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The freshwater red algae (*Batrachospermales, Rhodophyta*) of Africa and Madagascar I. New species of *Kumanoa*, *Sirodotia* and the new genus *Ahidranoa* (*Batrachospermaceae*)

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Abstract. Our knowledge of the diversity of African freshwater red algae is rather limited. Only a few reports exist. During our field work in the last five years we frequently encountered freshwater red algae in streams in Rwanda and Madagascar. Here we describe four new species and one new genus of freshwater red algae from the *Batrachospermales*, based on morphological and molecular evidence: *Kumanoa comperei* from the Democratic Republic of the Congo and Rwanda is related to *K. montagnei* and *K. nodiflora*; *Kumanoa rwandensis* from Rwanda is related to *K. ambigua* and *K. gudjewga*; *Sirodotia masoalensis* is related to *S. huillensis* and *S. delicatula*; and the new genus and species *Ahidranoa madagascariensis* from Madagascar is sister to *Sirodotia*, *Lemanea*, *Batrachospermum* s.str. and *Tuomeya*. There is also evidence for the presence of *Sheathia*, which was recorded as yet-unidentifiable *Chantransia* stages. These are among the first new descriptions since 1899 from the African continent and since 1964 from Madagascar. A short history of the exploration of freshwater red algae from Africa and Madagascar is provided. All new taxa are accompanied by illustrations and observations on their ecology.

Key words: *Batrachospermaceae*, tropical Africa, Madagascar, taxonomy

Introduction

The history of the exploration of freshwater red algae in Africa and Madagascar

'Very little is known concerning the freshwater algae from Africa' (West & West 1897). This is still true more than 120 years after that statement. While interest in the long-neglected group of freshwater red algae has increased in the Northern Hemisphere (e.g., Entwisle et al. 2009; Eloranta et al. 2011; Vis et al. 2012; Knappe & Huth 2014; Salomaki et al. 2014), South America (e.g., Necchi 1990; Necchi et al. 2010, 2019) and Australia (e.g., Entwisle & Foard 2007; Entwisle et al. 2016), there are only limited data available for Africa.

The first collection of a freshwater red alga from Africa was made by W. G. Schimper, who collected a *Lemanea* in 1840 in the Simien Mountains of Ethiopia ('in latere medio boreali montis Silke'). This specimen was subsequently described by Kützing (1849) as *Lemanea abyssinica*. The first species of *Batrachospermum* was published as *B. patens* (Suhr 1840) from Kroemsrivier (today Kromrivier) in the Cape region of South Africa, collected by Drège (without date). Szinte et al. (2020) place *Batrachospermum patens* into synonymy with *Torularia atra* (see below).

The next collections of freshwater red algae from Africa were made by Bishop Johann Christian Breutel in South Africa at the Herrenhut Mission of Gnadenthal (= Genadendal in Western Cape Province) in 1853–1854 (Rabenhorst 1855). Breutel collected the first two species of *Batrachospermum* from Africa, *Batrachospermum africanum* ('*afrikanum*') and *Batrachospermum breutelii* (Rabenhorst 1855). A few years later, a third species was described from this area: '*Batrachospermum dimorphum* Kütz., im Paviansfluss bei dem Herrenhuter Missionsort Gnadenthal in Süd-Africa. Mitgetheilt vom Herrn Pfarrer Wenck in Neu-Dieten' (Kützing 1857). This name is currently regarded as a synonym of *Batrachospermum breutelii* (Rabenhorst 1855).

The most extensive collections of freshwater red algae in Africa were made by Friedrich Welwitsch between 1855 and 1860 in Angola. The results were published by West & West (1897) almost 40 years later. The recorded species are *Batrachospermum angolense* [= *Sirodotia angolensis* according to Guiry (2019) but considered a heterotypic

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synonym of *Torularia atra* (= *Atrophycus ater*) in the previous literature, e.g., Entwisle 1992], *Batrachospermum nigrescens* (*Sirodotia nigrescens* = *Torularia puiggariana*), *Batrachospermum gracillimum* (= *Kumanoa gracillima*), *Batrachospermum huillense* (= *Sirodotia huillensis*), *Hildenbrandia rivularis* and *H. angolensis*. West & West (1897) remark that it is 'interesting to note that the earliest collection of algae made in Africa has been found to be more extensive and representative than any hitherto described' (West & West 1897: 1–2). None of these species has been re-collected from Africa but they were later recorded from South America or Europe. One of the last new descriptions from the African continent is *Batrachospermum bohneri* (Schmidle 1899a) from Cameroon, which is assigned by its author to section *Helminthosum* and is said to have a large stalked trichogyne. Unfortunately it is not mentioned in the subsequent literature and is also omitted from AlgaeBase (Guiry 2019). As the type probably has been destroyed and the protologue is not accompanied by any illustration, it is considered a doubtful name here. Separately published illustrations from this material (Schmidle 1899b) led Szinte et al. (2020) to identify it as *Montagnia macrospora*. A collection from Rwanda by Johannes Mildbraed in 1907 was identified as *Batrachospermum bohneri* (Lemmermann 1914: Rugege Wald, kalter Quellbach des Rukarara) but the specimen was destroyed in Berlin and the record is considered doubtful. Several other red algae were collected at this locality during our research but no specimen matched the description of *Batrachospermum bohneri*.

In his review of the subaerial and freshwater algal flora of the Tropics, Fritsch (1907) listed for Africa the five species described by West and West (1897) and Schmidle (1899a) but ignored the records of *Lemanea*. Thus, nine species of freshwater red algae were known from tropical Africa in 1907, and for 112 years not much progress was made. Borge (1928) listed two species of *Batrachospermum*, *B. dillenii* (= *Torularia atra*) and *B. vagum* (= *B. turfosum*) from Tanzania (eastern Usambara, Kilimandscharo) but the identifications are considered doubtful, as no specimens could be retrieved, so they serve only as an indication that there are freshwater red algae present in the mountains of eastern Tanzania. The same is true for the record of *Tuomeya fluviatilis* (= *T. americana*) from eastern Usambara (Borge 1928). In some papers on the diversity of freshwater algae, Compère (1975) recorded *Audouinella hermannii* from Chad, and Da et al. (1999) and Alika & Akoma (2012) listed *Batrachospermum turfosum* (as *B. vagum*) for the Ivory Coast and Nigeria, these latter records probably erroneous. By coincidence, another paper has just appeared independently (Szinte et al. 2020) in which the authors describe the new species *Kumanoa bouwmanii*, *Sheathia murpheyi* and *Sirodotia kennedyi*, all from Zambia, and they name a *Chantransia* stage as *C. azurea* from South Africa. They also give an overview of available herbarium specimens, mainly from BR and PC (abbreviations after Thiers 2019), the majority of which are not identifiable.

For South Africa, the taxon described by Suhr (1840) and the two species described by Rabenhorst (1855) are known, with the recent additions of *Sirodotia suecica* (Lam et al. 2012) and *Kumanoa iriomotensis*, collected in Western Cape Province in 2006 (Necchi & Vis 2012). The only records of freshwater red algae from Madagascar are *Batrachospermum gelatinosum* (Fritsch 1914, record probably erroneous) and *Nothocladus afroaustralis* (Skuja 1964), known only from the Fort Dauphin region in southeastern Madagascar.

Phylogenetic relationships of *Batrachospermum* and related genera

With about 112 species recognized, the genus *Batrachospermum* with the type species *B. gelatinosum* was considered the most species-rich genus of freshwater red algae, and was divided into two subgenera (*Batrachospermum*, *Acarposporophytum*), the former containing eight sections (Kumano 2002). However, based on molecular data from phylogenetic studies (Vis et al. 1998; Vis & Entwisle 2000; Vis et al. 2005; Entwisle et al. 2009), this genus has been shown to be paraphyletic. Early accepted segregates are *Sirodotia* and *Nothocladus*. Entwisle et al. (2009) proposed acceptance of different sections for the time being: *Acarposporophytum*, *Aristata*, *Batrachospermum*, *Helminthoidea*, *Macrospora*, the informal 'Australasica group', *Setacea*, and *Turfosa* and *Virescentia*. The sections *Contorta* and *Hybrida* were placed in the new genus *Kumanoa* (Entwisle et al. 2009). Subsequently, Salomaki et al. (2014) placed members of section *Helminthoidea* in the new genus *Sheathia*. More recently the new genus *Nocturama* (Entwisle et al. 2016) was erected, now comprising two species from Australia and South America (Necchi et al. 2016). In the first paper the genus *Nothocladus*, formerly containing three species from Madagascar and Australia (which now constitute section *Nothocladus*) was enlarged to comprise most of the old informal 'Australasica-group' with the new sections *Australasicus*, *Theaquus* and *Kraftii*, and also section *Setaceus*. Contrary to the arguments of Entwisle et al. (2016), Rossignolo and Necchi (2016) subsequently raised section *Setacea* to generic level and included three species. For nomenclatural reasons the generic name *Setaceus* had to be replaced by *Atrophycus* (Rossignolo et al. 2017). Wynne (2019) showed that the name *Torularia* (Bonnemaison 1828) has priority over *Atrophycus*, and thus the three recognized members of the former section *Setacea* were placed in the genus *Torularia*. Section *Virescentia* was raised to genus level under the name *Virescentia* (Necchi et al. 2018). Sections *Acarposporophytum* and *Aristata* were raised to generic status under the names *Acarposporophycus* and *Visia* (Necchi et al. 2019b), and section *Macrospora* to genus *Montagnia* (Necchi et al. 2019a). Two new genera were recently added: *Volatus* (Chapuis et al. 2017) with three species from North America and Europe, and the monotypic *Lympha* with *Lympha mucosa* (Evans et al. 2017). Thus the genus *Batrachospermum* s.str. comprises only *Batrachospermum gelatinosum* with a few related species, while section *Turfosa* is still not assigned to a definite genus and is thus kept as *Batrachospermum* s.l. For a summary of the taxonomic changes and the currently accepted taxonomy we refer to Table 1.

Table 1. Historical overview and currently accepted taxonomy of the *Batrachospermaceae*.

Kumano 2002	Entwisle et al. 2009	Entwisle et al. 2016	Accepted taxonomy
Batrachospermum Subg. *Acarposporophytum* Necchi	*Batrachospermum* Sect. *Acarposporophytum*	–	*Acarposporophycus* Necchi et al.
Batrachospermum Subg. *Batrachospermum*	–	–	–
Batrachospermum Sect. *Batrachospermum*	*Batrachospermum* Sect. *Batrachospermum*	–	*Batrachospermum* Roth s.str.
Batrachospermum Sect. *Setacea*	*Batrachospermum* Sect. *Setacea*	*Nothocladus* Sect. *Setacea*	*Torularia* Bonnemaison (= *Setacea* Rossignolo & Necchi, *Atrophycus* Rossignolo et al.)
Batrachospermum Sect. *Turfosa* Sirodot	*Batrachospermum* Sect. *Turfosa*	–	*Batrachospermum* Sect. *Turfosa*
Batrachospermum Sect. *Virescentia* Sirodot	*Batrachospermum* Sect. *Virescentia*	–	*Virescentia*
Batrachospermum Sect. *Gonimopropagulum* Sheath & Wittick	–	–	*Batrachospermum* Section *Gonimopropagulum* Sheath & Wittick
Batrachospermum Sect. *Hybrida* De Toni	*Kumanoa* Entwisle et al.	–	*Kumanoa* Entwisle et al.
Batrachospermum Sect. *Contorta* Skuja	*Kumanoa* Entwisle et al.	–	*Kumanoa* Entwisle et al.
Batrachospermum Sect. *Aristata* Skuja	*Batrachospermum* Sect. *Aristata* Skuja	–	*Visia* Necchi et al.
Batrachospermum Subsect. *Macrospora* Kumano	*Batrachospermum* Sect. *Macrospora* (Kumano) Entwisle et al.	–	*Montagnia* Necchi et al.
–	*Batrachospermum* Sect. *Helminthoidea* Sirodot ex De Toni	–	*Sheathia* Salomaki et al.
–	*Batrachospermum Australasica* Group	*Nothocladus* Sect. *Australasica*	*Nothocladus* Skuja
–	*Nothocladus*	*Nothocladus* Sect. *Nothocladus*	*Nothocladus* Skuja
Sirodotia Kylin	*Sirodotia* Kylin	–	*Sirodotia* Kylin
Tuomeya Harvey	*Tuomeya* Harvey	–	*Tuomeya* Harvey
–	–	*Nocturama* Entwisle & Vis	*Nocturama* Entwisle & Vis
–	–	–	*Lympha* J. R. Evans et al.
–	–	–	*Volatus* I. S. Chapuis & M. L. Vis
–	*Petrohua* G. W. Saunders	–	*Petrohua* G. W. Saunders
Lemanea Bory	*Lemanea* Bory	–	*Lemanea* Bory
Paralemanea (Silva) Vis & Sheath	*Paralemanea* (Silva) Vis & Sheath	–	*Paralemanea* (Silva) Vis & Sheath
Psilosiphon Entwisle	*Psilosiphon* Entwisle	–	*Psilosiphon* Entwisle
Ballia Harvey	*Balliopsis* G. W. Saunders & Necchi	–	*Balliopsis* G. W. Saunders & Necchi

Since 2011, several freshwater red algae have been collected from tropical Africa (Gabon, Rwanda, Burundi) and Madagascar. Most of them could not be identified with the available literature. The aim of this study is to reconstruct the phylogenetic relationships between these taxa based on molecular and morphological evidence, and to characterize the taxa collected in tropical Africa and Madagascar. In this first paper we deal with collections of the genera *Ahidranoa*, *Kumanoa* and *Sirodotia* from Rwanda and Madagascar, and we describe one genus and four species new to science. We also provide evidence for the occurrence of the genus *Sheathia*, albeit only collected as *Chantransia* stages.

