

The hornworts *Dendroceros* Nees and *Megaceros* Campb. in São Tomé e Príncipe (Africa, Gulf of Guinea) with the description of *Dendroceros paivae* sp. nov.

César GARCIA^{a*}, Cecília SÉRGIO^{a,b}, Juan C. VILLARREAL^c,
Manuela SIM-SIM^{a,b} & Francisco LARA^d

^aUniversidade de Lisboa, Museu Nacional de História Natural,
Jardim Botânico/Centro de Biologia Ambiental,
Faculdade de Ciências da Universidade de Lisboa, Rua da Escola Politécnica,
58, 1250-102 Lisboa, Portugal

^bUniversidade de Lisboa, Departamento de Biologia Vegetal/Centro de Biologia
Ambiental, Faculdade de Ciências da Universidade de Lisboa,
1749-016 Lisboa, Portugal

^cUniversity of Connecticut. Department of Ecology
and Evolutionary Biology. Storrs, CT, 06269-3043, U.S.A.

^dUniversidad Autónoma de Madrid. Departamento de Biología (Botánica),
c/ Darwin 2, E-28049 Madrid, Spain

(Received 16 May 2011, accepted 29 August 2011)

Abstract – Based on herbaria specimens and especially on samples recently collected in the area, a revision of the hornwort genera *Dendroceros* and *Megaceros* in the African archipelago of São Tomé e Príncipe is presented. The four resulting species are described and illustrated, with comments on their distribution and ecology. A new species of *Dendroceros* is proposed, *D. paivae* C. Garcia, Sérgio *et* Villarreal sp. nov., which is distinguished by delicate thallus, long and slender capsules, distinct spore ornamentation and a particular epiphyllous ecology, growing closely adherent to living leaves. The new hornwort is rare and localized but abundant where found. Also the presence of *Dendroceros crispatus* Nees in Africa is confirmed. The genus *Megaceros* is reported for the first time from São Tomé e Príncipe, corresponding to the second report from Africa of *M. flagellaris* (Mitt.) Steph. A key to the Dendrocerotaceae from São Tomé e Príncipe is presented.

Anthocerotophyta / Anthocerotaceae / Hornworts / African Bryophytes / Atlantic Islands / Taxonomy / West Africa

* Correspondence and reprints: cgarcia@fc.ul.pt

INTRODUCTION

The first bryophyte collections on these islands were made by Friedrich Welwitsch in 1853 and 1860, as part of his expeditions supported by the Portuguese government to Angola (Dolezal, 1974). Since then and until 1956 several other collections were made, with a maximum of activity in the second half of the 19th Century (Sérgio & Garcia, 2011). Since 2007, new field work has been carried out in different habitats of this archipelago along an altitudinal gradient, aiming to improve our knowledge on its bryophyte flora and ecology.

The genera *Dendroceros* Nees and *Megaceros* Campb. belong to the family Dendrocerotaceae (Milde) Hässel (Stotler & Crandall-Stotler, 2005). They share some characters including: capsules without stomata, pseudoelaters with helical thickening bands and a single antheridium in each antheridial chamber (Hasegawa, 1994; Renzaglia *et al.*, 2009). The two genera are distinguished from each other by gametophyte features: the presence of a midrib and perforation of the thallus wings, and the presence of a conspicuous pyrenoid in each monoplastidic cell are characteristics of *Dendroceros* (Vaughn *et al.*, 1992). Conversely, *Megaceros* has a broad thallus and, typically, each cell contains numerous chloroplasts without pyrenoids. Other important distinguishing features are the spores: *Dendroceros* spores are multicellular and endosporic with low ornamentation, while *Megaceros* spores are tuberculate, exosporic and unicellular (Proskauer, 1953; Renzaglia, 1978).

Dendroceros is a well-defined genus within Anthocerotaceae, with *ca* 47 extremely specialised species (Duff *et al.*, 2007; Villarreal *et al.*, 2010). The epiphytes or epiphyllous habit of *Dendroceros* differs from all other Anthocerotophyta, which are mainly terrestrial (Campbell, 1898; Hasegawa, 1980; 1983; Renzaglia & Vaughn, 2000; Gradstein *et al.*, 2001; Wigginton, 2004). Endosporic germination is considered to be an adaptation to this desiccation-prone environment (Schuette & Renzaglia, 2010). Growth from a hemidiscoid apical cell and chloroplasts with spherical pyrenoids containing opaque inclusions are also specific characteristics that distinguish *Dendroceros* from all other described genera (Campbell, 1898; Crandall-Stotler, 1981; Mishler & Churchill, 1985; Vaughn *et al.*, 1992; Schuette & Renzaglia, 2010). The genus has a Pantropical distribution (Gradstein & Costa, 2003; Villarreal *et al.*, 2010).

There are few reports of *Dendroceros* and *Megaceros* from Africa, although this may be due to the paucity of bryological studies in this continent. Only few species of *Dendroceros* have been reported: *D. adglutinatus* (Hook.f. *et* Taylor) Gottsche *et al.*, is endemic from St. Helena island, *D. africanus* Steph. from Bioko, Cameroun and Tanzania; *D. borbonicus* Steph. from Mauritius, Reunion and Seychelles, and *D. crispatus* Nees from São Tomé island. However *D. crispatus* was considered doubtful by Wigginton (2004), and has been recently excluded from the African flora by Infante (2010). *Dendroceros javanicus* (Nees) Nees was reported from Tanzania (Hasegawa, 1995; Wigginton, 2009), while *D. herasii* Infante was recently described from Annobón and São Tomé (Infante, 2010). Within the genus *Megaceros* the only species known in Africa, *M. flagellaris* (Mitt.) Steph., was reported from Tanzania, (Hasegawa, 1995; Wigginton & Grolle, 1996; Wigginton, 2009). *Megaceros lacerus* (Nees) Steph., reported from the African continent is likely a synonym of *Anthoceros fuciformis* Mont. (Arnell, 1956).

The aim of the present work is to contribute new knowledge on the genera *Dendroceros* and *Megaceros* in Africa, in particular in São Tomé e

Príncipe. We describe the diversity of these genera in the archipelago and provide morphological characterization of the species. Distribution patterns and some ecological aspects in these islands are also considered for these hornworts.

METHODS

During 2007 and 2008 field work was conducted in São Tomé e Príncipe. Distribution patterns of species in the different islands, with emphasis on endemism and rare species were recorded. Field work was carried out in different forest types and altitudinal gradients. More than 300 sites were analyzed and georeferenced with a GPS (Garmin 60 CSX); elevation calibrations in known altitudes were carried out twice a day.

Twenty-four samples of *Dendroceros* and *Megaceros* were obtained from the field work and specimens of these genera from BM, PC, H, NICH, LISU, VIT and PMA herbaria were revised.

Scanning electron microscopy (SEM) observations of dry plant material were made with a JEOL (JSM 5200 LV) at FCUL (Faculty of Sciences of the University of Lisbon).

RESULTS AND DISCUSSION

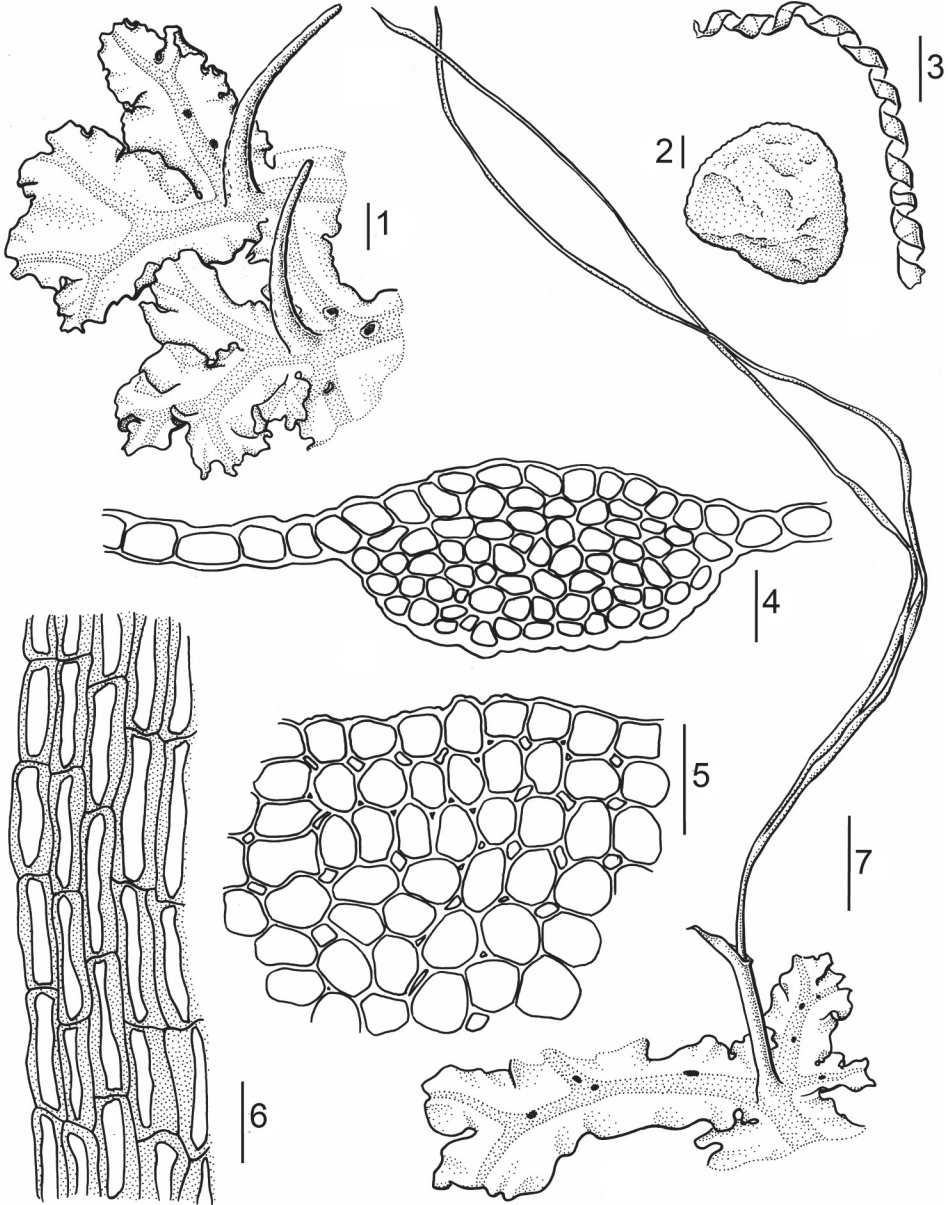
Dendroceros paivae C. Garcia, Sérgio et J.C. Villarreal sp. nov. **Figs 1-9; 26; 51-53**

