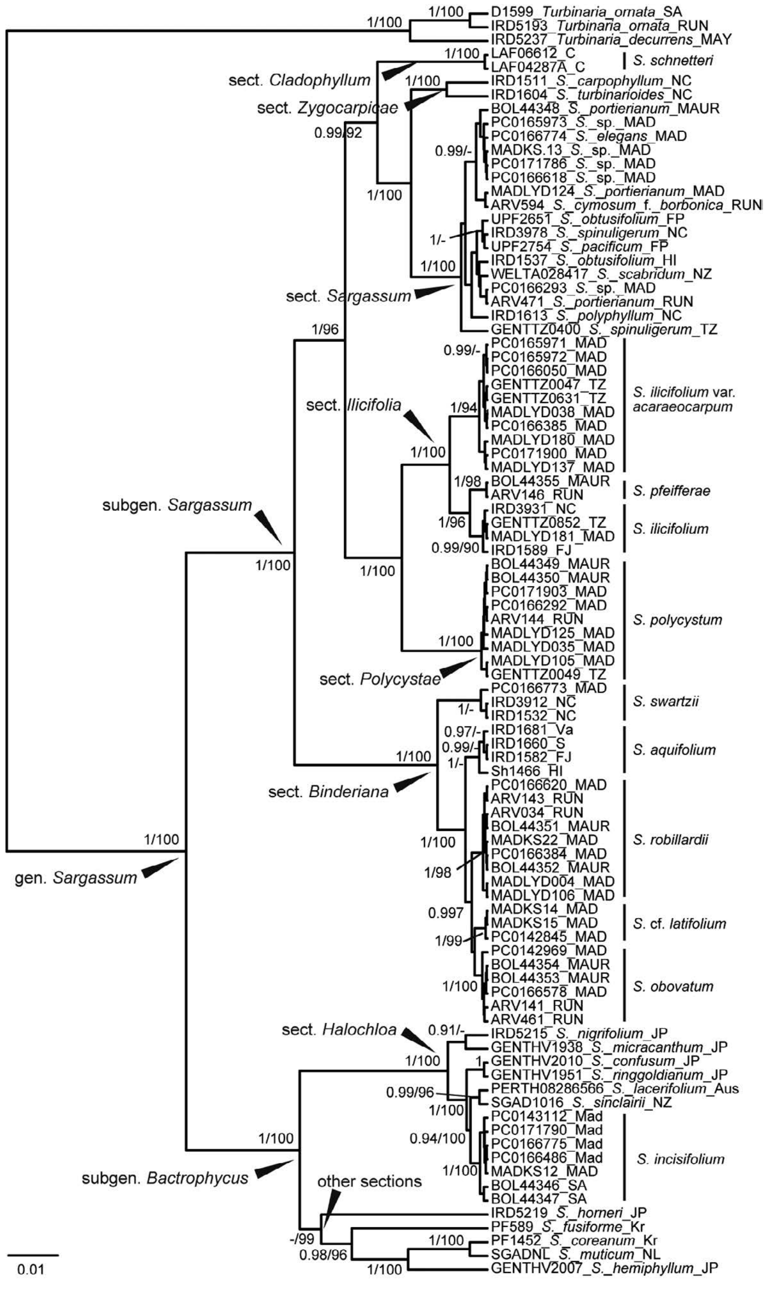

Fig. 1. Partitioned BEAST Bayesian Inference consensus tree based on partitioned ITS2, cox3, partial RuBisCO and mt23S; posterior probabilities greater than 0.9 and ML bootstrap greater than 90% are displayed. Country abbreviations: Aus, Australia; C, Colombia; HI: Hawaii; FJ: Fiji; FP, French Polynesia; Kr, Korea; JP, Japan; MAD, Madagascar; MAUR, Mauritius; MAY, Mayotte; NL, Netherlands; NC, New Caledonia; NZ, New Zealand; RUN, Réunion; Va: Vanuatu; SA, South Africa; Kr, South Korea; TZ, Tanzania.