Material and methods

Sampling and investigations

Freshwater red algae were sampled between 2014 and 2018 from four locations in Rwanda and two in Madagascar. Herbarium vouchers with specimens preserved in 70% alcohol were deposited in BR, TAN and KOBL (abbreviations after Thiers 2019, Table 2). Their morphology was examined and photographed with a KEYENCE VHX-S15 digital microscope.

DNA isolation

Silica-dried plant material was homogenized in a 2 ml Eppendorf cap (round bottom) with two glass beads (ø 5 mm) and a small amount (tip of spatula) of autoclaved sand at 30 hz for 2 min. using a TissueLyser II (QIAGEN, Venlo, Netherlands). From the obtained powder, genomic DNA was extracted using a NucleoSpin Plant II Kit (Marchery-Nagel, Düren, Germany), following the customized protocol of the supplier.

Amplification and sequencing

Amplification of COI followed Saunders (2005) using the primers GazF1 and GazR1, while new primers were designed for amplification of *rbc*L (rbcL-redF: TGCYAAAATGGGWTAYTGG; rbcS-redR:

CCTTGTGTTARTCTCAC). All PCR reactions were performed in 25 µl volumes for each sample. Each PCR reaction contained 1 µl DNA (> ~10 ng/µl), 10.35 µl H_2O, 5 µl 5x *Taq* Flexi Buffer, 2.5 µl 25 mM $MgCl_2$, 4 µl of dNTPs (each 1.25 mM), 1 µl of the respective forward and reverse primer (20 pm/µl) and 0.15 µl *Taq* Polymerase (5 units/µl). The PCR profile for the *rbc*L fragment comprised two steps: 1 cycle (94°C 120 s, 50°C 60 s, 68°C 120 s) followed by 38 cycles (94°C 30 s, 48°C 60 s, 68°C 120 s) and final extension of 20 min. at 72°C. For amplification of COI the following PCR profile was used: 94°C 3 min. followed by 34 cycles (94°C 60 s, 45°C 60 s, 72°C 60 s) and final extension of 10 min. at 72°C. Newly generated sequences were deposited in GenBank (Table 2).

Table 2. Locality data and new GenBank accession numbers.

Species	Country	Location	Elevation	Date	Collection number	Lab ID	rbcL	cox1
Kumanoa comperei (spec. A)	Rwanda	Nyungwe National Park, Kamiranzovu	1980 m	23.03.2017	RW 294/17	AC039	MT109256	MT109267
Kumanoa comperei (spec. A)	Rwanda	Nyungwe National Park, Gisakura	2000 m	23.03.2017	RW 305/17	AC040	MT109257	MT109268
Kumanoa comperei (spec. A)	Rwanda	Nyungwe National Park, Gisakura	2000 m	17.09.2016	RW 447/16	AC041	MT109258	MT109269
Kumanoa comperei (spec. A)	Rwanda	Nyungwe National Park, Kamiranzovu	1980 m	17.09.2016	RW 453/16	AC042	MT109259	MT109270
Kumanoa comperei (spec. A)	Dem. Rep. Congo	Kahuzi-Biéga National Park, Mulolo	1100 m	06.01.2018	C17/2018	AC079	MT109260	N.A.
Kumanoa rwandensis (spec. B)	Rwanda	Nyungwe National Park, Rwasenkoko	2450 m	08.09.2017	RW 678/17	AC068	MT109261	MT109271
Kumanoa rwandensis (spec. B)	Rwanda	Nyungwe National Park, Rukarara	2100 m	08.09.2017	RW 682/17	AC071	MT109262	MT109272
Ahidranoa madagascariensis	Madagascar	Masoala, Riv. Ambanizana	270 m	30.09.2017	799/17	AC076	MT109263	MT109273
Sheathia spec. (Chantransia)	Rwanda	Nyungwe National Park, Rwasenkoko	2450 m	08.09.2017	RW 679/17	AC069	MT109265	MT109275
Sheathia spec. (Chantransia)	Rwanda	Nyungwe National Park, Rukarara	2100 m	08.09.2017	RW 687/17	AC074	MT109264	MT109274
Sirodotia masoalensis	Madagascar	Masoala, Riv. Ambanizana	270 m	07.10.2015	181/15	AC027	MT109266	MT109276

Contig assembly, alignment and phylogenetic analyses

Quality control of the pherograms, contig assembly and alignment was done in PhyDE1 (available at www.phyde.de). In order to place the African taxa in phylogenetic context, a representative set of freshwater red algae *rbc*L and COI sequences were downloaded from GenBank (Table 3) and aligned with the newly generated sequences, using PhyDE1. Sampling was guided by Entwisle et al. (2009).

Maximum likelihood (ML) analyses were performed using RAxML-NG (Kozlov et al. 2019) via the RAxML BlackBox (raxml-ng.vital-it.ch), applying the GTR + Γ + I model. Bootstrap analysis was performed with the automatic bootstrapping option in effect at a cutoff of 0.3. Bayesian analyses were performed with MrBayes v.3.2.5 (Ronquist et al., 2012), applying the GTR + Γ + I model. Four runs with four chains (10^7 generations each) were run simultaneously, with chain sampling every 1000th generation. Tracer v.1.7.1 (Rambaut & al., 2018) was used to examine log likelihoods to determine the effective sampling size and stationarity of the MCMC search. Calculations of the consensus tree, including clade posterior probability (PP), were performed using the relburnin function in MrBayes; that is, the first 25% of the trees were discarded. Consensus topologies and support values were compiled and drawn using TreeGraph v.2 (Stöver & Müller, 2010). Bootstrap support (BS > 50) is depicted above and posterior probability (PP > 0.8) below the branches of the maximum likelihood tree. Support values in the text are given as BS/PP.

Phylogeny

Phylogenetic results

The concatenated data set comprised 1943 characters (*rbc*L: 1280; COI: 663) for 68 taxa (Tables 2 & 3, Fig. 1, S1, S2). Bayesian inference resulted in a resolved and well-supported phylogeny of the *Batrachospermales*. In principle, two large sister clades were resolved, one containing *Kumanoa*, *Virescentia* and *Visia* (clade A; 55/0.95), the other *Batrachospermum*, *Tuomeya*, *Lemanea*, *Sirodotia*, *Sheathia*, *Nocturama*, *Torularia* and *Nothocladus* (clade B; 88/1). Within the latter clade, *Nocturama*,

Table 3. Accession numbers of *rbcL* and COI gene sequences used from GenBank.

Species	Accession number	
	rbcL	COI
Audouinella hermannii	KC134346	–
Balbiania investiens	AF132293	KM055323
Bangia atropurpurea	DQ408162	DQ191330
Batrachospermum spermatoinvolucrum	AF029146	–
Bostrychia arbuscula	KM502821	KM502796
Bostrychia moritziana	AY920809	MF093965
Bostrychia scorpioides	AY920825	MF094019
Chantransia azurea	MN974515	MN974520
Hildenbrandia rubra	K-284724	KF649304
Kumanoa abilii	GQ368883	JN604915
Kumanoa ambigua	AY423390	EU095970
Kumanoa americana	KX284725	JN604910
Kumanoa bouwmanii	MN974516	MN974521
Kumanoa breviarticulata	GQ368886	EU636718
Kumanoa capensis	JX504698	J-504695
Kumanoa cipoensis	GQ368887	JN604919
Kumanoa curvata	JN590012	JN604925
Kumanoa equisetoidea	GQ368889	EU636716
Kumanoa globospora	GQ368891	JN604923
Kumanoa gracillima	AY423395	JN604927
Kumanoa gudjewga	JN590003	JN604908
Kumanoa intorta	AY423397	EU636717
Kumanoa iriomotensis	JN590011	–
Kumanoa louisianae	JN590005	JN604924
Kumanoa montagnei	AY423396	EU636713
Kumanoa nodiflora	AY423398	EU636714
Kumanoa skujana	JN590008	JN604922
Kumanoa tabagatenensis	JN590009	JN604914
Kumanoa virgato-decaisneana	AF029148	–
Lemanea fluviatilis	AF029150	KC130145
Lemanea fucina	KJ825959	KU672391
Nocturama antipodites	KT802839	KT802754
Nocturama novamundensis	KX764640	–
Nothocladus discors	AF257778	KT802759
Nothocladus kraftii	KT802854	KT802760
Nothocladus pseudogelatinosus	AF209983	KT802761
Nothocladus wattsii	AF209986	KT802765
Sheathia boryana	JX669773	JX669707
Sheathia confusa	DQ393133	JXX669712
Sheathia heterocortica	DQ393136	EU636740
Sheathia involuta	AF029143	–
Sheathia murpheyi	MN974517	MN974522
Sirodotia aff. *huillensis*	JF344717	–
Sirodotia delicatula	KC951862	KF010486
Sirodotia huillensis	AF126410	EU636739
Sirodotia kennedyi	MN974518	–
Sirodotia suecica	AF029158	EU636737
Thorea hispida	KC511078	KC511076
Torularia (*Nothocladus*) *atra* NZ	KT802841	KT802756
Torularia (*Nothocladus*) *atra* ZA	MN974519	MN974525
Torularia (*Setacea*) *atro-brasiliensis*	KT183023	KT894749
Torularia (*Setacea*) *puiggariana*	KP203886	KX703028
Tuomeya americana	AF029159	KM055330
Virescentia viride-brasiliense	KM097039	KM260002
Visia cayennensis	AY423392	EU095971

Sheathia, *Torularia* and *Nothocladus*, as well as a new genus, build a grade towards a strongly supported core clade (98/1) consisting of *Batrachospermum*, *Tuomeya*, *Lemanea* and *Sirodotia*. The African taxa, including the samples from Madagascar, are resolved in three different genera or are placed solitary (AC076) (Fig. 1). In Nyungwe National Park (Rwanda), two different species were found: one (*K. rwandensis*) clusters as sister to a clade consisting of *Kumanoa ambigua*, *K. abilii* and *K. gudjewga*, while the second (*K. comperei*) is sister to *Kumanoa bouwmanii* within a clade including *Kumanoa montagnei* and *K. nodiflora. Kumanoa comperei* is also found in the Democratic Republic of the Congo (AC079); it retains a sister group relation to the samples from Rwanda. The two samples from Madagascar (Masoala, Riv. Ambanizana) are resolved with significant support in clade B. While one sample (AC027, *Sirodotia masoalensis*) was resolved within *Sirodotia* as sister to *S. kennedyi*, the other (AC076, *Ahidranoa madagascariensis*) was resolved sister to the '*Batrachospermum-Lemanea-Sirodotia-Tuomeya*' clade. In addition, the two *Chantransia* stages from Nyungwe National Park (Rwanda) are resolved within *Sheathia* sister to *Sheathia murpheyi* with maximal support (Fig. 1). It is noteworthy that both *Torularia atra* samples do not form a clade.

Phylogenetic discussion

The well-resolved and highly supported phylogeny of the *Batrachospermales* indicates that the current concept of the generic boundaries seems to be settled. All genera in which more than one taxon was included, such as *Kumanoa*, *Batrachospermum*, *Lemanea*, *Sirodotia*, *Sheathia*, *Nocturama*, *Torularia* and *Nothocladus*, are monophyletic and receive significant if not maximal support. Specifically, this new analysis supports recognition of the genus *Torularia*, as proposed by Rossignolo & Necchi (2016), which based on an earlier tree (Entwisle et al. 2016) would have resulted in a paraphyletic *Nothocladus*. However, our tree has limited taxa sequenced within the *Nothocladus* clade, and recognition of *Torularia* still runs counter to the concern raised in Entwisle et al. (2016) around the proliferation of less informative small genera. With respect to *Batrachospermum* more analyses need to be done, as indicated by Entwisle et al. (2009). The resolution of both Madagascan specimens within the '*Batrachospermum-Lemanea-Sirodotia*' clade points to an interesting aspect related to the speciation and biogeography of red algae on the island, requiring further investigations.