Holotype: São Tomé e Príncipe. Ilha de São Tomé. Caminho para a Roça Trás-os-Montes. 32NKF3129. 1038 m. 19-07-2007. Epiphyllous on leaves of *Syzygium jambos* (L.) Alston. C. Garcia ST 125 (LISU 237201).

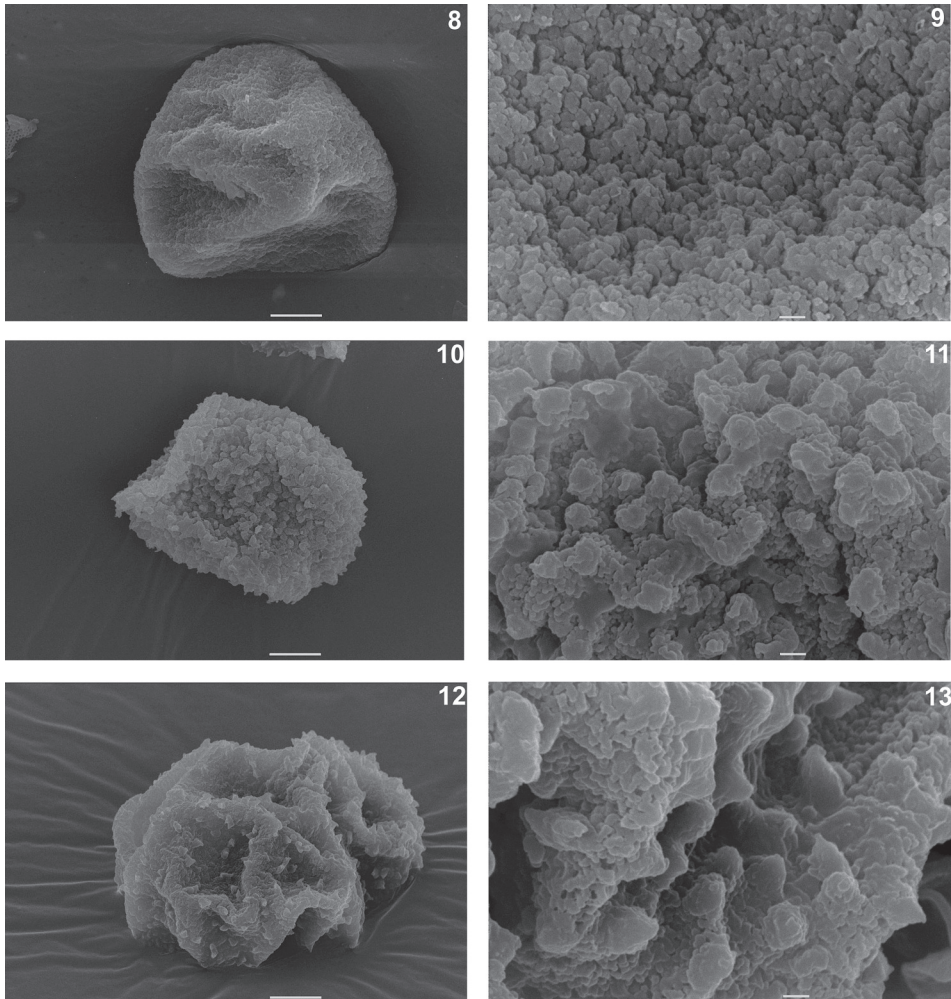
Monoica. Planta parva, dilute viridis ad atrovirens, ad arborum folia valde appressa. Thallus regulariter vel irregulariter subpinnate ramosus, 3-4 cm longus, marginibus breviter crispatis. Costa solida, 7(8) cellulis longa. Cuticula subtiliter papillosa. Capsula 3-4 cm longa gracillimaque, maturitate ad apicem bipartita, cellulis epidermalibus valde incrassatis, oblongis; stomata nulla. Sporae verrucosae, subglobosae, multicellulares, 50-63 × 45-62(65) µm, virides, pseudoelateribus in spiram tortis, non ramosis, 400-450 µm longis, 7.5-10 µm latis, papillosis.

Plants small, pale to dark green, strongly adherent to living leaves. Thalli (0.8)1.0-2.0(3.0) mm wide, (2)3-4 cm long, regularly to irregularly subpinnately branched, with divergent branches. Costa 150-270 µm wide, (7)8-10 cells long, more or less flat dorsally and convex ventrally, in cross-section cells 15-30 × 17-20 µm. Lamina unistratose, moderately crispate, undulate and sub-entire; cuticle slightly papillose; cells 17-25 × 25-35 µm at margin, 17-28 × 20-38 µm in middle part, thin-walled, with small and relatively large perforations. Rhizoids small and pale, 8-12 µm wide, present on the nerve. *Nostoc* colonies embedded in the thallus, scattered on dorsal and ventral sides of costa, especially in older parts.

Monoicous; androecia scattered on main branches; antheridia solitary, rounded-ovoid 150 µm wide. Involucre shortly squamulose (0.5)0.7-0.8 mm long. Capsules



Figs 1-7. *Dendroceros paivae* sp. nov. **1.** Thallus with two young capsules. **2.** Spore. **3.** Pseudoelater. **4.** Transverse section of costa. **5.** Epidermal cells of capsule. **6.** Superficial view of wing cells. **7.** Thallus with a long mature sporophyte (Scales: 1-100 μm ; 2-10 μm ; 3 and 6-25 μm ; 4 and 5-50 μm ; 7-0.25 cm).



Figs 8-13. SEM microphotographs of spores. **8-9.** *Dendroceros paivae* sp. nov. (LISU 237201). **10-11.** *Dendroceros crispus* (Sw.) Nees, from Panamá (JC742). **12-13.** *Dendroceros crispus* (Sw.) Nees, from Guadeloupe (BM000746118) (Scales: 8, 10 and 12-10 μm ; 9, 11 and 13-1 μm).

long and slender, 3.0-4.0(4.5) cm long, 190-230(240) μm in diameter, bivalved when mature; epidermal cells rectangular, elongate (30)40-60 \times 8-12 μm , with narrow lumens and strongly thickened walls, prorate at the tips of cells. Spores rounded globose, 50-63 \times 45-62(65) μm , green, multicellular with 10 or more cells, papillose, densely covered by verruca-like processes. Pseudoelaters pale brown, unbranched, 400-450(500) μm long, 7-10 μm wide, papillose, with a single helical band.

Etymology: The new hornwort is named in honour of Professor Jorge Paiva from University of Coimbra, as a tribute to his great dedication to nature conservation and to European and African floras, particularly the botany of São Tomé e Príncipe archipelago, that he enthusiastically studied for more than 35 years.

Dendroceros paivae is distinct from most other species of the genus in its ecology, gametophyte and sporophyte characters, resembling only the Bornean *D. foliicola* J. Haseg. (Hasegawa, 1980). In comparison to the type material of *D. foliicola*, *D. paivae* has a narrower sporophyte diameter, *c.f.*, 190-230(240) μm against ca. 320 μm in *D. foliicola*. The thallus of *D. paivae* does not form rosettes, the cuticle is weakly papillose and apices are plane to undulate, while *D. foliicola* forms rosette-like patches with strong crispate margins, even at branches apices, and the cuticle is slightly papillose.

Another comparable species is *Dendroceros crispus* (Sw.) Nees, with a similar gametophyte morphology and sporophyte length. After studying the type material (BM) and a specimen of this species from Panamá (PMA), it can be concluded that *D. crispus* clearly differs from *D. paivae* in spore ornamentation (Figs 8-13).