six sections of *S.* subgenus *Sargassum* (*S.* sect. *Binderiana*, *Cladophyllum*, *Ilicifolia, Polycystae, Sargassum* and *Zygocarpicae*). Sequences recently published for the three sections *S.* sect. *Herporhizum*, *Horridum* and *Lapazeanum* endemic to the Gulf of California (Andrade-Sorcia *et al.*, 2014), were not included in the present analyses. Sequences obtained from specimens collected in Madagascar clustered in all sections except *S.* sect. *Cladophyllum* and *Zygocarpicae*. The clade for *S.* sect. *Polycystae* was not significantly further subdivided. Further subdivisions of the *S.* sect. *Sargassum* clade were not supported by the ML analysis and most, except two, also not supported by the Bayesian analysis. The *S.* sect. *Binderiana* clade was subdivided into five fully to moderately supported subclades (PP = 1, BS = 74-100%), four of which contained previously-identified and GenBank-published sequences for *S. aquifolium* (Turner) C. Agardh, *S. obovatum* Harvey, *S. robillardii* (Grunow) Mattio *et al.* and *S. swartzii* C. Agardh. Sequences for seven Malagasy specimens clustered in the *S. obovatum, S. robillardii* and *S. swartzii* subclades, while three others formed the fifth subclade that did not contain previously-identified GenBank-published sequences. The *S.* sect. *Ilicifolia* clade was subdivided into three well supported subclades (PP = 1, BS = 94-98%). Two of them were represented by previously identified and GenBank-published sequences for *S. pfeifferae* Grunow and *S. ilicifolium* (Turner) C. Agardh, respectively. A sequence obtained for one Malagasy specimen clustered within the *S. ilicifolium* subclade, while eight others formed the third subclade of *S.* sect. *Ilicifolia* together with two new sequences obtained from Tanzanian specimens.

Species identification

A total of eleven morphotaxa were discriminated based on morphological characters and comparison to type specimens when available (Tables 2 & 3). Ten of them were identified to the following currently accepted names: *S. elegans* Suhr, *S. ilicifolium*, *S. ilicifolium* var. *acaraeocarpum* Grunow, *S. incisifolium, S.* cf. *latifolium* (Turner) C. Agardh, *S. obovatum*, *S. polycystum* C. Agardh, *S. portierianum* Zanardini, *S. robillardii* and *S. swartzii.* The remaining morphotaxon, collected from the southern region of Madagascar, could not be identified to species with confidence and is referred to hereafter as *Sargassum* sp. The morphology of the above mentioned morphotaxa is synthetised in Table 3.

Finally, the three *S.* sect. *Sargassum* morphotaxa, although morphologically different, were not significantly distinct molecularly (Fig. 1 and Table 3). Most specimens collected in the south of the island, and referred to as *S.* sp., were morphologically similar to each other but not to any species previously listed for Madagascar. These samples share, however, some characters with *S. cymosum* var. *scabriusculum* Grunow described from South Africa (Grunow, 1916: 142), but do not agree fully with it. Further study in the South West Indian Ocean region is needed to uncover its identity. The two other *S.* sect. *Sargassum* morphotaxa were similar to *S. elegans* and *S. portierianum*, though only one specimen of each was collected from Port Dauphin in the south-east (PC0166774) and Marovasa Be in the north-west (MAD-LYD124), respectively. Morphotaxa were then compared to results of the partitioned BEAST analyses (Fig. 1). As detailed above, the sequences newly obtained for Malagasy specimens appeared in nine distinct and well supported clades thus confirming the distinctness of at least nine of them. *Sargassum incisifolium* is the only member of *S.* subgenus *Bactrophycus* in Madagascar; its morphological distinctness (incl. three-sided axes and incised leaves; see Mattio *et al.*, 2015 and Table 3) led easily to its identification which was confirmed by the grouping of its

Table 2. Taxa listed in the literature for Madagascar with publication details and species recorded during the present study (bold), type information and taxonomic comment/revision when applicable.