Taxonomy

The genus *Kumanoa*

The genus *Kumanoa* (Entwisle et al. 2009) was proposed to accommodate the members of *Batrachospermum* sections *Contorta* and *Hybrida*. One of the main distinguishing characters is the twisted or curved carpogonial branch. An expanded molecular phylogeny of *Kumanoa* was provided by Vis et al. (2012), with additions by Necchi et al.

(2010). At present, 35 species are accepted, and the genus shows the highest diversity in tropical and subtropical regions (Necchi & Vis 2012). Only 13 species occur on more than one continent, and the majority of taxa show a narrow distribution, often known only from the type locality. According to Necchi & Vis (2012), 20 species are narrow endemics: five species are endemic to Brazil, four to Australia, three each to Portugal and the USA, two to French Guiana, and one each to China, Hawaii and Papua New Guinea. Ganesan and West (2013) attributed seven

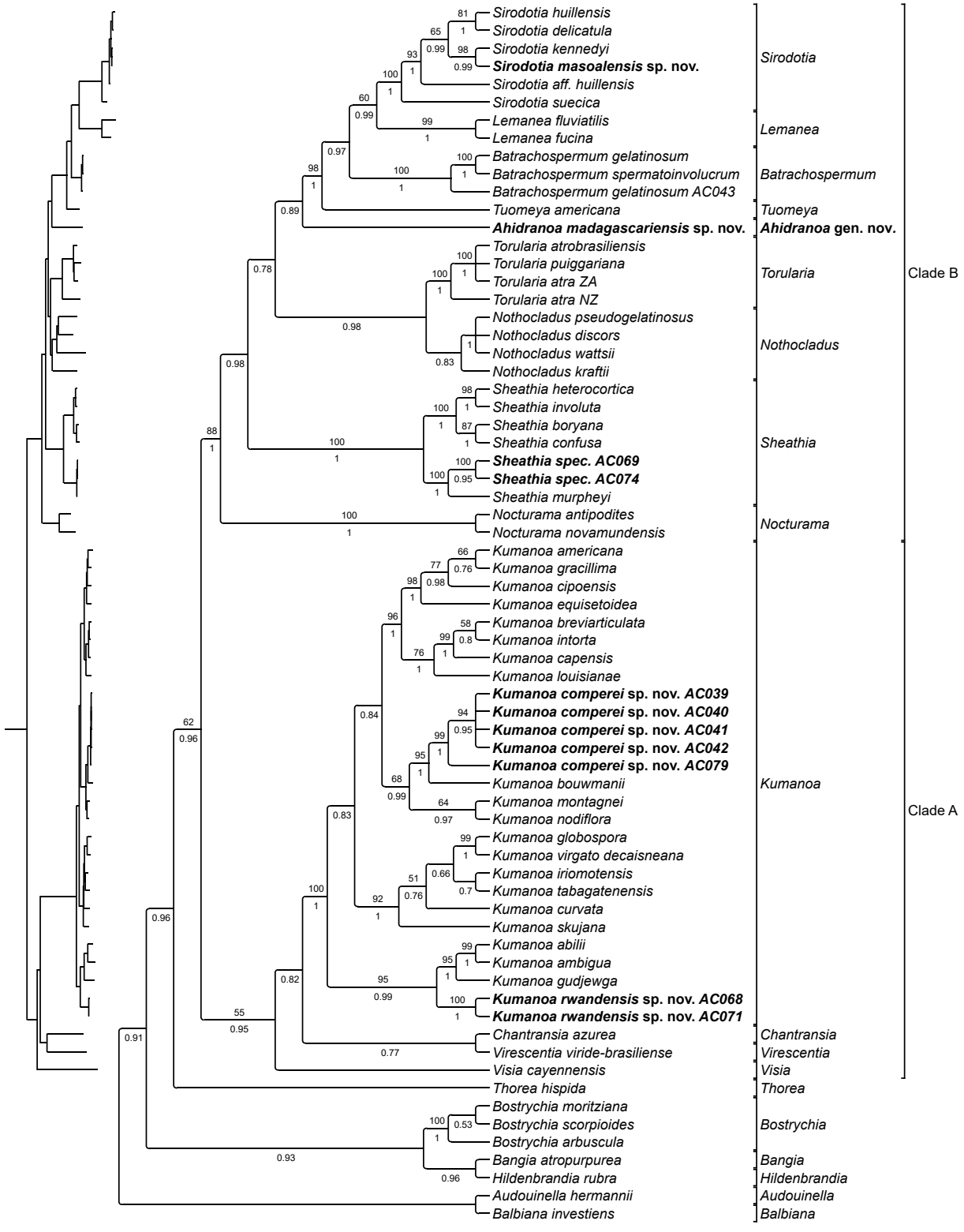

Figure 1. Likelihood tree based on concatenated *rbc*L and COI sequences. The numbers associated with the nodes indicate support values, while maximum likelihood bootstrap support (BS > 50) is depicted above the branches; posterior probability (PP) for the Bayesian analysis can be found below them. The phylogram structure is indicated next to the ML tree.

further species from India to *Kumanoa*, most of them known only from the type specimens, but their treatment relied entirely on literature studies, without consulting the relevant herbarium material. Johnston et al. (2014) added two further species from Indonesia. Szinte et al. (2020) describe *Kumanoa bouwmanii* from Northern Province, Zambia. Here we describe two new species from Rwanda and the Democratic Republic of the Congo, based on morphological and molecular evidence.

Kumanoa comperei Eb. Fisch., Killmann & D. Quandt, sp. nov. (Figs 2–4)

Diagnosis: Differs from *Kumanoa montagnei* in the shorter trichogyne, the carposporophyte higher than the whorls, sometimes two per whorl, and the secondary fascicles usually shorter than primary fascicles. It differs from *K. nodiflora* in the well-developed whorls. It differs from *K. bouwmanii* in the shape of the trichogyne.

Type: Rwanda, Western Province, Nyungwe National Park, stream in montane forest S of Kamiranzovu Swamp, along main road RN6, 2°29′09.14″S, 29°09′55.37″E, 2102 m, Fischer RW 294/17 (AC 039), 23 March 2017 (BR – holotype; KOBL – isotype).

Description. Plants moderately mucilaginous, thalli 3–14 cm high, branching irregular and abundant. Whorls reduced, composed of primary fascicles, 157–389 µm in diameter, barrel-shaped or obconic, slightly distant to confluent with age. Internode 120–190 µm long. Primary fascicles straight, with 7–8 cell-storeys. Secondary fascicles abundant, covering the entire internode, usually shorter than the primary fascicles, 2–3(–8) cell-storeys.

Monoecious. Spermatangia spherical, 5–6 µm in diameter, on primary and secondary fascicles. Carpogonial branches helically twisted, 35–38 µm long, composed of 4–6 cells, involucral filaments short, dense, carpogonia 25–35 µm long, trichogynes club-shaped, 25–30 × 10 µm, unstalked. Carposporophytes 1(–2) per whorl, hemispherical, usually higher than whorls, dense, 270–300 µm long, 210–250 µm in diameter, gonimoblast filaments 6–8 cell-storeys, carposporangia obovoid or elliptical, 5–7 × 4–5 µm.

Ecology and distribution. *Kumanoa comperei* occurs in small acidic streams in montane forest between 1100 and 2100 m. The streams are slow-flowing and half-shaded, with usually no aquatic vegetation except an unidentified *Cladophora* species at very low abundance. No aquatic bryophytes have been observed. So far the new species is known only from two localities in Nyungwe National Park in Rwanda and one locality in Kahuzi-Biéga-National Park in the Democratic Republic of the Congo.

Etymology. The species is dedicated to Pierre Compère (1934–2016), algologist at the National Botanical Garden of Meise, Belgium, who published numerous papers on African algae and a flora of freshwater red algae for Belgium.

Notes. In the phylogenetic tree (Fig. 1), *Kumanoa comperei* is sister to the almost simultaneously published *Kumanoa bouwmanii* (Szinte et al. 2020) but differs morphologically in the shape of the trichogyne, and molecularly in having distinct genetic differences. While among *Kumanoa comperei* samples the *rbc*L sequences are identical and for COI the divergence is only 0.4%, the differences from *Kumanoa bouwmanii* are conspicuous (*rbc*L: 2,6%; COI: 7.3%) and fall in the range of the observed divergence between species in the genus *Kumanoa* (*rbc*L: 1.5–8.4%; COI: 3.2–16.2%). *Kumanoa comperei-K. bouwmanii* cluster with *Kumanoa montagnei* (Entwisle et al. 2009) (= *Batrachospermum guyanense* nom. illeg.) and *K. nodiflora* (Entwisle et al. 2009). *Kumanoa montagnei* has long carpogonia, usually more than 45 µm (–65 µm) in length, and loose carposporophytes 150–230 µm in diameter, and unstalked long cylindrical or club-shaped trichogynes. *Kumanoa comperei* has carpogonia 25–35 µm long, trichogynes club-shaped, 25–30 × 10 µm, unstalked, and carposporophytes not exceeding 160 µm in diameter. *Kumanoa nodiflora* has reduced whorls and dense carposporophytes 200–400 µm in diameter that are higher than the whorl radius, and large carposporangia 15–20 µm in length (vs. 5–7 µm in *K. comperei*).

Specimens examined. DEMOCRATIC REPUBLIC OF THE CONGO. Kahuzi-Bièga National Park, Mulolo, ~1100 m (AC 079), B. & L. Dumbo C17/2018, 6 January 2018 (KOBL). RWANDA, Western Province, Nyungwe National Park, stream in montane forest S of Kamiranzovu Swamp, along main road RN6, 2°29′09.14″S, 29°09′55.37″E, 2102 m, Fischer RW 453/16 (AC 042), 17 September 2016 (BR, KOBL); Western Province, Nyungwe National Park, stream in montane forest near main road RN6 SE of Gisakura, 2°27′54.27″S, 29°06′02.93″E, 1909 m, E. Fischer RW 305/17 (AC 040), 23 March 2017 (KOBL); ibid. E. Fischer 447/16 (AC 041), 17 September 2016 (KOBL).

Kumanoa rwandensis Eb. Fisch., Killmann & D. Quandt, sp. nov. (Figs 5–6)

Diagnosis: The new species differs from *Kumanoa ambigua* and *K. gudjewga* in the distinctly shorter secondary fascicles and the carposporophyte being as high or higher than the whorl radius.

Type: Rwanda, Southern Province, Nyungwe National Park, Rwasenkoko stream in Rwasenkoko Swamp, along main road RN6, 2°31′43.60″S, 29°21′12.62″E, 2338 m, E. Fischer 678/17 (AC 068), 8 September 2017 (BR – holotype; KOBL – isotype).

Description. Plants moderately mucilaginous, thalli 3–3.5 cm high, branching irregular and abundant. Whorls well developed, composed of primary fascicles, 360–548 µm in diameter, barrel-shaped or obconic, slightly distant to confluent with age. Internodes 190–210 µm long. Primary fascicles straight, with 10–11 cell-storeys. Secondary fascicles abundant, covering the entire internode, usually shorter than the primary fascicles, 2–3 cell-storeys.

