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

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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:** *Batrachospermaeae*, 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 & Foad 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 Gnadalental (=Genadal 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., in Paviaischenfluss bei dem Herrenhuter Missionsort Gnadalental in Süd-Africa. Mitgetheilt vom Herrn Pfarrer Weneck 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 (= Atrophybus ater) in the previous literature, e.g., Entwisle 1992. Batrachospermum nigrescens (Sirodotia nigrescens = Torularia puiggariana), Batrachospermum graciilimum (= Kumanao gracillima), Batrachospermum hulense (= Sirodotia hulensis), Hildenbrandia rivalaris 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, Kili-mandscharo) 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 flaviatilis (= 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 Aliko & 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) which describes the new species Kumanao bouwmanii, Sheathia murpheyi and Sirodotia kennedyi, all from Zambia, and they name a Chantrasia 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 Nothocladas africanaustralis (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, Acrarposporophyta), 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 Nothocladas. Entwisle et al. (2009) proposed acceptance of different sections for the time being: Acrarposporophyta, Aristata, Batrachospermum, Helminthoidea, Macrospora, the informal ‘Australasica group’, Setacea, and Turfosa and Virescentia. The sections Contorta and Hybridra 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 Nothocladas, formerly containing three species from Madagascar and Australia (which now constitute section Nothocladas) was enlarged to comprise most of the old informal ‘Australasica-group’ with the new sections Australasicus, Theaquus and Krafitii, and also section Setaceus. Contrary to the arguments of Entwisle et al. (2016), Rossignolo and Necchi (2016) subsequently raised section Setaceus to generic level and included three species. For nomenclatural reasons the generic name Setaceus had to be replaced by Atrophybus (Rossignolo et al. 2017). Wynne (2019) showed that the name Torularia (Bonnemaison 1828) has priority over Atrophybus, and thus the three recognized members of the former section Setaceus were placed in the genus Torularia. Section Virescentia was raised to genus level under the name Virescentia (Necchi et al. 2018). Sections Acrarposporophyta and Aristata were raised to generic status under the names Acrarposporophycus 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.
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 (0.5 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 *rbcL* (rbcL-redF: TGCYAAAATGGGWTAYTG; rbcS-redR:...
PCR reactions were performed in 25 µl volumes for each sample. Each PCR reaction contained 1 µl DNA (> ~10 ng/µl), 10.35 µl H2O, 5 µl 5x Taq Flexi Buffer, 2.5 µl 25 mM MgCl2, 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 rbcL 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).