Distribution and ecology – *Dendroceros paivae* is abundant at the type locality on the island of São Tomé, the only locality where it has been found in spite of an intense search in other 300 sites in São Tomé e Príncipe archipelago (Figs 49-51). The new species grows on leaves of the tree *Syzygium jambos* (L.) Alston (Myrtaceae), where it develops numerous sporophytes (Figs 52-53).

***Dendroceros herasii* Infante**

Figs 14-25; 51

This taxon was recently described from Annobón (Equatorial Guinea) and São Tomé (Infante, 2010). We collected several new specimens from São Tomé that, although showing some differences with respect to the original description of *Dendroceros herasii*, correspond to this species, including ornamentation of spores as viewed by scanning electron microscopy (Figs 21-25). The main distinguishing features of the new material are the presence of yellow-green gemmae on thallus margins and longer pseudoelaters than previously reported. Gemmae are multicellular, elongate, 50-150 μm wide, and develop along thallus margins. Pseudoelaters are unbranched, (350) 400-450 μm , 10 μm wide, smooth, and contain a single helical band. Spores in our collections, are spheroid, 42.5-47.5 \times 40-50(65) μm , green, composed of 12 or more cells when mature. Spore surface ornamentation is a “broken-reticulum” covered by sparsely verruca-like processes (Figs 21-25), conferring to the spores a spiniform appearance under the light microscope.

Dendroceros herasii is unlike other *Dendroceros* species in its lamina structure with crispate or undulate, strongly gemmiferous margins.

Distribution and ecology – *Dendroceros herasii* is endemic to Annobón and São Tomé Islands (Infante, 2010). The new collections from São Tomé have been found on tree trunks at altitudes between 920 and 1260 m (Fig. 51).

Specimens examined

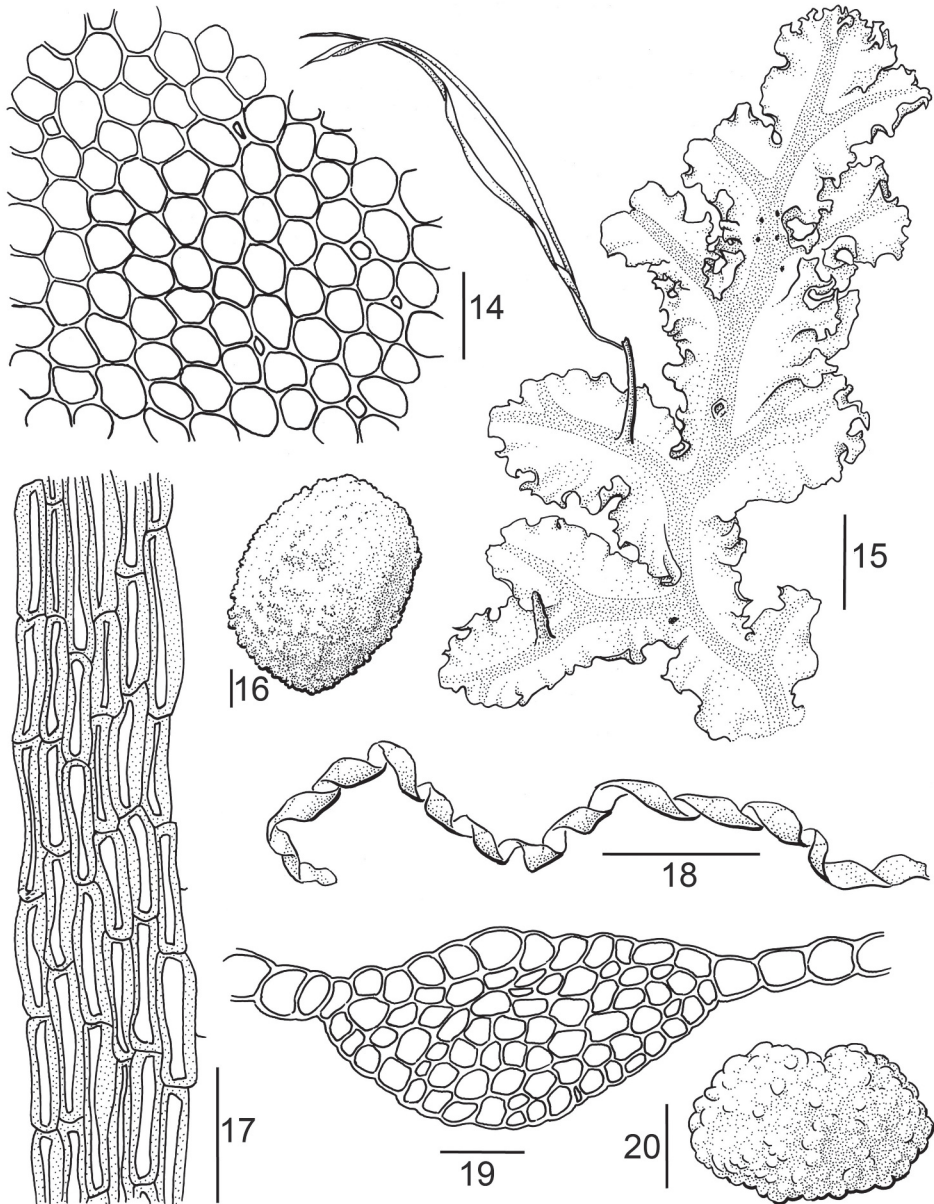
São Tomé e Príncipe. Ilha de São Tomé. Interior do Parque Obô. Caminho para a Roça Trás-os-Montes. A seguir ao cruzamento para o Pico. 32NKF3130. 1256 m. 19-07-2007. Epiphyte. *C. Garcia ST120* (LISU 237201); Caminho para a Roça Trás-os-Montes. 600 m da Roça. 32NKF3229. 916 m. 19-07-2007. Epiphyte. *C. Garcia ST130* (LISU 237203).

***Dendroceros crispatus* Nees**

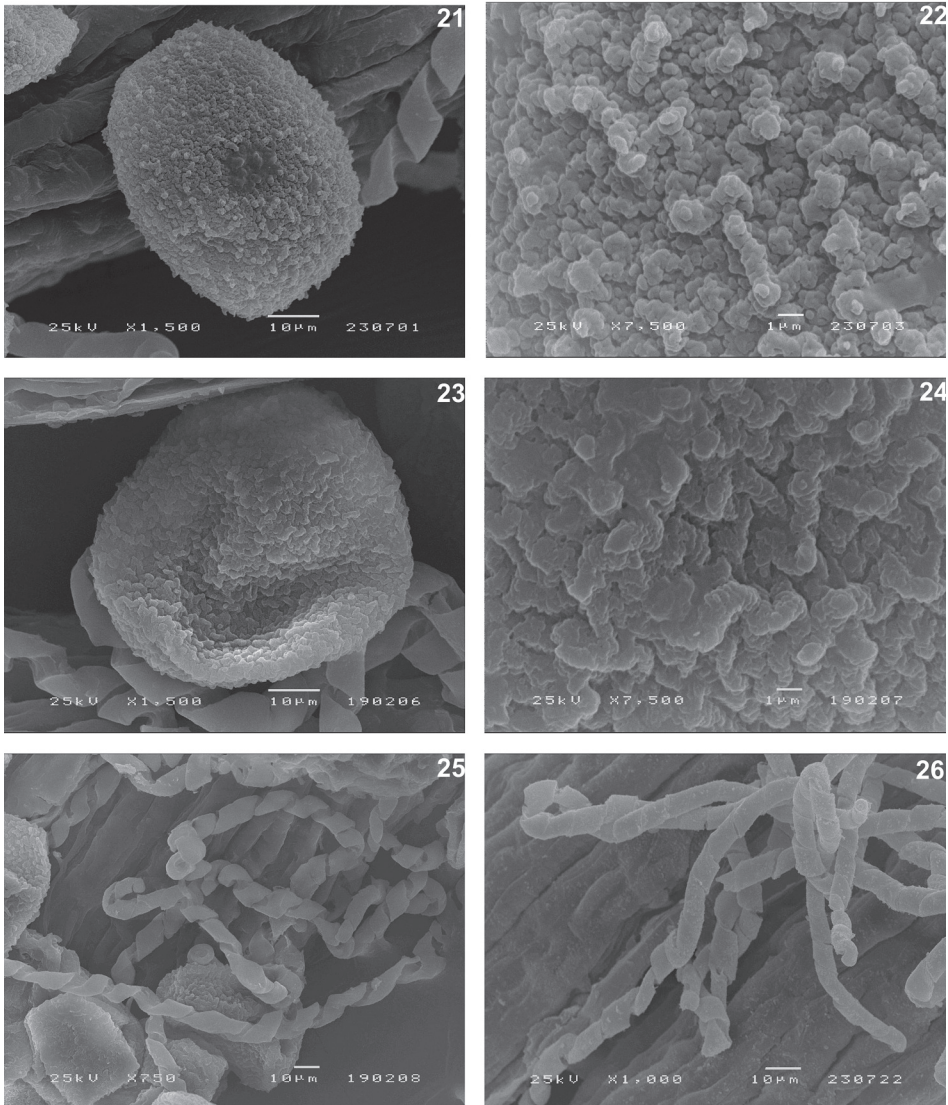
Figs 27-36; 51

≡ *Monoclea crispata* Hook., *Botanical miscellany* 1:117, 1829

Plants small, green to dark green, on tree trunks. Thalli (1.2)3-4 mm wide, (1.2)1.5-2 cm long, irregularly dichotomously branched, forming irregular mats. Costa 150-