Taxa	Recorded by	Type information	Taxonomic comment
Sargassum aquifolium (Turner) C. Agardh	Rabesandratana, 1996 (as *S. binderi* Sonder ex J. Agardh); Mattio *et al.*, 2010	Sunda Strait, Indonesia; Lectotype: BM 563434	This species was not collected again. It was recorded by (Mattio *et al.*, 2010) based on one specimen from Tulear identified with a *mtsp* sequence, but it was not possible to use this sequence in the present dataset; this record could be a misidentification of one of the *S.* sect. *Binderiana* species recorded in the present paper.
Sargassum baccularia (Mertens) C. Agardh	Silva *et al.*, 1996	Unknown	This species belongs to *S.* sect. *Sargassum*; the present record could not be confirmed with specimens at hand. The type specimen must be studied.
Sargassum cinctum J. Agardh	Bornet, 1885	Souliperon (Ceylon), Indonesia; Syntypes: LD2569, 2570	This record could be a misidentification of *S. elegans*, which is morphologically close and distributed in the region, while *S. cinctum* is mainly recorded for Asia and Westyern Pacific.
Sargassum cinctum var. *thiebautii* Grunow	Grunow, 1916; Silva *et al.*, 1996	Near Majunga (Mahajanga) and Tamatave (Toamasina), Madagascar; Type not seen, probably in W	No specimen similar to the short description of Grunow was collected from the type locality during the present study. The type specimen needs to be studied.
Sargassum densifolium Zanardini	Silva *et al.*, 1996	Suez, Egypt; Type not seen	No specimen similar to the diagnosis of Zanardini (1858) was collected during the present study
***Sargassum elegans* Suhr**	New record	"Am Kap der guten Hoffnung" (between Omsamculo (Umzimkulu) and Omcomas (Umkomaas) rivers, Natal, South Africa; Type not seen	A specimen similar to *S. elegans* (type and specimen from type locality) was collected during the present study
Sargassum gracile var. *pseudogracile* Grunow	Grunow, 1916; Silva *et al.*, 1996	China Sea, Madagascar, Papua New Guinea, Sri Lanka; probably in W	This taxon could be a synonym of *S. polycystum.* The type specimen needs to be studied, but Grunow's diagnosis seems to agree with *S. polycystum*

Table 2. Taxa listed in the literature for Madagascar with publication details and species recorded during the present study (bold), type information and taxonomic comment/revision when applicable. *(continued)*

Taxa	Recorded by	Type information	Taxonomic comment
***Sargassum ilicifolium* (Turner) C. Agardh**	Rabesandratana, 1996 (as *S. duplicatum* J. Agardh nom illeg.), Silva *et al.*, 1996 (as *S. cristaefolium* C. Agardh)	Sunda Strait, Indonesia; Type: BM 562953	This species was collected again from Sainte Marie in the north-west section of the island
***Sargassum ilicifolium* var. *acaraeocarpum* Grunow**	new record	Zanzibar, Tanzania; Type not seen.	This taxon was collected from both northern and southern Madagascar. It looks similar to Grunow's diagnosis (Grunow, 1915: 407-408) and sequences clustered with specimens from the type locality. Whether or not the name should be considered a synonym of some other species occurring in the region or be elevated to species level requires the study of further specimens in the region.
***Sargassum incisifolium* (Turner) C. Agardh**	Dixon *et al.*, 2014	Cape of Good Hope, South Africa (Basyonym *Fucus incisifolius*); Type not seen	This species was collected again from southern Madagascar.
***Sargassum latifolium* (Turner) C. Agardh**	Rabesandratana, 1996	Red Sea; Type: BM000561585	Specimens similar to this species were collected from Sainte Luce and Fort Dauphin.
Sargassum latifolium var. *seychellense* Grunow	Grunow, 1916; Silva *et al.*, 1996	Seychelles (leg. Pervillé), Madagascar boreali orientalis (leg. Pervillé); Type not seen, probably in W	Specimens similar to *S. latifolium* were collected from Sainte Luce and Fort Dauphin, Grunow's syntype specimen from Madagascar needs to be checked to conclude on the occurrence of variety "*seychellense*" in Madagascar
***Sargassum obovatum* Harvey**	new record	Cap Malheureux, Mauritius; Type: TCD0000076	This species was collected in southern Madagascar at Lokaro and Roche Choumare.
Sargassum parvifolium (Turner) C. Agardh	Grunow, 1916; Silva *et al.*, 1996	Unknown.	This species was not collected during the present study; according to Grunow's diagnosis it could be closely related to, or similar to *S. ilicifolium* var. *acaraeocarpum.*