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 rbcL 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 re-burnin 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 (rbcL: 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 |
|---------|-----------------|
| Aulouinella hermannii | KC134346 – |
| Balbiania investiens | AF132293 KM055323 |
| Bangia atropurpurea | DQ408162 DQ191330 |
| Batrachospermum spermatoinvolutum | AF029146 – |
| Bostrychia arbuscula | KM502821 KM502796 |
| Bostrychia moritziana | AY920809 MF093965 |
| Bostrychia scorpioides | AY920820 MF094019 |
| Chantransia azurea | MN974515 MN974520 |
| Hildenbrandia rubra | K-284724 KF649304 |
| Kumanoa americana | KX284725 JN604910 |
| Kumanoa breviarticulata | KF649304 |
| Kumanoa cipoensis | JN590014 – |
| Kumanoa curvata | AY423395 JN604927 |
| Kumanoa equisetidea | GQ368889 EU636716 |
| Kumanoa globospora | GQ368891 JN604923 |
| Kumanoa gracillima | JN590003 JN604908 |
| Kumanoa gudjewga | KM055323 |
| Kumanoa intorta | AY423397 EU636717 |
| Kumanoa iriomotensis | JN900011 – |
| Kumanoa louisianae | AY423396 EU636713 |
| Kumanoa nodiflora | GQ368887 JN604919 |
| Kumanoa skujana | GQ368891 JN604923 |
| Kumanoa tabagatenensis | JN900003 JN604914 |
| Kumanoa virgato-decaisneana | AY423390 EU636717 |
| Lemanea fluviatilis | AF029150 KM055323 |
| Lemanea fucina | KC130145 |
| Nocturama antipodites | KJ825959 KU672391 |
| Nocturama antipodites | KT802839 KT802754 |
| Nocturama novamandensis | KX764640 – |
| Nothocladus discors | AF257778 KT802759 |
| Nothocladus kraftii | KT802854 KT802760 |
| Nothocladus pseudogelatinosus | AF209983 KT802761 |
| Nothocladus watissi | AF209986 KT802765 |
| Sheathia boryana | JX669773 JX669707 |
| Sheathia confusa | DQ393133 JX669712 |
| Sheathia heterocortica | DQ393136 EU636740 |
| Sheathia involuta | AF029145 – |
| Sheathia murpheyi | MN974517 MN974522 |
| Sirodotia aff. huillensis | JF344717 – |
| Sirodotia deliciatula | 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) atrro-brasilensis | KT183023 KT894749 |
| Torularia (Setacea) puiggariana | KP203886 KX703028 |
| Tuomeya americana | AF029159 KM055330 |
| Virentia 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. rwan-densis) 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 Notho-cladus. 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 Madagascar 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 Hybridra. 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.
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 rbcL 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″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 obvoid 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-overflowing and half-shaded, with usually no aquatic vegetation except an unidentified *Cladophora* species at very low abundance. No aquatic macrophytes 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), algaologist 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 rbcL sequences are identical and for COI the divergence is only 0.4%, the differences from *Kumanoa bouwmanii* are conspicuous (rbcL: 2.6%; COI: 7.3%) and fall in the range of the observed divergence between species in the genus *Kumanoa* (rbcL: 1.5–8.4%; COI: 3.2–16.2%). *Kumanoa comperei*- *K. bouwmanii* cluster with *Kumanoa montagnei* (Entwisle et al. 2009) (= *Batrachospermum guynense* 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 carposporophores 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 carposporophores not exceeding 160 μm in diameter. *Kumanoa nodiflora* has reduced whorls and dense carposporophores 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-Biéga 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″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, Rwansenkoko stream in Rwansenkoko 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, gonomoblast filaments 6–8 cell-stores, carposporangia obvoid or elliptical, 4–4.5 × 6–7 µm.

**Ecology and distribution.** *Kumanoa rwandensis* is found in acidic streams in Rwasebkoko swamp, surrounded by a vegetation of *Cyperus denudatus*, *Cyperus aterrimus* and ericaceous shrubs (*Erica rugegensis*, *Hypericum revol- tum*, *Cliffortia nitidula*, *Ankistrodesmus usambarensis*) 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 Rukara, which later becomes the Nyabarongo and Akagera and thus one of main sources of the Blue Nile. There *Kumanoa 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, Rukara 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 Hemispheric 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. novamun-densis* (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 *Nocturama* 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 mucilaginous, abundantly and irregularly branched, up 5–8 cm long. Rhizoidal cells not inflated, cylindrical, 120–130 × 100–450 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-stores, distal cells ellipsoid or obvoid, 380–410 × 77–80 µm. Secondary fascicles present, below the whorls of primary fascicles, composed of 2–8 cell-stores, not covering the whole internode.

Monoeccious. Spermatangia 4.5–6 µm in diameter, on primary fascicles. Carpogonial branches straight, composed of 11–13 cell-stores, 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 pedicillate to almost sessile, 1 per whorl, dense, spherical, 58–70 µm in diameter, carposporangia obvoid, 4.5 × 5–6 µm.

**Ecology and distribution.** *Ahidranoa madagascariensis* occurs in the Marojéy 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 mosaloensis* (see below) is growing in full sun. *Ahidranoa madagascariensis* is so far restricted to northeastern Madagascar.

**Specimens examined.** MADAGASCAR. Antsiranana, Parc National Marojéy, 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 Chantrasia stages of the genus Batrachospermum. Necchi & Zucchi (1997) support this suggestion. Also, Chen et al. (2014) could show that Audouinella heterospora is the Chantrasia 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 Chantrasia 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′29.50″E, 2338 m, E. Fischer RW 679/17 (AC 069), 8 September 2017 (KOBL); Southern Province, Rukara River at Kuyu, 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 carpogonial and the indeterminate gonimoblast filaments in the carposporephyte (Lam et al. 2012). From the eight taxa accepted by Kumano (2002), Sirodotia goebelii (Entwistle & Forord 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 suecica 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 Ambianizana, 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 mucilaginous, 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-stores, 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-stores, straight, up to 20–22 µm long, not covering the whole internode.

**Ecology and distribution.** Known only from small tributaries of the River Ambianizana 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 rcl; 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

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