Monoecious. Spermatangia spherical, 5–6 µm in diameter, on primary and secondary fascicles. Carpogonial branches helically twisted, 34–38 µm long, composed of 5–6 cells, involucral filaments short, dense, carpogonia up to 32–38(–71) µm long, trichogynes club-shaped, 10–12 µm in diameter, unstalked. Carposporophytes 1(–2) per whorl, hemispherical, usually higher than whorls,

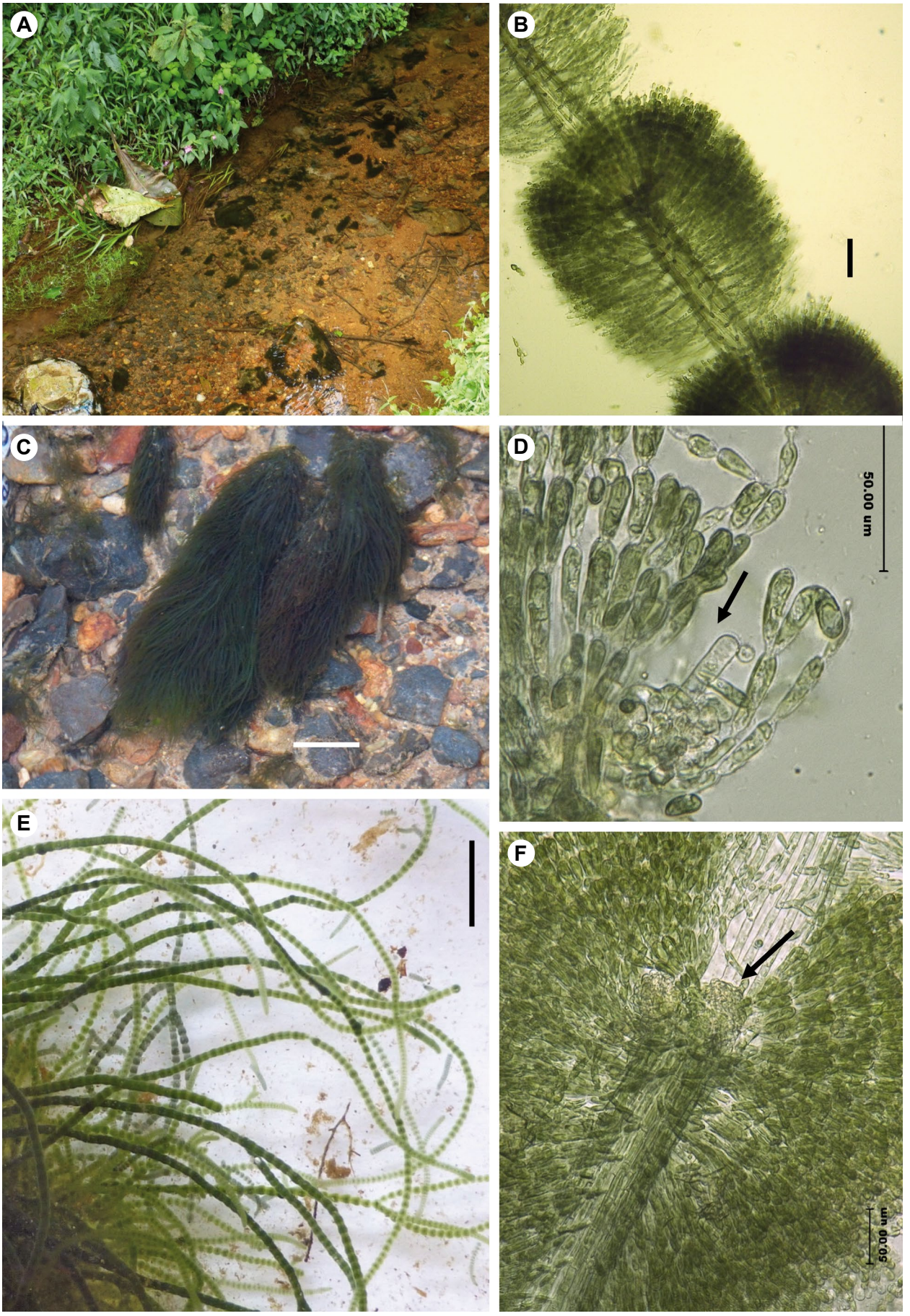

Figure 2. *Kumanoa comperei*. A – habitat in Kamiranzovu stream, Rwanda; B – whorls; C – habit in situ, Kamiranzovu stream; D – carpogonium with trichogyne (arrow); E – detail of habit; F – detail of whorl, showing primary and secondary fascicles and carpogonium (arrow). (A–F, Fischer RW 453/16, AC 042). Scales: B, D–F = 50 µm; C, E = 1 cm.

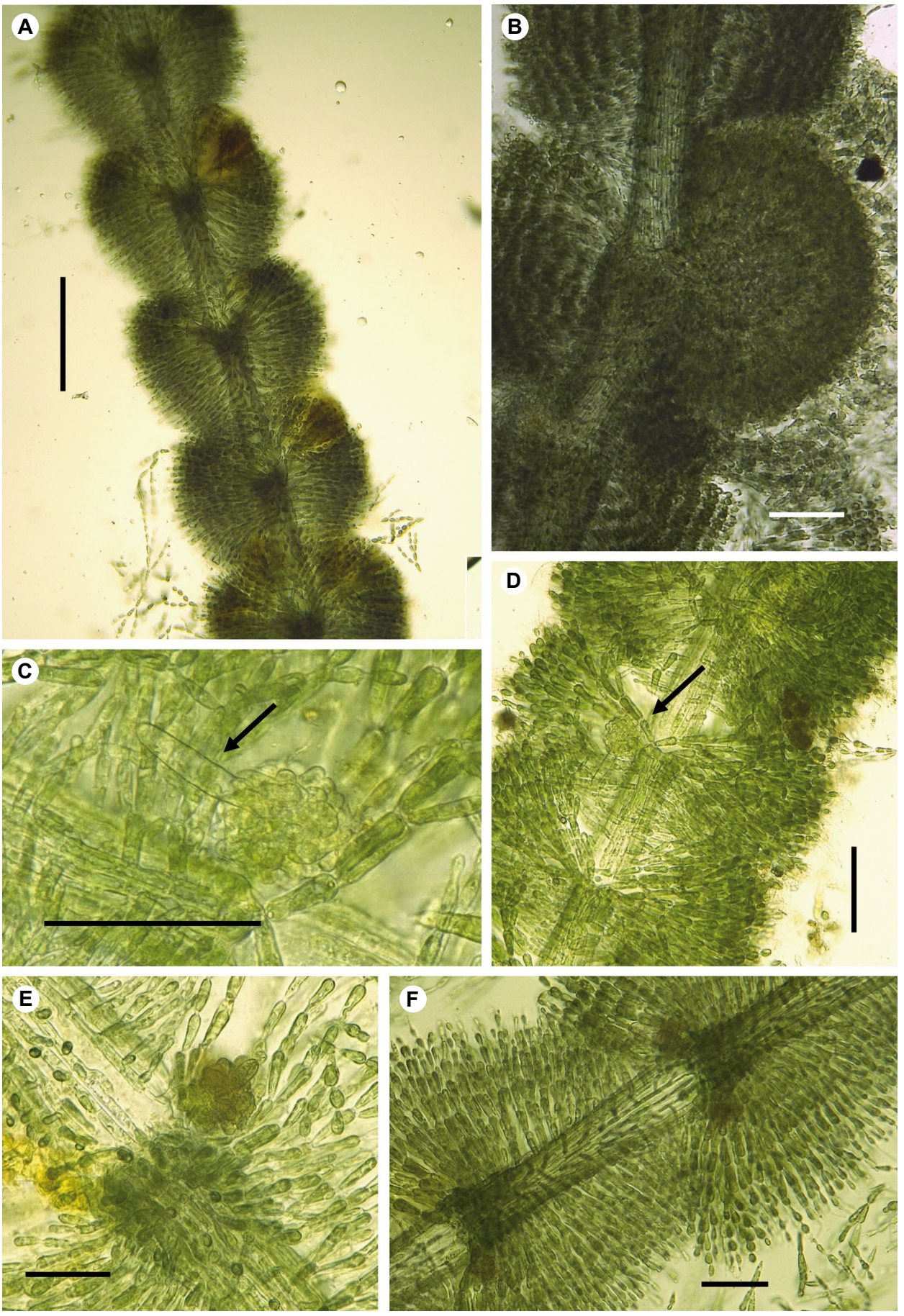

Figure 3. *Kumanoa comperei*. A, F – whorls with primary and secondary fascicles; B – carposporophyte; C–E – carpogonia with trichogyne (arrow). (A–F, Fischer RW 294/17, AC 039). Scales: A = 250 µm; B = 100 µm; C–F = 50 µm.

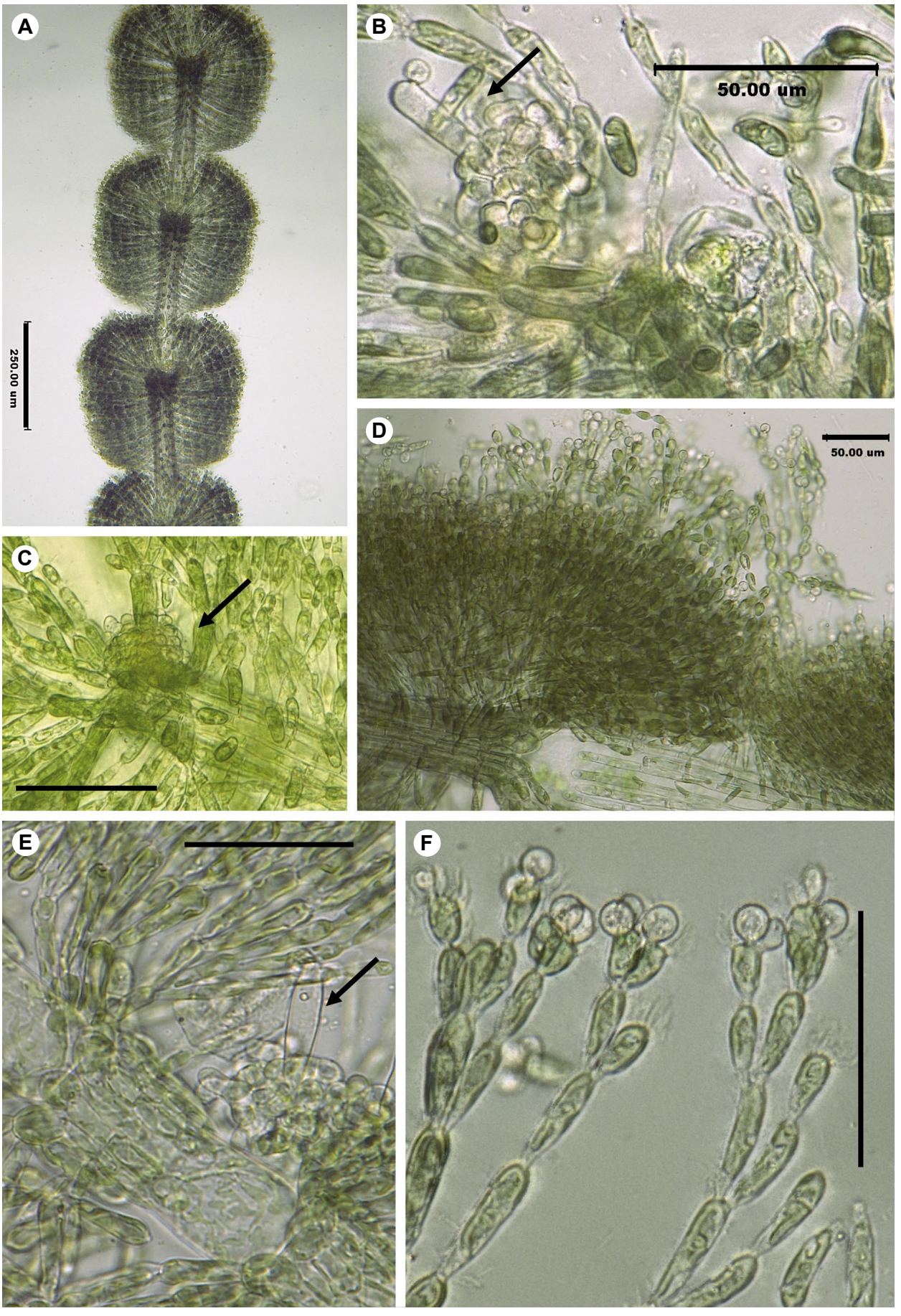

Figure 4. *Kumanoa comperei*. A – whorl; B–C, E – carpogonium with trichogyne; D – carposporophyte; F – spermatangia; (A–F, Fischer RW 453/16, AC 042). Scales: A = 250 µm; B–F = 50 µm.