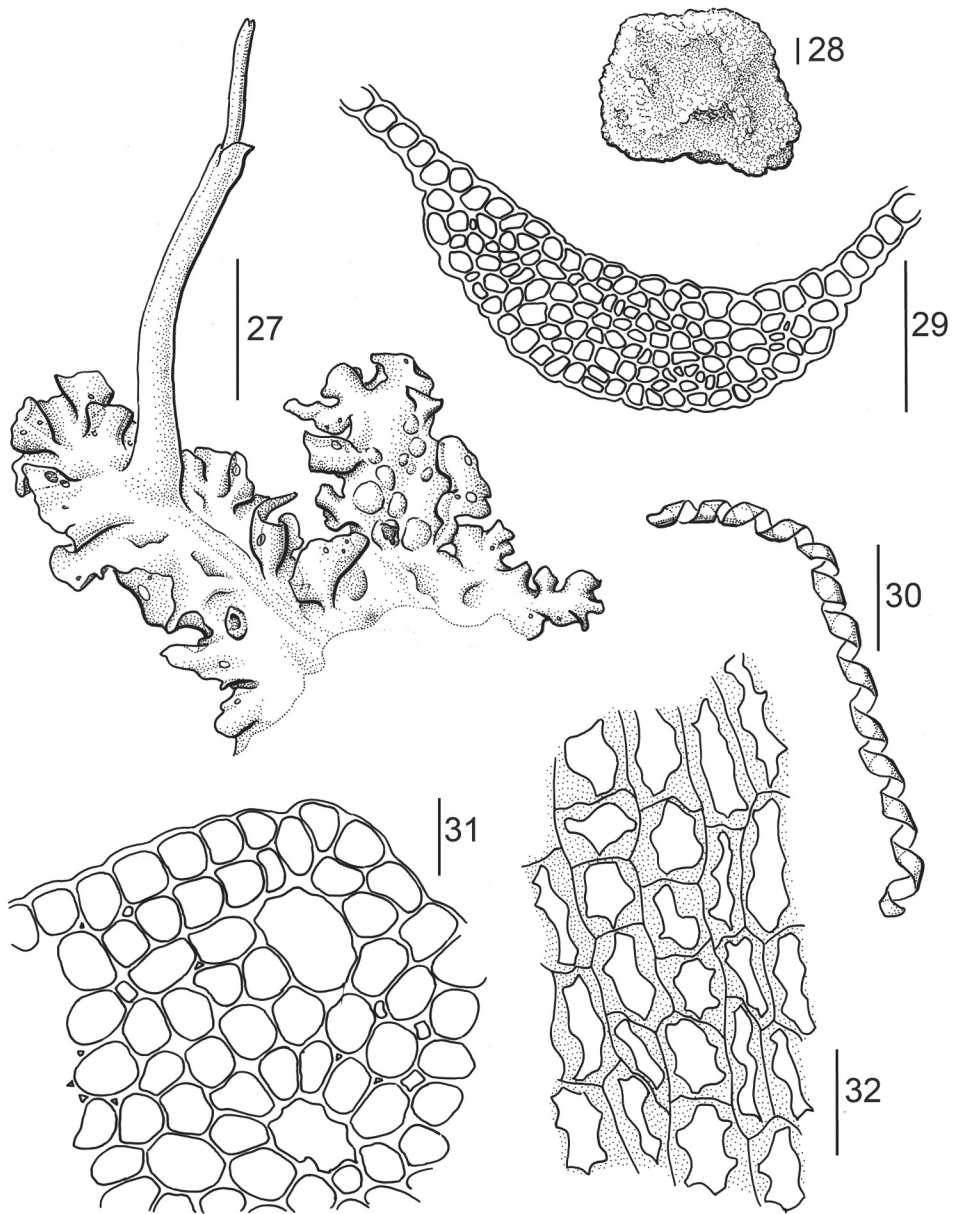


Figs 14-20. *Dendroceros herasii* Infante (LISU 237201). **14.** Superficial view of wing cells. **15.** Thallus with mature capsule. **16.** Spore. **17.** Epidermal cells of the capsule. **18.** Pseudoelater. **19.** Transverse section of costa. **20.** Gemmae (Scales: 14 and 17-50 μm ; 15-0.25 mm; 16-10 μm ; 18-100 μm ; 19-30 μm ; 20-25 μm).

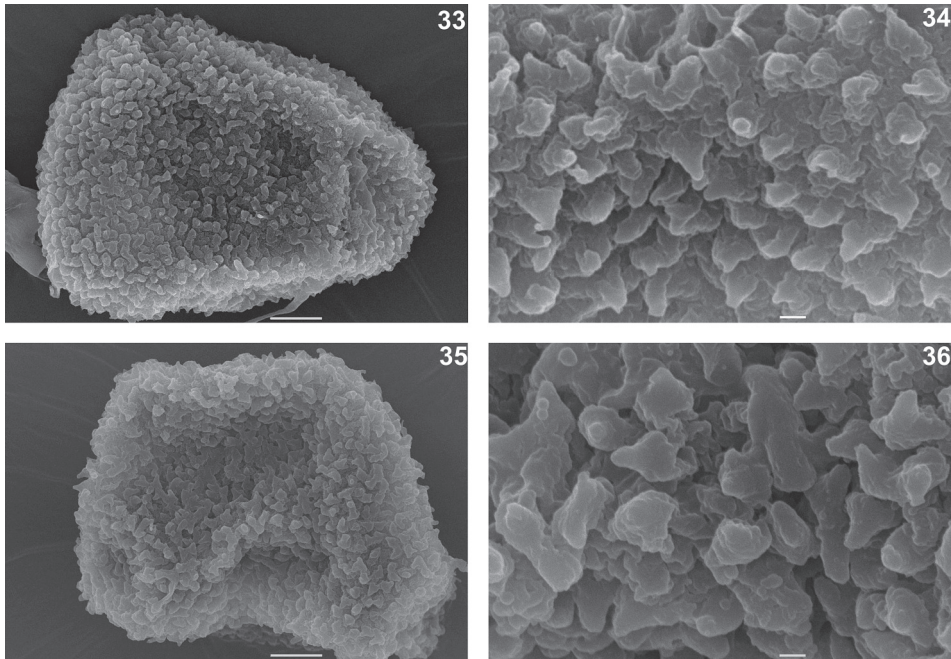


Figs 21-26. SEMs of spores and pseudoelaters: **21-24**. Spores of *Dendroceros herasii* Infante, **21-22**. from LISU 237201. **23-24**. from holotype (VIT 25366). **25**. Smooth pseudoelaters of *D. herasii* Infante -VIT 25366 (1295/00 holotype). **26**. Papillose pseudoelaters of *Dendroceros paivae* C. Garcia, Sérgio *et al.* J.C. Villarreal (LISU 237201) (Scales: 21, 23, 25 and 26-10 μm ; 22 and 24-1 μm).

300(900) μm wide, 9-10 cells high, flat dorsally and convex ventrally, in cross-section cells 17.5-30.0(35.0) \times 17.5-20.0(22.5) μm . Lamina unistratose, frequently perforated, moderately crispate or undulate with entire margins; branches and lobes strongly galeate, with large perforations 50-200 μm in diameter, more commonly in the margin; cuticle slightly papillose; cells 20.0-22.5 \times 25.0-27.5 μm at margin, 17.5-27.5 \times 20.0-37.5(40.0) μm in middle part, thin-walled. Rhizoids small



Figs 27-32. *Dendroceros crispatus* Nees (LISU 237209). **27.** Thallus with capsule. **28.** Spore. **29.** Transverse section of costa. **30.** Pseudoelater. **31.** Superficial view of wing cells. **32.** Epidermal cells of capsules (Scales: 27-0.25 mm; 28-10 μ m; 29-100 μ m; 30 and 32-50 μ m; 31-33 μ m).



Figs 33-36. SEM microphotographs of *Dendroceros crispatus* Nees. **33-34.** Spores from São Tomé e Príncipe collections (LISU 237209). **35-36.** Spores from the type material (BM000746080) (Scales: 33 and 35-10 μm ; 34 and 36-1 μm).

and scarce on the nerve. *Nostoc* colonies embedded in the thallus, scattered on dorsal and ventral sides of costa.

Monoicous; androecia scattered on main branches; antheridia solitary. Involucres (500)650-700 μm high. Capsules 1.0-1.4 cm long, 350-400 μm in diameter, bivalved when mature; epidermal cells quadrate to rectangular, to sinuose hexagonal, nodulose, 37.5-42.5(50.0) \times 17.5-25.0 μm , with narrow and stellate lumens and strongly thickened walls; cuticle on the epidermal cells irregularly papillose. Spores rounded to elongated, 50.0-60.0 \times 62.5-70.0(87.5) μm , green, with 10-15 or more cells, densely covered by verruca-like processes. Pseudoelaters unbranched, 250-300(320) μm long, 10-11 μm wide, smooth, with a single helical band.