Table 2. Taxa listed in the literature for Madagascar with publication details and species recorded during the present study (bold), type information and taxonomic comment/revision when applicable. *(continued)*

Taxa	Recorded by	Type information	Taxonomic comment
***Sargassum polycystum* C. Agardh**	Bornet, 1885; Silva *et al*., 1996	Sunda Strait, Indonesia; Syntypes: TCD 1108, 1109.	This species was collected again during the present study from both northern and southern Madagascar.
Sargassum portierianum Zanardini	new record	Koseir (Quseir), Egypt; Type not seen.	This species was collected from Marovasa Be in the north-west of the Island.
Sargassum pulchellum var. *gracilensis* Grunow	Grunow, 1916; Silva *et al*., 1996	Madagascar; Type not seen, probably in W.	Only known from Madagascar; this record could be a misidentification of *S. elegans* with which Grunow's diagnosis seems to agree;the type specimen needs to be studied
Sargassum robillardii* (Grunow) Mattio *et al.	new record	Mauritius; Holotype: Grunow's collection no. 70 W2012-00786	This species was collected from both northern and southern Madagascar
***Sargassum swartzii* C. Agardh**	new record	India; Lectotype: BM 563461	This species was collected from Baie des Galions near Fort Dauphin in southern Madagascar.
***Sargassum* sp.**	new record	unknown	One species collected during the present study could not be identified to species with confidence. It belongs to the morphologically variable section *Sargassum*. It is not similar to any species listed for Madagascar, although it shares some characters with *S. cymosum* var. *scabriusculum* Grunow but does not agree fully with it.

Table 3. Synthetic morphological description of the 11 morphotaxa identified in the present study.

Taxa	Systematic position	Holdfast	Axis	Leaves	Vesicles	Receptacles
S. ilicifolium	*S.* subgen. *Sargassum* sect. *Ilicifolia*	not observed	terete to compressed, smooth	round to ovate-spathulate, stiff-hard texture, pedicel short or absent, base round, margin serrate to dentate, midrib faint or inconspicuous, cryptostomata thin and scattered, apex round and forming a cup-like depression	not observed	not observed
S. ilicifolium* var. *acaraeocarpum	*S.* subgen. *Sargassum* sect. *Ilicifolia*	discoid	terete , smooth	lanceolate, oblong or slightly spathualte, pedicel short or absent, base cuneate-asymmetrical, margin irregularly serrate, midrib faint or inconspicuous, cryptostomata scattered or aligned, apex acute or obtuse	pedicel terete or compressed with serrate margin, very short; vesicle spherical to ovate, mostly smooth	in racemes, simple, flattened, serrate margins
S. incisifolium	*S.* subgen. Bactrophycus sect. *Halochloa*	conical	compressed, three-sided, smooth	linear-oblong to lanceolate, leathery texture, pedicel short, base cuneate-asymmetrical, margin entire to deeply serrate, midrib percurrent, Cryptostomata inconspicuous, midrib percurrent, apex obtuse or round	not observed	in racemes, simple, flattened, shallow serrate margins
S. elegans	*S.* subgen. *Sargassum* sect. *Sargassum*	discoid	terete, with some spines	linear to oblong-lanceolate, thick but soft texture, pedicel short, base cuneate-asymmetrical, margin entire, midrib percurrent, cryptostomata faint or inconspicuous, apex obtuse	not observed	not observed
S.* cf. *latifolium	*S.* subgen. *Sargassum* sect. *Binderiana*	not observed	compressed to flattened, smooth,	oblong-lanceolate, base cuneate-asymmetrical, marginal most entire to deeply dentate, midrib almost percurrent, cryptostomata scattered, apex obtuse	not observed	not observed
S. obovatum	*S.* subgen. *Sargassum* sect. *Binderiana*	not observed	compressed, smooth,	spatulate, thick leathery in texture, pedicel short or absent, base cuneate, margin dentate, midrib inconspicuous, cryptostomata raised and scattered, apex round and sometimes duplicated	not observed	in tight clusters, compressed, serrate margins