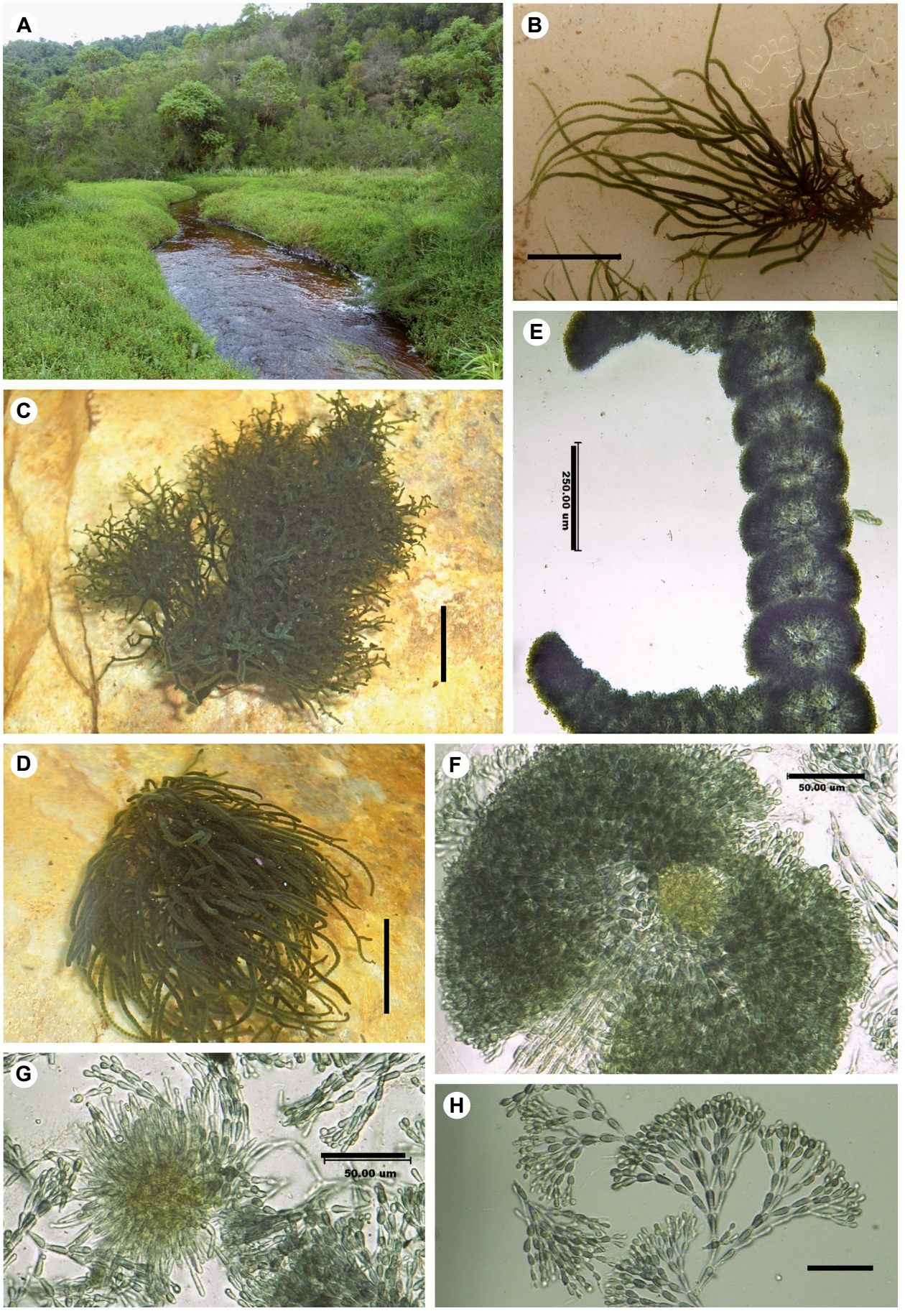

Figure 5. *Kumanoa rwandensis*. A – Habitat with Rwasenkoko stream, Rwanda; B–D – habit; E – whorls; F – carposporophyte; G – young carposporophyte; H – primary fascicles. (B–H, Fischer RW 678/17, AC 068). Scales: B–D = 1 cm; E = 250 µm; F–H = 50 µm.

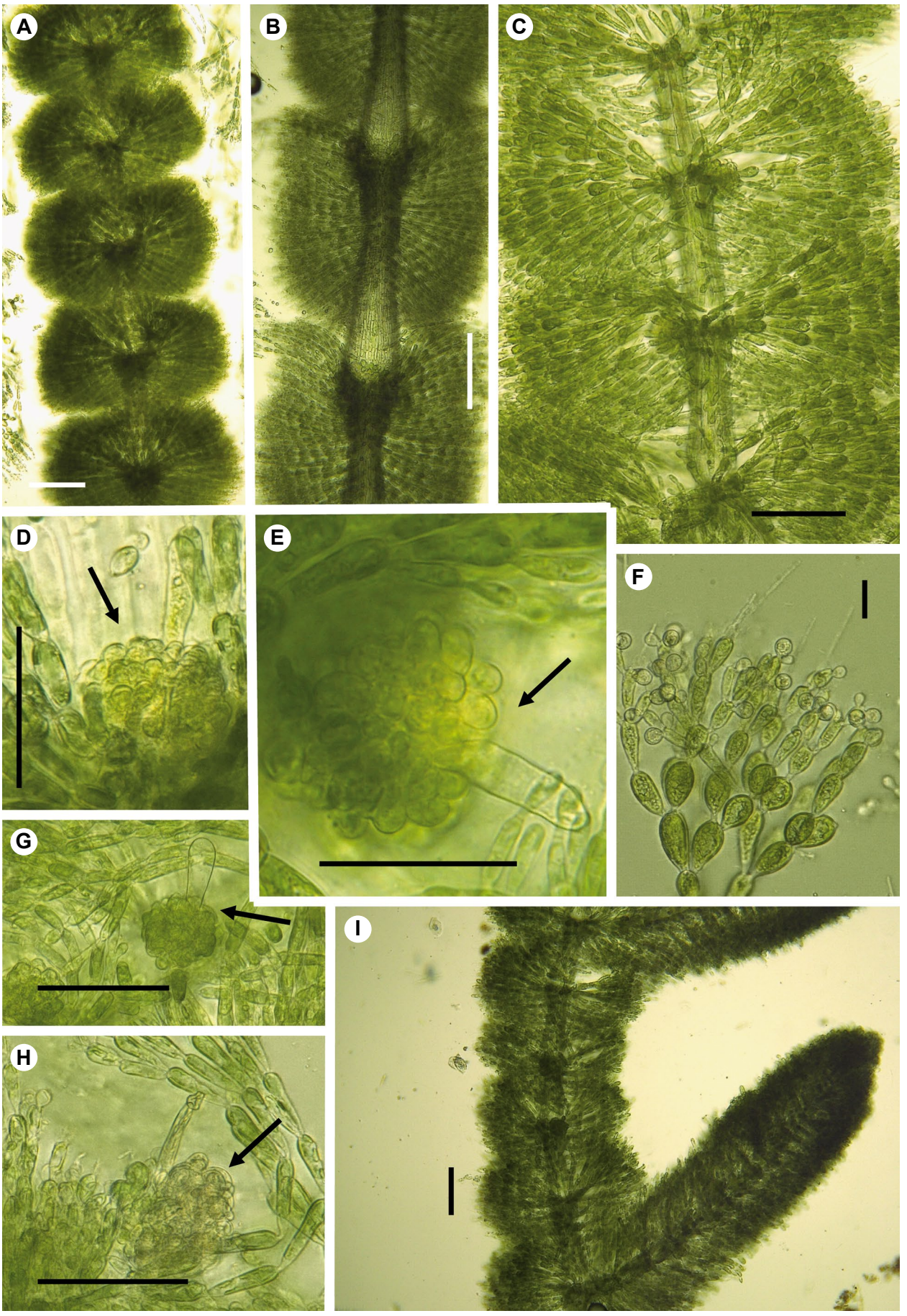

Figure 6. *Kumanoa rwandensis*. A–C, I – whorls; D–E, G–H – carpogonium with trichogyne (arrow); F – spermatangia. (A–F, Fischer RW 678/17, AC 068). Scales: A–C, I = 100 µm; D–E, G–H = 50 µm; F = 10 µm.

up to 100–119 µm long and 210–241 µm in diameter, gonimoblast filaments 6–8 cell-storeys, carposporangia obovoid or elliptical, 4–4.5 × 6–7 µm.

Ecology and distribution. *Kumanoa rwandensis* is found in acidic streams in Rwasenkoko swamp, surrounded by a vegetation of *Cyperus denudatus*, *Cyperus aterrimus* and ericaceous shrubs (*Erica rugegensis*, *Hypericum revolutum*, *Cliffortia nitidula*, *Anthospermum usambarense*) and *Hagenia abyssinica*. The populations grow on quartzitic stones together with *Chantransia* stages of *Sheathia* (see below). An aquatic macrophyte occurring in the stream is *Potamogeton thunbergii*. The second locality is an open sunny and fast-flowing stream outside the forest, the Rukarara, which later becomes the Nyabarongo and Akagera and thus one of main sources of the Blue Nile. There *Kumamoa rwandensis* is associated with several yet-unidentified freshwater red algae and a new species of *Paralemanea* (Fischer et al. in prep.).

Notes. In the phylogenetic tree (Fig. 1), *Kumanoa rwandensis* clusters with *Kumanoa ambigua*, known from Central America to northern South America, and *K. gudjewga* M. L. Vis et al. from Australia. It differs from *Kumanoa ambigua* and *K. gudjewga* in the distinctly shorter secondary fascicles and the carposporophyte being as high or higher than the whorl radius [120–300(–450) µm in *K. ambigua*, 150–410(–600) µm in *K. gudjewga*, up to 119–241 µm in *K. rwandensis*]. The carposporangia of *Kumanoa rwandensis* are much smaller (4.5–7 µm) than those of *K. ambigua* (10–17 µm) and *K. gudjewga* (14–26 µm).

Specimens examined. RWANDA. Southern Province, Rukarara River at Kunyu, 2°27′16.08″S, 29°27′20.71″E, 2016 m, E. Fischer 682/17 (AC 071), 8 September 2017 (KOBL).

The new genus *Ahidranoa*

While comparing two samples of a freshwater red alga, they seemed at first similar to the Southern Hemispherean genus *Nocturama* that was established to accommodate a single species from Australia and New Zealand, *Batrachospermum antipodites* (Entwisle 1995). This species was formerly included in a cluster of Australian and New Zealand species that was distinguished by carpogonia subtended by a relatively short filament of modified cells (Entwisle & Foard 1997, 2007). The other taxa included in this cluster are now placed in the expanded genus *Nothocladus* (Entwisle et al. 2016). Necchi et al. (2016) described a second species of *Nocturama*, *N. novamundensis* (Necchi et al. 2016) from Brazil, Rio Grande do Sul. Molecular evidence, however, supports the recognition of a new genus. This taxon is well supported as sister to a clade with *Sirodotia*, *Lemanea*, *Batrachospermum* s.str. and *Tuomeya* (Fig. 1). *Nocturama*, on the other hand, is sister to *Nothocladus*, *Torularia* and *Sheathia*.

Ahidranoa Eb. Fisch., Killmann & D. Quandt, gen. nov.

Diagnosis: *Ahidranoa* is similar to *Batrachospermum* s.str. and *Nocturam*a but is characterized by curved primary fascicles, the presence of rather abundant secondary fascicles, the curved and shorter cells of the carpogonial branches different from primary fascicle cells, and the pear-shaped trichogyne which is widest in the lower third.

Generic type: *Ahidranoa madagascariensis* Eb. Fisch., Killmann & D. Quandt

Etymology. The name of the new genus is derived from the Malagasy word for alga: ahidrano.

Ahidranoa madagascariensis Eb. Fisch., Killmann & D. Quandt, sp. nov. (Figs 7–8)

Type: Madagascar, Antsiranana, Parc National de Masoala, River Ambanizana, 15°26′59.88″S, 50°00′29.45″E, 335 m, E. Fischer 799/17 (AC 076), 30 September 2017 (TAN – holotype; KOBL – isotype).

Description. Thalli brownish to reddish-brownish, moderately mucilagineous, abundantly and irregularly branched, up 5–8 cm long. Rhizoidal cells not inflated, cylindrical, 120–130 µm in diameter. Whorls spherical or barrel-shaped, 150–500 µm in diameter. Internodes 160–280 µm long. Primary fascicles curved, composed of 10–13 cell-storeys, distal cells ellipsoid or obovoid, 380–410 × 77–80 µm. Secondary fascicles present, below the whorls of primary fascicles, composed of 2–8 cell-storeys, not covering the whole internode.

Monoecious. Spermatangia 4.5–6 µm in diameter, on primary fascicles. Carpogonial branches straight, composed of 11–13 cell-storys, 234–244 × 80–83 µm, differentiated from primary fascicle cells, curved and shorter than primary fascicle cells. Carpogonia symmetric, 30–45 µm long, trichogyne pear-shaped, widest in lower third, sessile, 13–15 µm in diameter. Carposporophyte indistinctly pedicellate to almost sessile, 1 per whorl, dense, spherical, 58–70 µm in diameter, carposporangia obovoid, 4–5 × 5–6 µm.