Dendroceros crispatus was first reported from São Tomé by Mitten (1863), a record considered doubtful by Wigginton (2004) and recently attributed by Infante (2010) to *D. herasii*, excluding *D. crispatus* from the African flora. However, based on our new collections, the presence of this species in West Africa can be confirmed. After the comparison of the new specimens from São Tomé with the type material of *D. crispatus*, several significant characters in common have arisen. Specifically, the spore ornamentation revealed in scanning micrographs is concordant (Figs 33-36), as are the galeate thallus spotted with frequent macroperforations (Figs 27-32).

Dendroceros crispatus differs from *D. paivae* and *D. herasii* mainly in the epidermal cells of the capsule, that are quadrate to rectangular or sinuose hexagonal in *D. crispatus* and rectangular-elongate in the two other species. The large perforations and galeate thallus in *D. crispatus* are also distinctive features.

We further compared these two recently described *Dendroceros* with the type material of the rare *D. africanus* Steph from Cameroon, and with a specimen of *D. borbonicus* Steph from Reunion Island. These two taxa are distinct from *D. paivae* and *D. herasii* because they have nodulose thickenings in the sporophyte epidermal cells. However, the phylogenetic relationships among the taxa with nodulose epidermal cells (*D. africanus*, *D. borbonicus*, *D. crispatus* and *D. granulatus*) remain to be investigated.

Dendroceros adglutinatus (Hook. f. et Taylor) Gottsche, Lindenb. et Nees, an endemic from St. Helena, was also studied, with major differences mainly in the capsule diameter, which is more similar to *D. crispus* (Sw.) Nees (Figs 10-13). Proskauer in his unpublished notes suggested that *D. adglutinatus* may be a synonym of the widespread Neotropical *D. crispus*.

Dendroceros javanicus (Nees) Nees another African species reported from Tanzania with narrow-rectangular epidermal cells of capsules (Hasegawa, 1995), differs from *D. crispatus* in the epidermal cells of the capsule, and from *D. herasii* and *D. paivae* by a network of micro and macropores on the thallus wings.

Hasegawa in his unpublished notes on isotype material of *D. crispatus*, suggested that this species is related to *Dendroceros granulatus* Mitt., which is widely distributed in the islands of tropical Asia and the South Pacific (Hasegawa, 1984).

Distribution and ecology – *Dendroceros crispatus* is mainly known from tropical America: Panamá (Dauphin *et al.*, 2006), Peru (Menzel, 1984), Costa Rica, Guadeloupe Island (Pagán, 1942). The species is also present in Australia (Cargill *et al.*, 2005). In Africa it is restricted to São Tomé where it was discovered in four localities growing on tree trunks, mainly on *Cyathea* species, within the altitude range of 916-1942 m.

Specimens studied

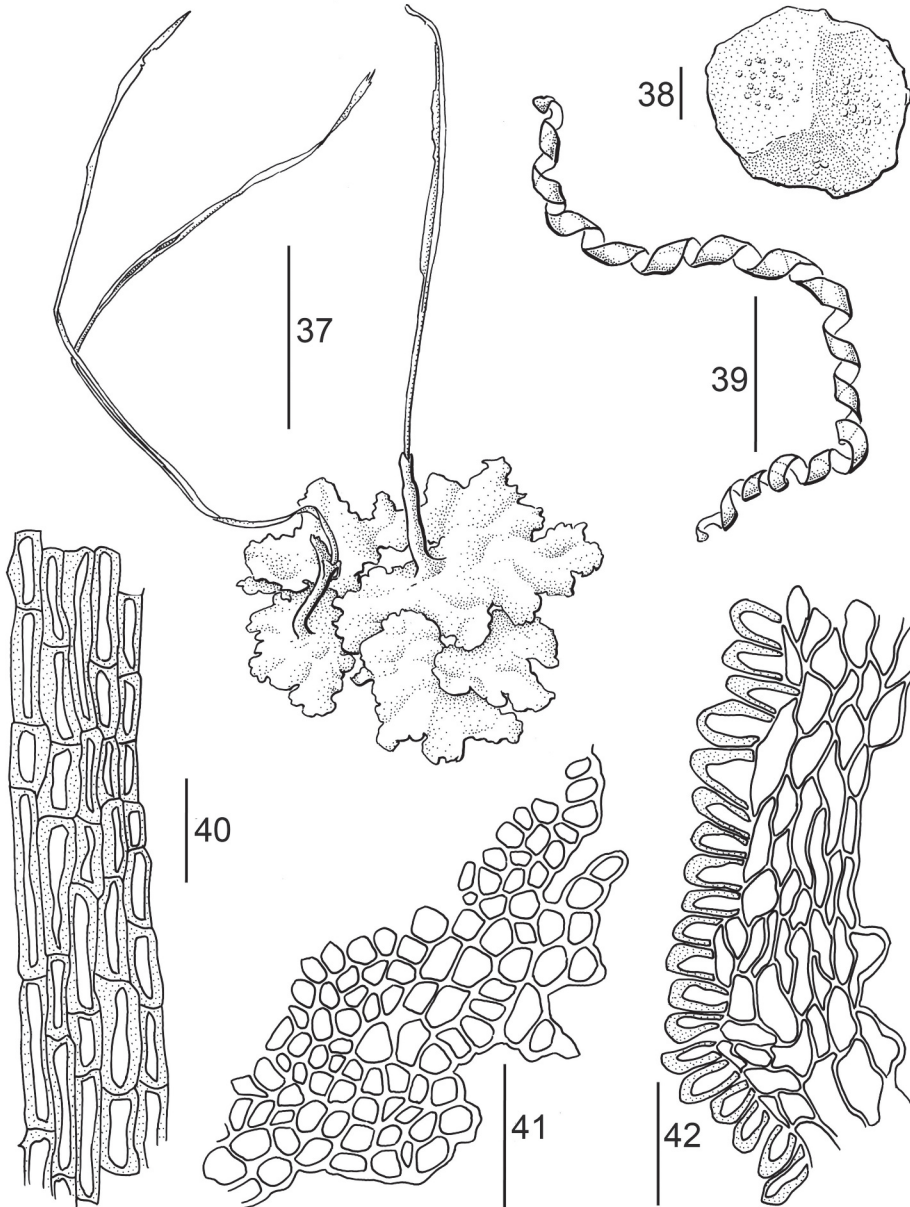
São Tomé e Príncipe. Ilha de São Tomé. Interior do Parque Obô. Caminho para o Pico, próximo do cruzamento para a Lagoa Amélia. 32NKF3230. 1409 m. 05-07-2007. Epiphyte. *C. Garcia ST42* (LISU 237209); Acampamento do Pico. Planalto. 32NKF2629. 1942 m. 05-07-2007. Epiphyte. *C. Garcia ST66* (LISU 237214); Caminho para a Roça Trás-os-Montes. A seguir ao Rio, antes de chegar à Roça. 32NKF3229. 916 m. 19-07-2007. Epiphyte. *C. Garcia ST130* (LISU 237205); Jardim Botânico do Bom Sucesso. 32NKF3431. 1164 m. 30-06-2007. Epiphyte on *Cyathea manniana* Hook. and *Cyathea welwitschii* Hook. *C. Garcia STBase* (LISU 237212).

Megaceros flagellaris (Mitt.) Steph.