Table 3. Synthetic morphological description of the 11 morphotaxa identified in the present study. *(continued)*

Taxa	Systematic position	Holdfast	Axis	Leaves	Vesicles	Receptacles
S. polycystum	*S.* subgen. *Sargassum* sect. *Polycystae*	small conical giving rise to stolon-like branches	terete, muricate, with smooth stolon-like axes borne from principal basal axis	linear to lanceolate, pedicel absent, base cuneate-asymmetrical, margin serrate, midrib inconspicuous, numerous scattered cryptostomata, apex obtuse to acute	pedicel tererete, shorter than the vesicle; vesicle spherical with a few raised cryptostomata, sometimes an apical mucron	not observed
S. portierianum	*S.* subgen. *Sargassum* sect. *Sargassum*	not observed	terete, smooth or with few spines	mostly simple but some leaves divided at the apex, oblong to oblanceolate, wavy in lateral view, pedicel short or absent, base round-asymmetrical, margin undulate to slightly serrate, midrib faint percurrent, cryptostomata faint scattered, apex obtuse or round	pedicel terete, same size as vesicle; vesicles spherical and smooth	not observed
S. robillardii	*S.* subgen. *Sargassum* sect. *Binderiana*	discoidal	compressed to flattened, smooth	linear-lanceolate, thick, pedicel short and flattened or absent, base cuneate-asymmetrical, margin dentate, midrib almost percurent, cryptostomata raised and mostly aligned, apex acute	pedicel terete, same size or shorter than vesicle; vesicle ovate, smooth	in tight clusters, compressed, serrate margins
***S.* sp.**	*S.* subgen. *Sargassum* sect. *Sargassum*	discoid	terete, slender, with some spines	narrow leaves divided 3 to 5 times, short flattened pedicel, base cuneate, margin almost entire to deeply serrate, midrib raised and percurrent, cryptostomata thin and aligned or inconspicuous, apex obtuse sometimes acute	pedicel terete smooth or flattened; vesicle spherical or ovate, smooth or with a short spine-like mucron	not observed
S. swartzii	*S.* subgen. *Sargassum* sect. *Binderiana*	not observed	compressed to flattened, smooth	linear-lanceolate, narrow, pedicel long, base cuneate-asymmetrical, margin irregularly dentate, midrib almost percurent, cryptostmata thin scattered or aligned, apex acute	pedicel terete, shorter than the vesicle; vesicle spherical to ovate, smooth	in tight clusters, compressed, serrate margins

sequences with previously published sequences including some from the type locality of the species (Table 2). The identification of *S. ilicifolium, S. obovatum, S. robillardii, S. polycystum* and *S. swartzii* were similarly confirmed by the clustering of South African sequences with Genbank sequences for the same species from various Indo-Pacific localities, including sequences from some of the type localities (Fig. 1, Table 2). Sequences for a total of nine specimens morphologically identified as *S. ilicifolium* var. *acaraeocarpum* clustered in a subclade of *S*. sect. *Ilicifolia*, sister to both *S. ilicifolium* and *S. pfeifferae*. This subclade also contained a sequence for a specimen from the type locality (IRD#TZ631; Zanzibar, Tanzania), confirming the morphological similarity to Grunow's diagnosis (Grunow, 1915: 407-408). The three specimens identified to *S*. cf. *latifolium* clustered on their own within the *S*. section *Binderiana* clade, lending support to the distinctness of this morphotaxon. We believe, however, that the epithet needs to be confirmed with a sequence from the type locality.