Ecology and distribution. *Ahidranoa madagascariensis* occurs in the Marojejy Massif in a small shaded stream just below Cascade d´Humbert. The second locality is the River Ambanizana on Masoala presque-île, which is quite sun-exposed. *Ahidranoa madagascariensis*, however, occurs between the leaves of a member of *Podostemaceae* and thus is also growing in shade. At the same locality, the new species *Sirodotia masoalensis* (see below) is growing in full sun. *Ahidranoa madagascariensis* is so far restricted to northeastern Madagascar.

Specimens examined. MADAGASCAR. Antsiranana, Parc National Marojejy, small stream near Cascade d´Humbert, 14°25′58.3″S, 49°46′22.7″E, 489 m, E. Fischer 28/14, 18 October 2014 (TAN, KOBL).

Evidence for the occurrence of the genus *Sheathia* in Central Africa

Two specimens of a bluish grey acrochaetioid alga were collected and tentatively identified as *Audouinella*. However, molecular data suggest that these are *Chantransia* stages of the genus *Sheathia*, and the two accessions accordingly cluster with other *Sheathia* species, but no mature gametophyte could be detected.

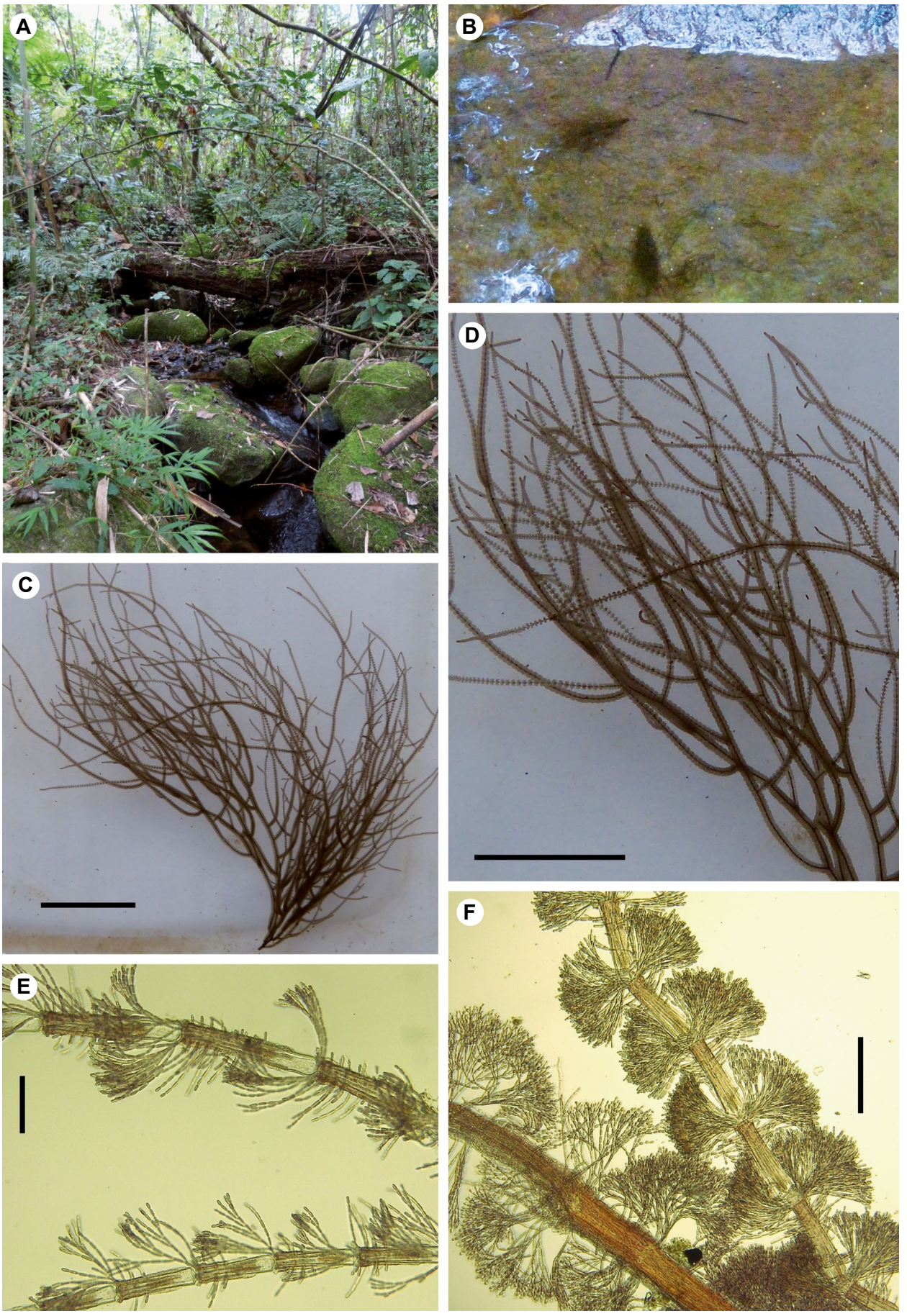

Figure 7. *Ahidranoa madagascariensis*. A–B – habitat, Parc National Marojejy, Madagascar; C–D – habit, Parc National Marojejy, Madagascar; E–F – whorls. (A–F, Fischer 28/14). Scales: C–D = 1 cm; E–F = 100 µm.

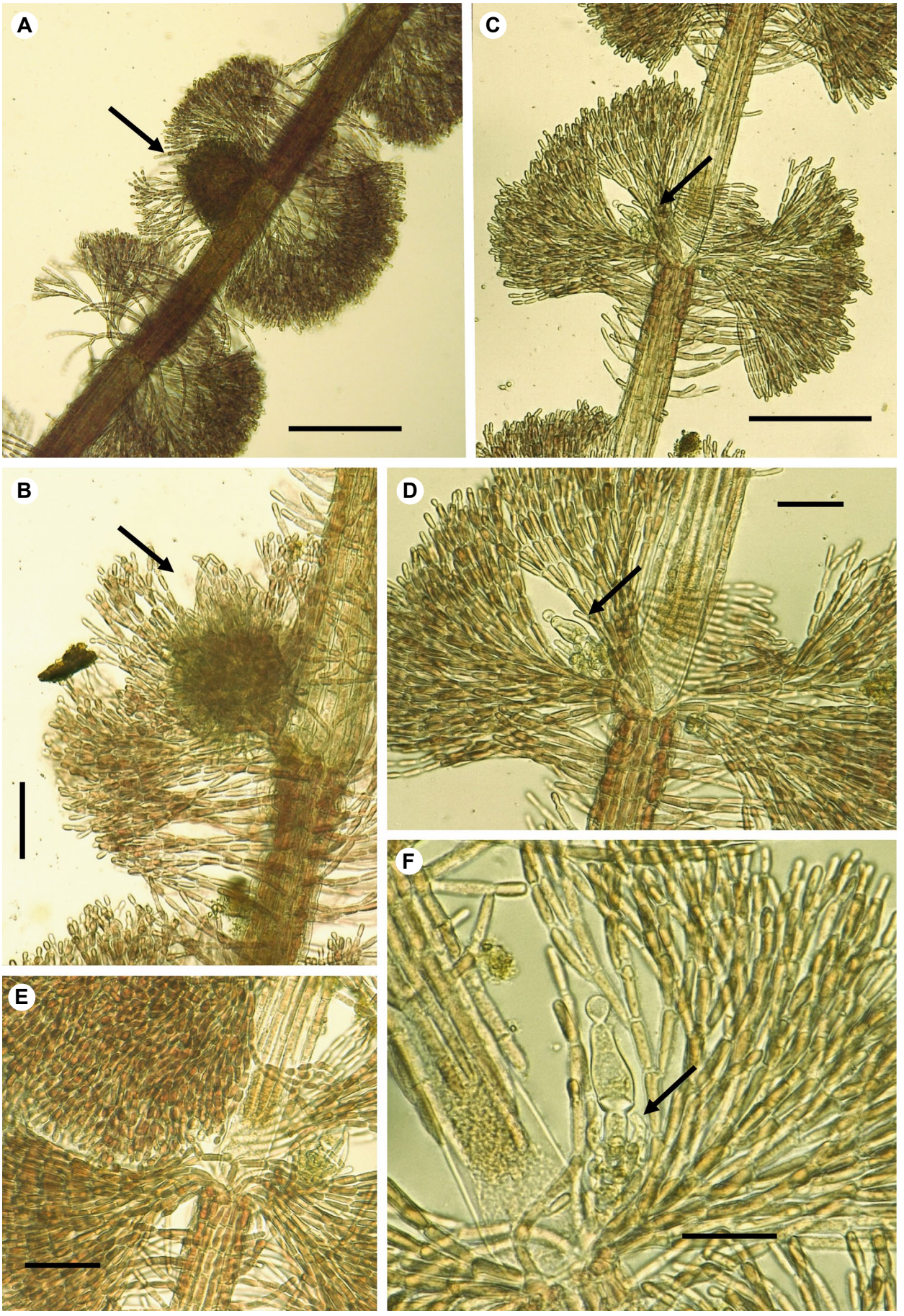

Figure 8. *Ahidranoa madagascariensis*. A–B – whorl with carposporophyte (arrow); C–D, F – whorls with primary and secondary fascicles, and carpogonium with trichogyne and spermatium (arrow); E – detail of whorl. (A–F, E. Fischer 799/17, AC 076). Scales: A–B = 100 µm; C–E = 50 µm; F = 20 µm.

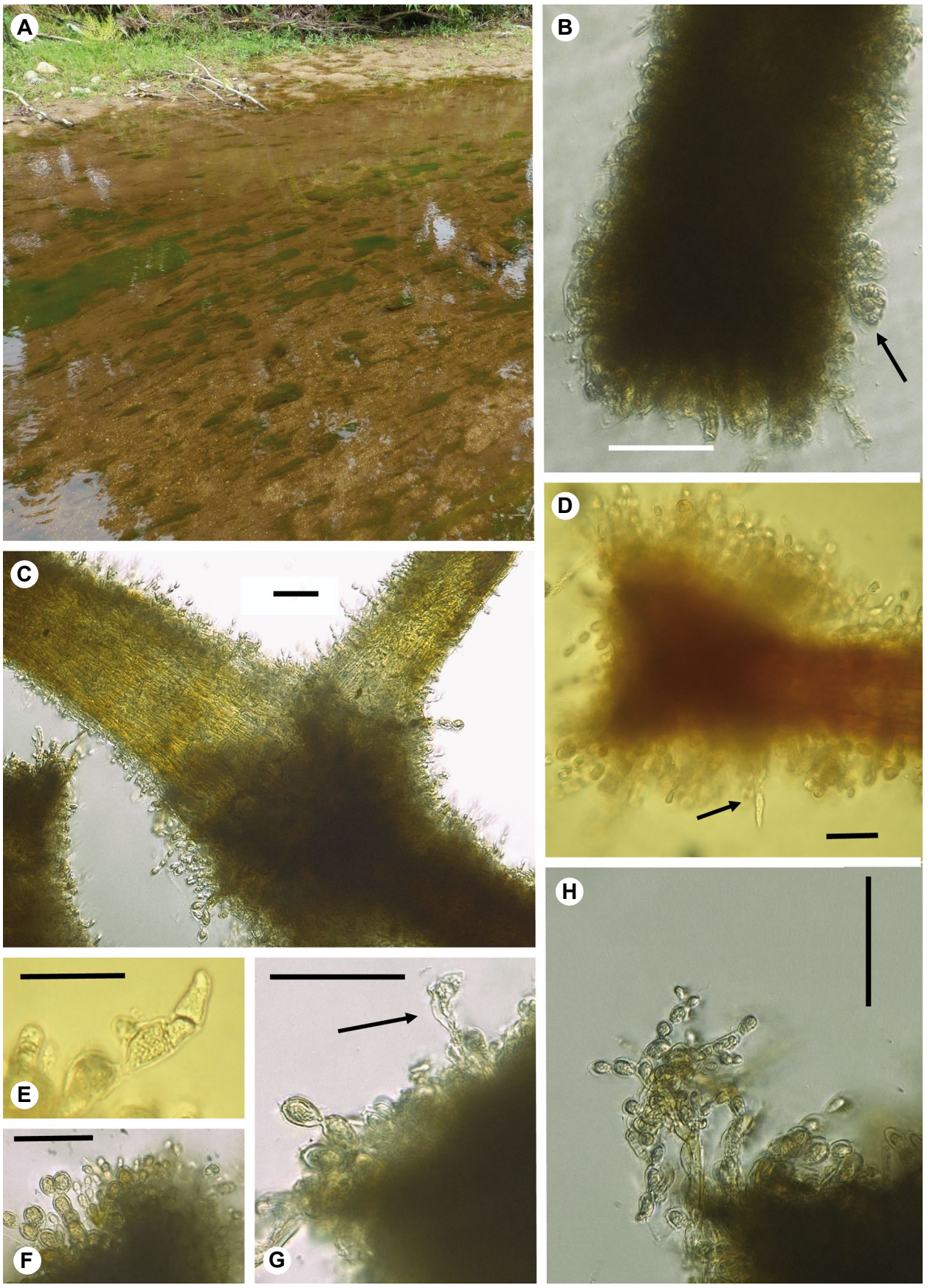

Figure 9. *Sirodotia masoalensis*. A – habitat; B – whorl with carpogosporophyte and carposporangia (arrow); C – thallus with ramification; D – whorl with spermatangia, and carpogonium with trichogyne (arrow); E, G – young carpogonium (arrow); F, H – carpogonium. (A–H, E. Fischer 181/15, AC 027). Scales: B–C, G–H = 50 µm; D–F = 20 µm.