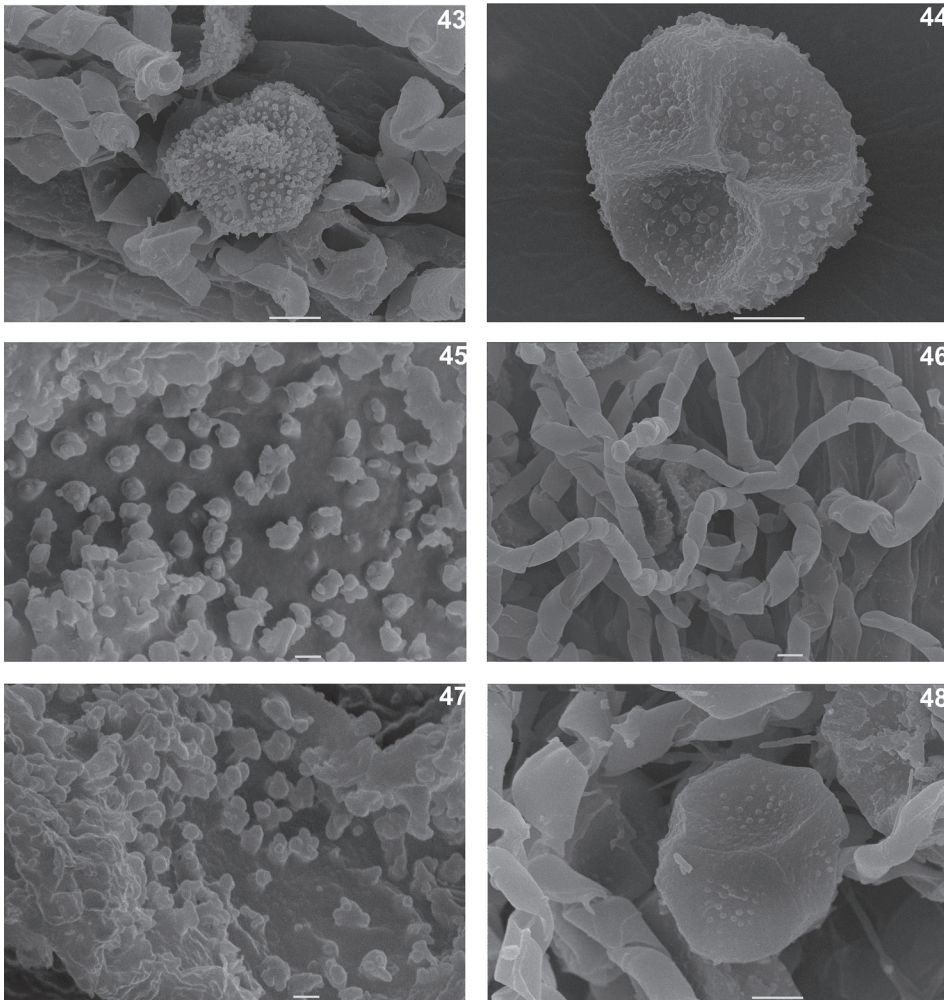
Figs 37-48; 51; 54-55

Plants large, pale green to olive green on bark of tree trunks. Thalli compact, forming colonies more than 20 cm wide, in patches divided into lobes with entire or crenulate margins. Branches in transverse section 6-12 cells thick in the middle, borders irregularly lacinate, formed by 1-4 rows of hyaline unistratose cells. Cuticle smooth, lamina cells 50-60 × 18-25(30) μm at margin, 25-35 × 15-33 μm in the middle, thin-walled. Chloroplast number 2-4 per cell, without a pyrenoid. Rhizoids in tufts scattered along the ventral surface, sometimes dendritic. *Nostoc* colonies not abundant, scattered in the interior of the thallus, on dorsal and ventral sides.

Monoicous: monandrous androecia scattered on main branches; antheridia ca. 500 × 700 μm. Involucres 0.4-0.5 mm high. Capsules erect, 2-3 cm long, 400-500 μm in diameter; epidermal cells rectangular, elongate 45-65 × 8-14 μm, with thickened slightly porose walls. Spores green, with thin exine, tetrahedral to



Figs 37-42. *Megaceros flagellaris* (Mitt.) Steph. **37.** Thallus with mature capsule. **38.** Spore in proximal view. **39.** Pseudoeleter. **40.** Epidermal cells of capsules. **41.** Cells of thallus lamina including the margin. **42.** Transverse section of capsule wall (Scales: 37-0.6 mm; 38-10 μ m; 39, 40, 41 and 42-50 μ m).



Figs 43-48. SEM micrographs of spores and pseudoelaters of *Megaceros flagellaris* (Mitt.) Steph. **43-45.** Material from São Tomé e Príncipe (LISU 237200). **46-48.** Material from Japan (NICH 193986) (Scales: 43, 44, 46 and 48-10 μm ; 45 and 47-1 μm).

irregular in shape, 23-25 \times 25-30(35) μm ; distal face with a central mamilla surrounded by abundant verrucose projections, proximal face with a faint trilete mark, each triangular face with round verrucae. Pseudoelaters unbranched, 225-250(300) μm long, 6-9(12) μm wide, slightly papillose, with a single helical band.

The diagnostic features of *Megaceros flagellaris* are spore characters: the central bump in the distal face and the tessellate pattern in the equatorial region (Villarreal *et al.*, 2010; Fig. 43), as well as the uniformly distributed verrucae on each triangular proximal face. São Tomé collections have spores similar to the “typical” spores of *M. flagellaris*, however the tessellate pattern in the equatorial region is less pronounced (Figs 43-48).

Distribution and ecology – According to Hasegawa (1983), *Megaceros flagellaris* is widespread in Asia and through the Pacific Islands, and shows a great morphological plasticity. Recent studies in Australasia and Asia conducted by C. Cargill suggest that *M. flagellaris* is widely distributed although it may be mistaken for species having similar thallus morphology such as *M. pellucidus/leptohymenius* (Villarreal *et al.*, 2010; Cargill *com. perss.*). The species is extensively distributed in tropical and subtropical Asia, China, Japan, India, Thailand, Philippines, Borneo, Indonesia, Papua New Guinea, New Caledonia, Samoa, Society Islands, Hawaii (Zhang, 2003), Vanuatu (Hasegawa, 2002), Australia (Vella & Cargill, 2003) and New Zealand (Campbell, 1984). Recently, it has been reported from Ulguro Mts in Tanzania (Hasegawa, 1995).

In São Tomé e Príncipe *Megaceros flagellaris* is rare and locally restricted, and it was found growing on a tree trunk. In the Neotropics some morphologically similar species, such as *Nothoceros vincentianus* (Lehm. *et* Lindenb.) J.C. Villarreal and *N. canaliculatus* (Pagan) J.C. Villarreal *et al.* grow on the base of palms and tree ferns (Villarreal unpub. data).

Specimens studied

São Tomé e Príncipe. Ilha de São Tomé. São Tomé. Interior do Parque Obô. Caminho para a Roça Trás-os-Montes. Depois do cruzamento que vai para o Pico, 32NKF3130, 1367 m. 02-07-2008. Epiphyte. *C. Garcia ST186* (LISU 237200).

IDENTIFICATION KEY

A dichotomous key for the known species of Dendrocerotaceae from São Tomé e Príncipe is presented:

1. Cells typically with more than two chloroplasts; thallus not differentiated into midrib and wings; spores unicellular at maturity; on moist or dripping rocks, bark, base of trees or rotten wood, mostly in rain forests *Megaceros flagellaris*
2. Cells with one large chloroplast; thallus differentiated into costa and lamina; spores multicellular at maturity; on bark or leaves **3**
3. Laminae with micro or macroporations; thallus strongly galeate; epidermal cells quadrate to rectangular (nodulose) *Dendroceros crispatus*
4. Laminae with micro or without perforations; thallus not galeate; epidermal cells variable in length, rectangular often elongate. **5**
5. Epiphytic plants; capsules 2-2.5 cm long; some thallus with gemmiferous margins, spores with a spiniform appearance; pseudoelaters smooth *Dendroceros herasii*
6. Epiphyllous plants; capsules 3-4 cm long, slender; gemmae absent; spores with verrucae-like processes densely arranged; pseudoelaters papillose *Dendroceros paivae*

CONCLUDING REMARKS

Dendroceros herasii and *D. paivae* are the most recently described species of the genus since *Dendroceros ogeramangus* was described from New Guinea (Piippo, 1993). The scattered reports of members of Dendrocerotaceae in Africa, Asia and the American continent suggest a worldwide revision of the family.

New material of *Dendroceros crispatus* from São Tomé represents the only known locality in Africa. Thus the species is not only present on the American continent, but also is the most common *Dendroceros* species on São Tomé Island (Fig. 51).

ADDITIONAL SPECIMENS EXAMINED

NICH:

Dendroceros foliicola J. Haseg. Holotype. East Borneo. 11-1953. Leg. W. Meijer B. 5018. 217811; *Megaceros flagellaris* (Mitt.) Stephani. Japan. Kyushu. Kumamoto-Ken, Ashikita-gun, Tanoura-Cho. 17-5-1985. Leg. H. Kaneda. 193986; Japan. Kyushu. Kumamoto-Ken, Ashikita-gun, Uchinoura-cho, Hetsuka, Ichino-tani. 100-200 m altitude. 22-11-1982. Leg. M. Mizutani. 189606; Japan. Kyushu. Kumamoto-Ken, Ashikita-gun, Uchinoura-cho, Gorôgamoto. On wet Boulder. 350 m altitude. 2311-1982. Leg. M. Mizutani. 189937; 473658.

LISU:

Dendroceros borbonicus Steph. Ile de la Réunion. Au sud-ouest de Saint- Benoît. Entre le Grand Etang et lar oute. Alt. Env. 400 m. dans une région deforestée en bordure d'une plantation de goyaviers, sur tronc d'Eucalyptus. 28-12-1973. Leg. J.L De Sloover 17829. LISU65238

PMA:

Dendroceros crispatus (Hook.) Nees. Panamá. Chiriqui. Leg. Juan Carlos Villareal. JC7981; *Dendroceros crispus* (Sw.) Nees. Panamá. Chiriqui. Leg. J.C. Villareal. JC742.