DISCUSSION

Sargassum diversity in Madagascar

Using a combined analysis of morphological characters and four concatenated molecular markers we highlighted the occurrence of 11 distinct *Sargassum* taxa in Madagascar, one belonging to *S*. subgenus *Bactrophycus* (*S. incisifolium*), and 10 to *S*. subgenus *Sargassum* (section *Binderiana*: *S*. cf. *latifolium*, *S. obovatum*, *S. robillardii* and *S. swartzii*; section *Ilicifolia*: *S. ilicifolium* and *S. ilicifolium* var. *acaraeocarpum;* section *Polycystae*: *S. polycystum*; section *Sargassum*: *S. elegans*, *S. portierianum* and *S*. sp.).

An inspection of the literature available for Madagascar revealed a list of 16 different epithets for *Sargassum*, of which 13 are regarded as currently accepted taxonomically (Table 2; Guiry & Guiry, 2014). Only four of these taxa were re-collected during the present study, while we add six new records and an unidentified species to the list. The nine taxa not re-collected during the present study could, in part, have been misidentified (cf. Table 2). A closer look at previous records indicated that four taxa have their type or syntype localities in Madagascar, and all of these appeared to be varieties described by Grunow (1915, 1916): *S. cinctum* var. *thiebautii* Grunow, *S. gracile* var. *pseudogracile* Grunow, *Sargassum latifolium* var. *seychellense* Grunow, *S. pulchellum* var. *gracilensis* Grunow. The present study adds one more to the list, *S. ilicifolium* var. *acaraeocarpum* Grunow; whether or not the name should be elevated to species level or considered a synonym of some other species requires the study of further specimens in the region. The situation is similar for the 33 remaining varieties and forms probably "over-enthusiastically" described by Grunow, and listed for the South West Indian Ocean region: we believe all are in critical need of revision. The most complete list of *Sargassum* taxa for Madagascar to date is provided in Table 2 and records a total of 20 species, 10 of which are still in need of taxonomic revision. Besides extending sampling locations to the west and east coast, we believe that these must be revised in a regional framework to assess region-wide morphological variations.

Biogeography

Out of the 11 taxa analysed for the purpose of the present study, a total of nine occurred in the south while only five occurred in the north. Although this difference could in part be explained by a larger sampling effort in the southern section of the Island, only three of the 11 taxa (*S. ilicifolium* var. *acaraeocarpum, S. polycystum* and *S. robillardii*) were found both in the southern and the Northern sections of the Island, highlighting existing differences in species assemblages. These different assemblages and the central geographic position of Madagascar in the south-western Indian Ocean raise interesting questions about the distribution and phylogeny of the genus in the region.

Sargassum spp. are known for their high dispersion/invasion potential (Paula & Eston, 1987; Hoek, 1987). Like *Macrocystis* (Macaya *et al.*, 2005), *Sargassum* can form rafts, drift long distances and release propagules upon arrival at new favourable habitats (Thiel & Gutow, 2005a b; Yatsuya, 2008; Mattio *et al.*, 2013). As a consequence, the distribution and connectivity of *Sargassum* populations are probably largely shaped by regional oceanic circulation. In a recent publication, Mattio *et al.* (2013) revised the *Sargassum* diversity in the Mascarene Islands and recorded six species of which three appear to be shared with northern Madagascar (*S. polycystum*, *S. portierianum* and *S. robillardii*). In the same paper, the authors discussed the distribution of the species in the region based on hydrodynamic models. Their results indicated that the likelihood of an export of particles (i.e. *Sargassum*) from the Mascarenes to the north-east of Madagascar is weak but possible in 40 days and not possible in the other direction. According to their results, the Mascarenes, Cargados and Tromelin are the only source of connectivity at a reasonable distance to the east of northern Madgascar, and given regional patterns of circulation described by Hancke *et al.*, (2014), more connection may be expected with the Seychelles, the Comoros or the coasts of Tanzania and Northern Madagascar.