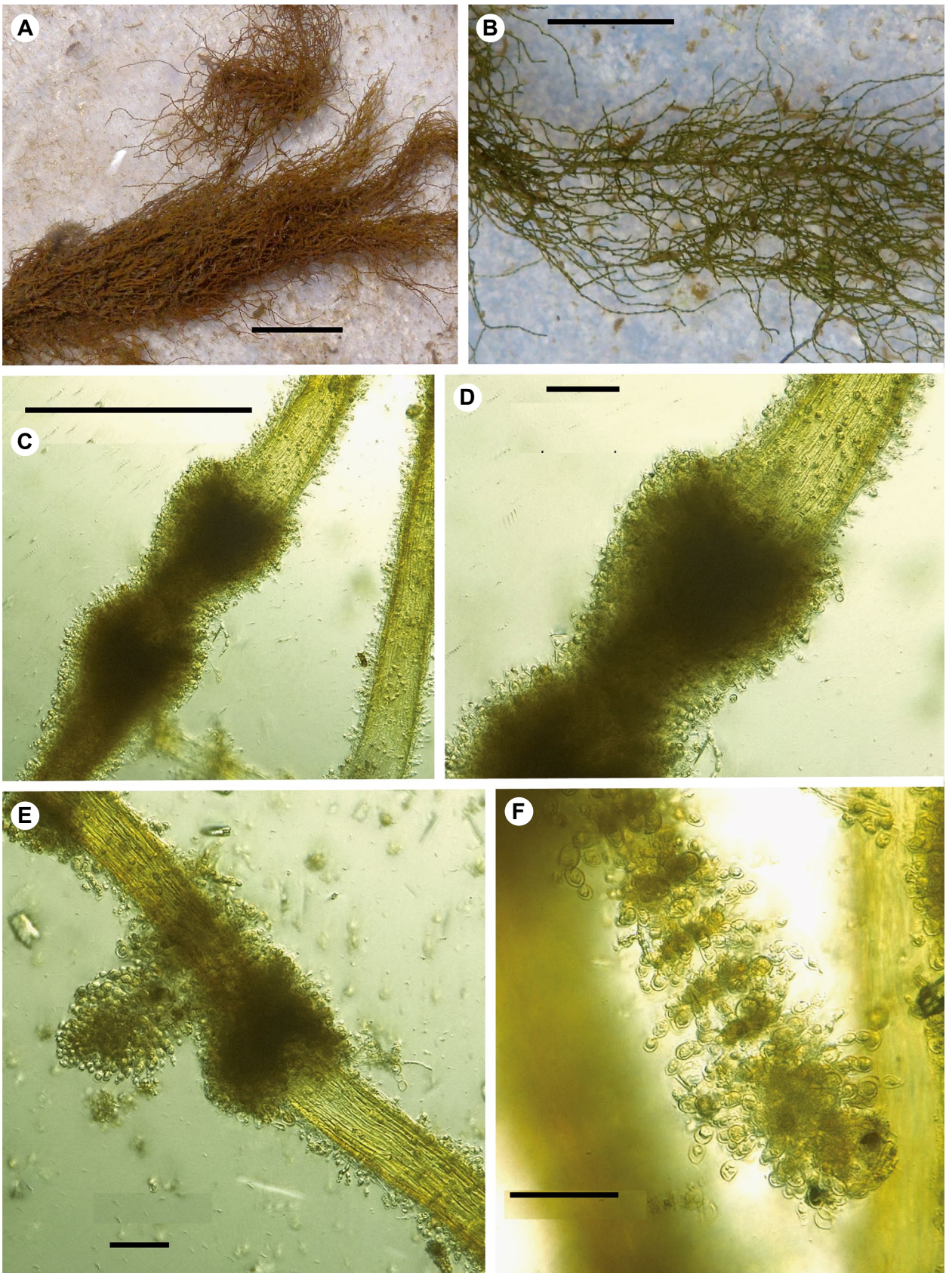

Figure 10. *Sirodotia masoalensis*. A–B – habit; C–D – whorl with internodes, showing primary and secondary fascicles; E–F – young branch with terminal spermatangia. (A–F, E. Fischer 181/15, AC 027). Scales: A–B = 1 cm; C = 250 µm; D–F = 50 µm.

Skuja (1934) assumed that only the red forms should be included in the genus *Audouinella*, and that the blue forms are young *Chantransia* stages of the genus *Batrachospermum*. Necchi & Zucchi (1997) support this suggestion. Also, Chen et al. (2014) could show that *Audouinella heterospora* is the *Chantransia* stage of *Thorea hispida*. Given that Szinte et al. (2020) described a *Sheathia* from northern Zambia as *S. murpheyi*, which was resolved sister to our *Chantransia* stages, our analysis provides further evidence for the occurrence of *Sheathia* in Central Africa. However, the species cannot be identified at present, and the genetic differences from *S. murpheyi* might indicate a new species.

Specimens examined. RWANDA. Southern Province, Nyungwe National Park, Rwasenkoko stream, on rocks in Rwasenkoko Swamp, along main road RN6, 2°31′43.60″S, 29°21′12.62″E, 2338 m, E. Fischer RW 679/17 (AC 069), 8 September 2017 (KOBL); Southern Province, Rukarara River at Kunyu, 2°27′16.08″S, 29°27′20.71″E, 2016 m, E. Fischer RW 687/17 (AC 074), 8 September 2017 (KOBL).

The genus *Sirodotia*

Sirodotia was segregated from *Batrachospermum*, mainly due to the asymmetrical base of the carpogonium and the indeterminate gonimoblast filaments in the carposporophyte (Lam et al. 2012). From the eight taxa accepted by Kumano (2002), *Sirodotia goebelii* (Entwisle & Foard 1999) was placed in synonymy with *S. suecica*, and *S. tenuissima* was confirmed as a synonym of *S. suecica* (Lam et al. 2012). In Africa, *Sirodotia huillensis* was described from Angola (see above) but has never been re-collected near the type locality. Material with DNA data has so far only been studied from the United States and Mexico (see Lam et al. 2012). A specimen identified as *Sirodotia* aff. *huillensis* from South Africa differed from the samples from Texas, Arizona and Mexico, and could well represent the typical *Sirodotia huillensis*. *Sirodotia suecia* is widespread and recorded from the United States, Europe, Australia and New Zealand, and one sample from South Africa. A new species, *Sirodotia kennedyi* (Szinte et al. 2020), has been described from northern Zambia and is sister to our sample but morphologically differs distinctly, and *Sirodotia masoalensis* is described here as a new species.

Sirodotia masoalensis Eb. Fisch., Killmann & D. Quandt, sp. nov. (Figs 9–10)

Diagnosis: The species differs from *S. suecica*, *S. huillensis* and *S. kennedyi* in the much shorter primary fascicles, thus more resembling in its habit *Torularia atra*. It differs from *S. suecica* in the lack of terminal hairs on primary fascicles.

Type: Madagascar, Antsiranana, Parc National de Masoala, River Ambanizana, 15°26′59.88″S, 50°00′29.45″E, 335 m, E. Fischer 181/15 (AC 027), 7 October 2015 (TAN – holotype; KOBL – isotype).

Description. Thalli robust, brownish to reddish-brownish, moderately mucilagineous, abundantly and irregularly branched, up 7–14 cm long. Whorls reduced, obconical to barrel-shaped, 115 µm in diameter. Internodes 250–380 µm. Primary fascicles straight, composed of 5–6 cell-storeys, branching 3–4 times, distal cells ellipsoid or obovoid, terminal hairs lacking. Secondary fascicles numerous, below the whorls of primary fascicles, composed of 2–3 cell-storeys, straight, up to 20–22 µm long, not covering the whole internode.

Monoecious. Spermatangia spherical, 6–8 µm in diameter. Carpogonial branches arising from intercalary fascicle cells. Carpogonia 26–35 µm long, base up to 15 µm in diameter, trichogyne indistinctly pedicellate, ellipsoid to cylindrical, 8–10 µm in diameter. Carposporangium-bearing filaments extending into outer cortex, carposporangia ellipsoidal, 10–12 µm long and 5–6 µm wide.

Ecology and distribution. Known only from small tributaries of the River Ambanizana on the Masoala Peninsula in Madagascar, where the species is associated with various green algae including *Chara* sp.

Notes. *Sirodotia masoalensis* is part of the *Sirodotia* clade (Fig. 1) and sister to *S. kennedyi*. Both cluster with *S. huillensis* and *S. delicatula*. Several characters of *Sirodotia masoalensis*, such as the origin of gonimoblast filaments, are not observed, but the new species differs from all congeners in the reduced primary fascicle whorls.

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Supplementary electronic material

Figure S1. Bayesian inference based on *rbc*L; posterior probabilities are located along the branches. Download file

Figure S2. Bayesian inference based on COI; posterior probabilities are located along the branches. Download file

References

Alika, F. O. & Akoma, O. C. 2012. Preliminary checklist of phytoplankton and periphyton in River Okhuo, Nigeria. *Current Research Journal of Biological Sciences* 4: 538–543.

Bonnemaison, T. 1828. Essai sur les hydrophytes loculées (ou articulées) de la famille des Épidermées et des Céramiées. *Mémoires du Muséum d'Histoire Naturelle, Paris* 16: 49–148, pls 3–8.

Borge, O. 1928. Teil VIII. Süßwasseralgen. In: Schröder, B.: Zellpflanzen Ostafrikas, gesammelt auf der akademischen Studienfahrt 1910. *Hedwigia* 68: 93–114.

Chapuis, I. S., Necchi, O. Jr., Zuccarello, G. C., Xie, S.-L., Aboal, M., Sánchez Castillo, P. M. & Vis, M. L. 2017. A new genus, *Volatus* and four new species of *Batrachospermum* sensu strict (*Batrachospermales*, *Rhodophyta*). *Phycologia* 56: 454–468.

Chen, L., Feng, J., Han, X.-J. & Xie, S.-L. 2014. Investigation of a freshwater acrochaetioid alga (*Rhodophyta*) with molecular and morphological methods. *Nordic Journal of Botany* 32: 529–535.

Compère, P. 1975. Algues de la region du lac Tchad III-Rhodophycées, Euglénophycées, Cryptophycées, Dinophycées, Chrysophycées, Xanthophycées. *Cahiers de l'ORSTOM, série hydrobiologique* 9: 167–192.

Da, K. P., Traore, D. & Assemien, A. P. 1999. Cyanophytes, Rhodophytes, et Pyrrhophytes de la mare et du complexe piscicole du Parc National du Banco (Côte d'Ivoire). *Systematics and Geography of Plants* 69: 161–183.

De Toni, G. B. 1897. *Sylloge Algarum omnium hucusque cognitarum*. IV. Florideae Sect. I. – Familiae I-XI. 1–388.

Eloranta, P. & Kwandrans, J. 1996. Distribution and ecology of freshwater red algae (*Rhodophyta*) in some central finnish rivers. *Nordic Journal of Botany* 16: 107–117.

Eloranta, P., Kwandrans, J. & Kusel-Fetzmann, E. 2011. *Süsswasserflora von Mitteleuropa, Bd. 7/Freshwater flora of Central Europe*, Vol. 7: *Rhodophyta* and *Phaeophyceae*. Spektrum Akademischer Verlag, Heidelberg.

Entwisle, T. J. 1992. The setaceous species of *Batrachospermum* (*Rhodophyta*): a re-evaluation of *B. atrum* (Hudson) Harvey and *B. puiggarianum* Grunow including the description of *B. dyatyches* sp. nov. from Tasmania, Australia. *Muelleria* 7: 425–445.

Entwisle, T. J. 1995. *Batrachospermum antipodites* sp. nov. (*Batrachospermaceae*): a widespread freshwater red alga in eastern Australia and New Zealand. *Muelleria* 8: 291–298.