BM:

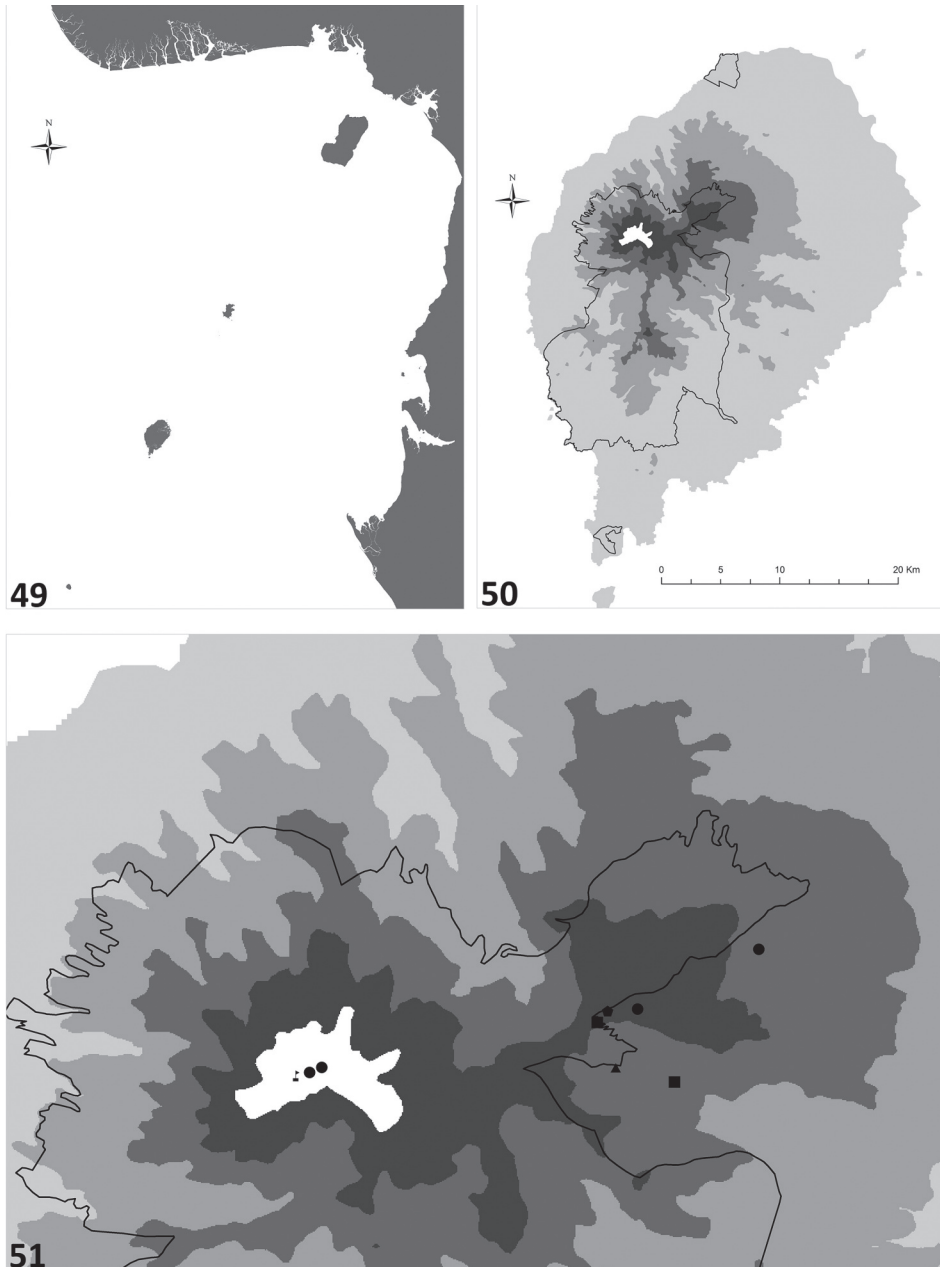
Dendroceros adglutinatus (Hook. f. et Taylor) Gottsche, Lindenb. & Nees. Santa Helena. Trunks of trees on Diana's Peak. 2100 ft. BM000746141; *Dendroceros africanus* Stephani. Isotype. Kamerum, Juli 1891; *Dendroceros crispatus* (Hook.) Nees. Type. Serra dos Orgãos. Brazil. Leg. Gardner. BM000746080; *Dendroceros brasiliensis* (Raddi) Gottsche, Lindenb. et Nees. Type. BM000746079; *Dendroceros brevicapsulus* Steph. Sandwich Islands. Kauai Island. Leg. Faurie 1910; *Dendroceros crispus* (Sw.) Nees. Guadeloupe Herb. F. Stephani. BM000746118; Type. Mts Liguanicis, Jamaica. Leg. Swartz BM000746120 (Rev. Proskauer, 1954), BM000746117; BM000746119; BM000746115; BM000746116. Other species examined: *Dendroceros cucullatus* Stephani; *Dendroceros difcillis* Stephani; *Dendroceros endiviaefolius* (Mont.) Prosk.; *Dendroceros foliatus* Spruce; *Dendroceros acutilobus* Steph.; *Dendroceros japonicus* Steph.; *Dendroceros javanicus* (Nees) Gott. et al.; *Dendroceros lacerus* Nees; *Dendroceros tubercularis* S. Hatt.; *Megaceros aenigmaticus* R.M. Schust.; *Megaceros tosanus* Stephani; *Megaceros vincentianus* (Lehm. & Lindenb.) Campb. (Type).

PC:

Dendroceros difcillis Stephani. Philippines. San António. La Laguna Luzon. M. Ramos. 1910. 12098; *Anthoceros endiviaefolius* Mont.; *Dendroceros hawaicus* St. Type. Sandwich Islands. Kauai Island. Faurie 1910. PC0102103; *Dendroceros japonicus* Steph. Japan. Kozagawa-Cho, Higashimuro-gun. Wakayama-ken. T. Kodama, 1975; *Dendroceros lacerus* Nees. Isotype. Bourbon Island. PC0102099; *Dendroceros pusillus* Stephani Isotype. New Caledonia. Pic. Pembai. PC0102101; *Dendroceros subplanus* Stephani. Vanuatu. Pentecôte Est.; *Dendroceros tahitensis* Angstr. Iles de la Société. Moorea.1975; *Dendroceros vesconianus* Gotts. Ms. Isotype. Tahiti. M. Vesco 1847. PC0102102.

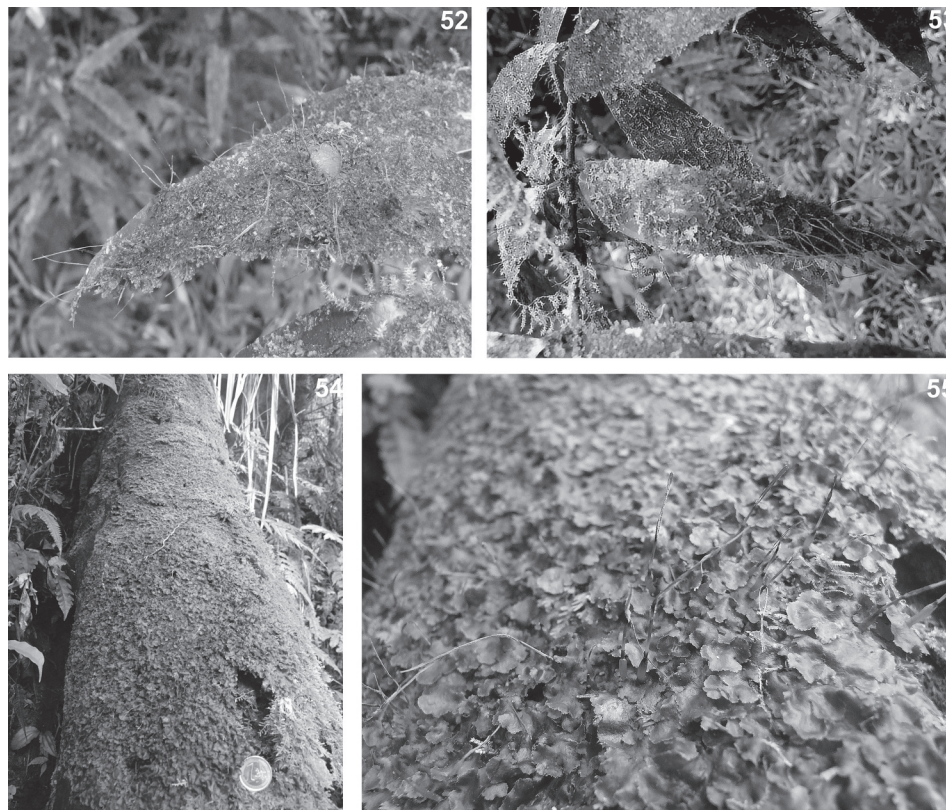
H:

Dendroceros crispatus Nees. Northern Queensland. Leg. T. Pócs 01109/A. 2001. H32201795; *Dendroceros acutilobus* Steph. Papua New Guinea. Morobe. Leg. T. Koponen. 1981. 32447. H3169986; *Dendroceros borbonicus* Steph. Ile de la Réunion. Leg. J.L de Sloover.1973. 17829. H3170013; *Dendroceros ogeramnangus* Piippo. Holotype. Papua New Guinea. Morobe. 1981. Leg. D. H. Norris. H3170022; *Dendroceros pedunculatus* Steph. Papua New



Figs 49-51. Gulf of Guinea Islands and known distribution of *Dendroceros* Nees and *Megaceros* Campb. in São Tomé. **49.** Gulf of Guinea Islands, from NE to SW: Bioko (Fernando Pó), Príncipe, São Tomé and Annobón (Ano Bom). **50.** São Tomé island with the Natural Park Óbo (black line), and altitudinal zones: 0-400 m; 401-800 m; 801-1200 m; 1201-1600 m; 1601-2024 m (white). **51.** Distribution of *Dendroceros* and *Megaceros* in São Tomé.

● *Dendroceros crispatus* ■ *Dendroceros herasii* ▲ *Dendroceros paivae* ◆ *Megaceros flagellaris*. The flag represent the Gago Coutinho or São Tomé peak (2024 m).