In the southern section of the Mozambique Channel, the warm temperate species *S. incisifolium* and *S. elegans* are found both in southeast Madagascar and in South Africa, raising some interesting question about connectivity between the two regions Interestingly, sea temperatures around the southeast of Madagascar may be seasonally cooler than surrounding tropical regions, due to localised upwelling events (Machu *et al.*, 2002), a situation that may be similar to what is observed along the eastern coast of South Africa (Smit *et al.*, 2013). There is limited, but growing, evidence for a number of species shared between the Southern coast of Madagascar and the warm temperate/sub-tropical coastline of South Africa, and southern Mozambique. This is the case in particular of a number of invertebrates (e.g. Jackson, Smale & Berry, 1991; Gopal *et al.*, 2006), but the similarity has also been show for the marine flora. Hence, *Laurencia complanata* (Suhr) Kützing (formerly considered to be a South African endemic) also grows in Southern Madagascar, as does *Laurencia natalensis* Kylin, another common and abundant Southern African species (Francis, 2014). The current study recording the occurrence of the most common South African *Sargassum* species, *Sargassum incisifolium* and *S. elegans,* in Madagascar and the sharing of four more species between the two regions, (*S. ilicifolium*, *S. ilicifolium* var. *acaraeocarpum*, *S. obovatum* and *S. polycystum*) is further evidence of this phenomenon. These similarities raise questions on the geographical origin of the species and their conspecificity. Are species links prior to the separation of Madagascar from the African continent (ca. 170 Ma ago) and have they maintained gene flow since, or have they colonized one region from the other more recently?

The Mozambique Channel, ca. 1,000 kms wide in its southern section, probably represents a geographical barrier difficult to cross for most coastal organisms. A study on the scalloped spiny lobster, Reddy *et al.* (2014) showed an absence of contemporary gene flow across the Mozambique Channel between Malagasy and South African populations. The African lineage appeared to be ancestral, and the source population for the Madagascan population. The molecular data presented in the present paper (FIG. 1) also showed a geographical pattern for *S. incisifolium* and produced two fully supported and distinct subclades grouping the Malagasy and South African morphologically similar specimens, respectively. The present-day pattern of circulation in the Mozambique Channel is highly complex and several studies have put forward mesoscale eddies as potential vectors of connectivity between Madagascar and the East coast of Africa (Quartly & Srokosz, 2004; de Ruijter *et al.*, 2004; Tew-Kai & Marsac, 2009; Marsac *et al.*, 2014). Mesoscale eddies have been shown to propagate westward from southern Madagascar and across the Mozambique Channel to reach southern Mozambique and the Kwazulu-Natal (KZN) region in South Africa (Marsac *et al.*, 2014). Although the propagation of those mesoscale eddies is relatively slow, experiments have demonstrated that particles travelling at the periphery of eddies, within corridors existing between contra-rotating eddies, could travel between southern Madagascar and southern Mozambique in less than 50 days (Hancke *et al.*, 2014). Yatsuya (2008) indicated that the floating period of *Sargassum* is dependent on species (specific density) and the timing (season) at which the individual is detached in its life cycle. According to these authors most of the detached sargassacean thalli in nature will float for 14 days or less, and very few of them have more than 42 days (maximum 98 days) longevity in floating conditions. These figures and travelling times measured by Hancke *et al.* (2014) support the hypothesis that *Sargassum* specimens from the southeast coast of Madagascar could cross the Mozambique Channel and settle on the coast of Southern Mozambique and Kwazulu Natal in South Africa. Although our results lend support to an absence of gene flow between the two regions, we believe the analysis of more specimens from each region is needed to clearly assess connectivity.

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