Entwisle, T. J. & Foard, H. J. 1997. *Batrachospermum* (*Batrachospermales*, *Rhodophyta*) in Australia and New Zealand: New Taxa and emended circumscriptions in sections *Aristata*, *Batrachospermum*, *Turfos*a and *Virescentia. Australian Systematic Botany* 10: 331–380.

Entwisle, T. J. & Foard, H. J. 1999. *Sirodotia* (*Batrachospermales*, *Rhodophyta*) in Australia and New Zealand. *Australian Systematic Botany* 12: 605–613.

Entwisle, T. J. & Foard, H. J. 2007. *Batrachospermales*. In Entwisle, T. J., Skinner, S., Lewis, S. H. & Foard, H. J. (eds) *Algae of Australia: Batrachospermales, Thoreales, Oedogoniales and Zygnemaceae*, pp. 1–25. ABRS, Canberra, CSTRO Publishing, Melbourne.

Entwisle, T. J., Vis, M. L., Chiasson, W. B., Necchi, O. Jr. & Sherwood, A. R. 2009. Systematics of the *Batrachospermales* (*Rhodophyta*) – A synthesis. *Journal of Phycology* 45: 704–715.

Entwisle, T. J., Johnston, E. T., Lam, D. W., Stewart, S. A. & Vis, M. L. 2016. *Nocturama* gen. nov., *Nothocladus* s.lat. and other taxonomic novelties resulting from the further resolution of paraphyly in Australasian members of *Batrachospermum* (*Batrachospermales*, *Rhodophyta*). *Journal of Phycology* 52: 384–396.

Evans, J. R., Chapuis I. S. & Vis, M. L. 2017. Adding to the freshwater red algal diversity in North America: *Lympha mucosa* gen. et sp. nov. (*Batrachospermales*, *Rhodophyta*). *Algae* 32: 171–179.

Fritsch, F. E. 1907. The Subaerial and Freshwater Algal Flora of the Tropics. *Annals of Botany* 82: 235–275.

Fritsch, F. E. 1914. Contributions to our knowledge of the freshwater algae of Africa. I. Some freshwater algae from Madagascar. *Annales de Biologie Lacustre* 7: 1–20.

Ganesan, E. K. & West, J. A. 2013. Nomenclatural changes for some freshwater red algae from India. *Algae* 28: 45–51.

Guiry, M. D. in Guiry, M. D. & Guiry, G. M. 2019. *AlgaeBase*. Worldwide electronic publication, National University of Ireland, Galway. http://www.algaebase.org [searched on 5 April 2019]

Johnston, E. T., Lim, P.-E., Buhari, N., Keil, E. J., Diawad, M. I. & Vis, M. L. 2014. Diversity of freshwater red algae (*Rhodophyta*) in Malaysia and Indonesia from morphological and molecular data. *Phycologia* 53: 329–341.

Kozlov, A. M., Darriba, D., Flouri, F., Morel, B., & Stamatakis, A. 2019. RAxML-NG: A fast, scalable, and user-friendly tool for maximum likelihood phylogenetic inference. Bioinformatics, btz305 doi:10.1093/bioinformatics/btz305

Kumano, S. 2002. *Freshwater red algae of the world*. Biopress Ltd., Bristol.

Kützing, F. T. 1849. *Species Algarum*, VI. Lipsiae F. A. Brockhaus.

Kylin, H. 1912. Studien über die schwedischen Arten der Gattungen *Batrachospermum* Roth und *Sirodotia* nov.gen. *Nova Acta Regii Societatis Scientiae Upsaliensis*, Ser. IV, Vol. 3,3: 1–40.

Lam, D. W., Entwisle, T. J., Eloranta, P., Kwandrans, J. & Vis, M. L. 2012. Circumscription of species in the genus *Sirodotia* (*Batrachospermales*, *Rhodophyta*) based on molecular and morphological data. *European Journal of Phycology* 47: 42–50.

Lemmermann, E. 1914. *Rhodophyceae*. In: Mildbraed, J. (ed.) *Wissenschaftliche Ergebnisse der Deutschen Zentralafrika-Expedition 1907–1908 unter Führung Adolf Friedrichs, Herzog zu Mecklenburg* 2: 94.

Necchi, O. Jr. 1990 Revision of the genus *Batrachospermum* Roth (*Rhodophyta*, *Batrachospermales*) in Brazil. *Bibliotheca Phycologia* 84: 1–201.

Necchi, O. Jr. & Vis, M. L. 2012. Monograph of the genus *Kumanoa* (*Rhodophyta*, *Batrachospermales*). *Bibliotheca Phycologia* 116: 1–79.

Necchi, O. Jr. & Zucchi, M. R. 1997. Taxonomy and distribution of *Thorea* (*Thoreaceae*, *Rhodophyta*) in Brazil. *Archiv für Hydrobiologie Supplement* 118: 83–90.

Necchi, O. Jr., Sheath, R. G. & Cole, K. M. 1993. Distribution and systematics of the freshwater genus *Sirodotia* (*Batrachospermales*, *Rhodophyta*) in North America. *Journal of Phycology* 29: 236–243.

Necchi, O. Jr., Entwisle, T. J., Branco, C. C. Z. & Paiano, M. O. 2016. First record of *Nocturama* (*Batrachospermales*, *Rhodophyta*) in South America, with the description of a new species, *N. novamundensis*. *Phytotaxa* 278: 273–280.

Necchi, O. Jr, Agostinho, D. C. & Vis, M. I. 2018. Revision of *Batrachospermum* Section *Virescentia* (*Batrachospermales*, *Rhodophyta*) with the establishment of the new genus *Virescentia* stat. nov. *Cryptogamie, Algologie* 39: 313–338.

Necchi, O. Jr., Fo, S. G., Paiano, M. O. & Vis, M. L. 2019a. Revision of *Batrachospermum* section *Macrospora* (*Batrachospermales*, *Rhodophyta*) with the establishment of the new genus *Montagnia*. *Phycologia* 58: 582–591.

Necchi, O. Jr., Garcia Filho, A. & Paiano, M. O. 2019b. Revision of *Batrachospermum* sections *Acarposporophytum* and *Aristata* (*Batrachospermales*, *Rhodophyta*) with the establishment of the new genera *Acarposporophycus* and *Visia*. *Phytotaxa* 395: 51–65.

Rabenhorst, L. 1855. Beitrag zur Kryptogamen-Flora Süd-Afrikas. Pilze und Algen. *Allgemeine Deutsche Naturhistorische Zeitung*, ser. 2, 1: 280–283.

Rambaut, A., Drummond, A. J., Xie, D., Baele, G. & Suchard, M. A. 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67: 901–904.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.-l., Darling, A., Höhna, S., Larget, B., Liu, l., Suchard, M. A. & Huelsenbeck, J. P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542.

Rossignolo, N. L. & Necchi, O. Jr. 2016. Revision of section *Setacea* of the genus *Batrachospermum* (*Batrachospermales*, *Rhodophyta*) with emphasis on specimens from Brazil. *Phycologia* 55: 337–346.

Rossignolo, N. L., Necchi, O. Jr. & Guiry, M. D. 2017. *Atrophycus*, a new genus name for '*Setacea* (De Toni) Necchi & Rossignolo'. *Notulae Algarum* 26: 1–2.

Salomaki, E. D., Kwandrans, J., Eloranta, P. & Vis, M. L. 2014. Molecular and morphological evidence for *Sheathia* gen. nov. (*Batrachospermales*, *Rhodophyta*) and three new species. *Journal of Phycology* 50: 526–542.

Saunders, G. W. 2005. Applying DNA barcoding to red macroalgae: a preliminary appraisal holds promise for future applications. *Philosophical Transactions of the Royal Society of London. Series B, containing papers of a Biological Character. London* 360: 1879–1888.

Schmidle, W. 1899a. Algologische Notizen VIII. *Batrachospermum Bohneri* Schmidle n. sp. *Allgemeine Botanische Zeitschrift* 5: 2–4.

Schmidle, W. 1899b. Einiges über die Befruchtung, Keimung und Haarinsertion von *Batrachospermum*. Botanische Zeitung 57: 125–135.

Sheath, R. G., Vis, M. L. & Cole, K. M. 1992. Distribution and systematics of *Batrachospermum* (*Batrachospermales*, *Rhodophyta*) in North America. 1. Section Contorta. *Journal of Phycology* 28: 237–246.

Sheath, R. G., Vis, M. L. & Cole, K. M. 1993. Distribution and systematics of *Batrachospermum* (*Batrachospermales*, *Rhodophyta*) in North America. 3. Section *Setacea*. *Journal of Phycology* 29: 719–725.

Sheath, R. G., Vis, M. L. & Cole, K. M. 1994a. Distribution and systematics of *Batrachospermum* (*Batrachospermales*, *Rhodophyta*) in North America. 4. Section *Virescentia*. *Journal of Phycology* 30: 108–117.

Sheath, R. G., Vis, M. L. & Cole, K. M. 1994b. Distribution and systematics of *Batrachospermum* (*Batrachospermales*, *Rhodophyta*) in North America. 6. Section *Turfosa*. *Journal of Phycology* 30: 872–884.

Sheath, R. G., Vis, M. L. & Cole, K. M. 1995. Distribution and systematics of *Batrachospermum* (*Batrachospermales*, *Rhodophyta*) in North America. 7. Section *Hybrida*. *Journal of Phycology* 34: 431–438.

Skuja, H. 1964. Weiteres zur Kenntnis der Süßwasserrhodophyceen der Gattung *Nothocladus*. *Revue Algologique* n.s. 7: 303–314.

Stöver, B. C. & Müller, K. F. 2010. TreeGraph 2: combining and visualizing evidence from different phylogenetic analyses. *BMC bioinformatics* 11: 7.

Suhr, J. N.v. 1840. Beiträge zur Algenkunde. *Flora* 23, 19: 289–298.

Szinte, A. L., Taylor, J. C., Abosede, A. T. & Vis, M. L. 2020. Current status of freshwater red algal diversity (*Rhodophyta*) of the African continent including descriptions of new taxa (*Batrachospermales*). *Phycologia* https://doi.org/10.1080/00318884.2020.1732149.

Thiers, B. M. 2019. Index Herbariorum Upgrade: A Project to Improve Access to Information about the World's Plant and Fungal Collections Assets https://www.nybg.org/science-project/index-herbariorum-upgrade/

Vis, M. L. & Entwisle, T. J. 2000. Insights into the phylogeny of the *Batrachospermales* (*Rhodophyta*) from rbcL sequence data of Australian taxa. *Journal of Phycology* 36: 1175–1182.

Vis, M. L., Chiasson, W. B. & Sheath, R. G. 2005. Phylogenetic relationships of *Batrachospermum* species (*Batrachospermales, Rhodophyta*) from coastal streams in French Guiana. *Phycologia* 44: 441–446.

Vis, M. L., Saunders, G. W., Sheath, R. G., Dunse, K. & Entwisle, T. J. 1998. Phylogeny of the *Batrachospermales* (*Rhodophyta*) inferred from *rbc*L and 18S ribosomal DNA gene sequences. *Journal of Phycology* 34: 341–350.

Vis, M. L. & Sheath, R. G. 1996. Distribution and systematics of *Batrachospermum* (*Batrachospermales*, *Rhodophyta*) in North America. 9. Section *Batrachospermum*: description of five new species. *Phycologia* 35: 124–134.

Vis, M. L., Necchi, O. Jr., Chiasson, W. B. & Entwisle, T. J. 2012. Molecular phylogeny of the genus *Kumanoa* (*Batrachospermales*, *Rhodophyta*). *Journal of Phycology* 48: 750–758.

Vis, M. L., Sheath, R. G. & Cole, K. M. 1994. Distribution and systematics of *Batrachospermum* (*Batrachospermales*, *Rhodophyta*) in North America. 8b. Section *Batrachospermum*: previously described species excluding *Batrachospermum gelatinosum*. *European Journal of Phycology* 31: 189–199.

West, W. & West, G. S. 1897. Welwitsch's African Freshwater Algae. *Journal of Botany* 35: 1–7.

Wynne, M. J. 2019. *Torularia* Bonnnemaison, 1828, a generic name to be reinstated for *Atrophycus* Necchi & Rossignolo, 2017. *Notulae algarum* 89: 1–4.

Zucchi, M. R. & Necchi, O. Jr. 2003. Blue-greenish acrochaetioid algae in freshwater habitats are '*Chantransia*' stages of *Batrachospermales* sensu lato (*Rhodophyta*). *Cryptogamie, Algologie* 24: 117–131.