Figs 52-55. **52-53.** *Dendroceros paivae* sp. nov. in the type locality. (LISU 237201). **54-55.** *Megaceros flagellaris* (Mitt.) Steph. growing on a tree trunk in the first known locality in São Tomé e Príncipe and the second one reported for the African Continent (LISU 237200).

Guinea. Morobe. Leg. T. Koponen. 1981. 33546. H3170023; *Dendroceros tahitensis* Ångstr. Ile de la Société. Mooréa. Leg. J.L de Sloover. 20:967. H3170024; *Megaceros flagellaris* (Mitt.) Steph. Japan. Ryukyu. Iriomote Isl. Leg. T. Yamaguchi. 1998. H3196477; *Megaceros endiviaefolius* (Mont.) Stephani. Tierra del Fogo. Leg. H. Roivainen. 1970. Det. J. Engel. H3181148; *Megaceros gracilis* (Reichardt) Stephani. Australia. New South Wales. Leg. J.A Curnow & H. Lepp. 1981. H3181177; *Megaceros tosanus* Stephani. Japan. Near Setoguchi. Leg. H. Inoue. 1978. H3181180.

VIT:

Dendroceros herasii Infante. Holotype. Annobón, Mte Quioveo. 590 m. Leg. M. Infante & P. Heras. VIT 25366 (1295/00).

Acknowledgements. The present study was supported by FCT (Fundação para a Ciência e a Tecnologia), contract POCTI/AFR/58699/2004 and SFRH/BPD/22304/2005. We are grateful to Telmo Nunes for the assistance with the SEM studies and to the curators of the following herbaria for kindly allowing us to study *in situ* the plant material and for the loan of specimens, including types: PC, G, BM, H, VIT and NICH. We thank Laura L. Forrest for her comments on language and grammar, Vicente Mazimpaka for the revision of the Latin diagnosis and Sara Simões for the illustrations. The first author is grateful to the *sãotomenses*, Salvador Pontes, Aurélio Espírito-Santo, Estevão Soares, Francisco Álamo and Mr. Lagoas (+) for their help during the fieldwork.

REFERENCES

- ARNELL S., 1956 — Hepaticae collected by K. Byström in Fernando Pó and Annobón, West Africa, 1953. *Svensk botanisk tidskrift* 50: 527-534.
- CAMPBELL D.H., 1898 — On the Structure and Development of *Dendroceros*, Nees. *Journal of the Linnean society of London, Botany* 33:467-478.
- CAMPBELL E.O., 1984 — Notes on some Anthocerotae of New Zealand (4). *Tuatara* 27: 105-120.
- CARGILL D.C., RENZAGLIA K.S., VILLARREAL J.C. & DUFF R.J., 2005 — Generic concepts within hornworts: historical review, contemporary insights and future directions. *Australian systematic botany* 18: 7-16.
- CRANDALL-STOTLER B., 1981 — Morphology/anatomy of Hepatics and Anthocerotes. *Advances in bryology* 1: 315-398.
- DAUPHIN G., PÓCS T., VILLARREAL J.C. & SALAZAR-ALLEN N., 2006 — Nuevos Registros de Hepáticas y Anthocerotófitas para Panamá. *Tropical bryology* 27: 73-85.
- DOLEZAL H., 1974 — *Friedrich Welwitsch. Vida e obra*. Lisboa, Junta de Investigações Científicas do Ultramar. (Traduzido e anotado por A.W. Exell e E.J. Mendes). 249 p.
- DUFF R.J., CARGILL D.C., VILLARREAL J.C. & RENZAGLIA K.S., 2007 — Progress and challenges toward developing a phylogeny and classifications of hornworts. *The bryologist* 110: 214-243.
- GRADSTEIN S.R., CHURCHILL S.P. & SALAZAR-ALLEN N., 2001 — *Guide to Bryophytes of Tropical America*. New York, New York Botanical Garden Press, 577 p.
- GRADSTEIN S.R. & COSTA, D.P., 2003 — The Hepaticae and Anthocerotae of Brazil. *Memoirs of the New York botanical garden* 87: 1-318.
- HASEGAWA J., 1980 — Taxonomical studies on Asian Anthocerotae III. Some Asian species of *Dendroceros*. *Journal of the Hattori botanical laboratory* 47: 287-309.
- HASEGAWA J., 1983 — Taxonomical studies on Asian Anthocerotae III. Asian species of *Megaceros*. *Journal of the Hattori botanical laboratory* 54: 227-240.
- HASEGAWA J., 1984 — Distribution of Japanese species of Anthocerotae. *Journal Hattori botanical laboratory* 56: 21-28.
- HASEGAWA J., 1994 — New classification of Anthocerotae. *Journal of the Hattori botanical laboratory* 76: 21-34.
- HASEGAWA J., 1995 — Four tropical Asian species of Anthocerotaceae newly found in continental Africa. *Fragmenta floristica et geobotanica* 40: 113-122.
- HASEGAWA J., 2002 — Studies on the bryophyte flora of Vanuatu. 6. Anthocerotae. *Annals of the Tsukuba botanical garden* 21: 103-107.
- INFANTE M., 2010 — Notes on the genus *Dendroceros* in West Africa and South Atlantic Islands. *Journal of bryology* 32: 283-287.
- MENZEL M., 1984 — Katalog der Lebermoose von Peru. *Willdenowia* 14: 473-523.
- MISHLER B.D. & CHURCHILL S.P., 1985 — Transition to a land flora: phylogenetic relationships of the green algae and bryophytes. *Cladistics* 1: 305-28.
- MITTEN W., 1863 — On the Musci and Hepaticae from the Cameroons Mountains and from the River Niger. *Journal and proceedings of the Linnean society, Botany* 7: 147-169.
- PAGÁN F.M., 1942 — Catalogue of the hepaticae of Guadeloupe. *The bryologist* 45: 76-110.
- PIIPPO S., 1993 — Bryophyte flora of the Huon Peninsula, Papua New Guinea. LIV. Anthocerotophyta. *Acta botanica Fennica* 148: 27-51.
- PROSKAUER J., 1953 — Studies on Anthocerotales IV. *Bulletin of the Torrey botanical club* 80: 65-75.
- RENZAGLIA K.S., 1978 — A comparative morphology and developmental anatomy of the Anthocerotophyta. *Journal of the Hattori botanical laboratory* 44: 31-90.
- RENZAGLIA K.S., J.C. VILLARREAL & R.J. DUFF., 2009 — New insights into morphology, anatomy and systematics of hornworts. In: B. Goffinet & J. Shaw (eds), *Bryophyte Biology, 2nd Edition*, Cambridge, Cambridge University Press, pp. 139-171.
- RENZAGLIA K.S. & VAUGHN K.C., 2000 — Anatomy, development and classification of hornworts. In J. Shaw and B. Goffinet [eds.], *The biology of bryophytes*, Cambridge, Cambridge University Press, pp. 1-35.
- SCHUETTE S. & RENZAGLIA K.S., 2010 — Development of multicellular spores in the hornwort genus *Dendroceros* (Dendrocerotaceae, Anthocerotophyta) and the occurrence of endospory in Bryophytes. *Nova Hedwigia* 91: 301-316.
- SÉRGIO C. & GARCIA C., 2011 — Bryophyte flora of São Tomé e Príncipe Archipelago: annotated catalogue based on past researches. *Cryptogamie, Bryologie* 32(2): 145-196.
- STOTLER R.E. & CRANDALL-STOTLER B., 2005 — A revised classification of the Anthocerotophyta and a checklist of the hornworts of North America, North of Mexico. *The bryologist* 108: 16-26.

- VAUGHN K.C., LIGRONE R., OWEN H.A., HASEGAWA J., CAMPBELL E.O., RENZAGLIA K.S. & MONGENAJERA J., 1992 — The Anthocerotae Chloroplast – a Review. *New phytologist* 120: 169-190.
- VELLA N. & CARGILL D.C., 2003 — [Abstract] The hornwort genus *Megaceros*: the Australian connection *In: Celebrating 150 Years of Plant Research in Australia*. Conference Abstract Book. Melbourne, Australia, National Herbarium of Victoria, University of Melbourne. p. 74.
- VILLARREAL J.C., GOFFINET B., DUFF R.J. & CARGILL D.C., 2010 — Phylogenetic delineation of *Nothoceros* and *Megaceros* (Dendrocerotaceae). *The bryologist* 113: 106-113.
- WIGGINTON M.J. & GROLLE R., 1996 — Catalogue of the Hepaticae and Anthocerotae of sub-Saharan Africa. *Bryophytorum bibliotheca* 50: 1-267.
- WIGGINTON M.J. (ed.), 2004 — *E. W. Jones's liverwort and hornwort flora of West Africa*. Scripta Botanica Belgica 30: xii + 443 pp.
- WIGGINTON M.J., 2009 — Checklist and distribution of the liverworts and hornworts of sub-Saharan Africa, including the East African Islands (edition 3, January 2009). *Tropical bryology research reports* 8: 1-116.
- ZHANG L., 2003 — An updated and annotated inventory of Hong Kong bryophytes. *Memoirs of the Hong Kong natural history society* 26: 1-133.