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New species of *Ipomoea* (Convolvulaceae) from South America

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Abstract

The importance of discovering, describing and cataloguing poorly known species in herbarium collections is discussed. It is a spur to efforts at rediscovery and consequent conservation efforts. The problems faced in describing species from limited material are discussed and our methods and criteria in making a decision are described. Prospects for future novelties are briefly assessed. Fifteen new species are described and illustrated with line drawings and distribution maps: *Ipomoea attenuata* J.R.I. Wood & Scotland, *I. cuscoensis* J.R.I. Wood & P. Muñoz, *I. dasycarpa* J.R.I. Wood & Scotland, *I. dolichopoda* J.R.I. Wood & R. Degen, *I. ensiformis* J.R.I.Wood & Scotland, *I. fasciculata* J.R.I. Wood & Scotland, *I. graminifolia* J.R.I. Wood & Scotland, *I. kraholandica* J.R.I. Wood & Scotland, *I. longirostra* J.R.I. Wood & Scotland, *I. revoluta* J.R.I. Wood & Scotland, *I. scopulina* J.R.I. Wood &. Scotland, *I. uninervis* J.R.I. Wood & Scotland, *I. veadeirosii* J.R.I. Wood & Scotland, *I. velutinifolia* J.R.I. Wood & Scotland, *I. walteri* J.R.I. Wood & Scotland. All species are narrow endemics except *I. velutinifolia* which is found in Brazil and Peru; of the others, 12 are found in Brazil and one each in Paraguay and Peru.

Keywords

Brazil, Caatinga, Cerrado, Chapada dos Veadeiros, endemic, inselbergs, Paraguay, Peru, taxonomy

Introduction

Ipomoea is a large genus in the Americas, where it is represented by around 430 species (Wood and Scotland 2017c). It is almost entirely restricted to the tropical and subtropical regions, and our studies show that the greatest diversity lies between latitudes 15° and 30° both south and north of the equator (Wood and Scotland 2017c).

Several recent papers have highlighted the number of unidentified or wrongly identified specimens lying in the cupboards of the world's herbaria (Bebber et al. 2010; Goodwin et al. 2015). Attention has been drawn to the importance of revising these, often old, collections, which may contain significant numbers of unrecognised new species that may subsequently be rediscovered as a result of focussed field work (Cavallin et al. 2016). Only by completing this task are we likely to get significantly closer to completing the inventory of the world's flowering plants and reaching a comprehensive understanding of the conservation threats faced by the world's flora.

As part of our monographic studies of *Ipomoea* at Oxford, we regularly come across unidentified specimens in material sent for determination or examined during visits to different herbaria. The majority of these unnamed specimens are readily identified but there usually remains a residue of problematic collections. Some of these are essentially unidentifiable, usually because they are sterile or lacking important diagnostic characters. In other cases, the specimen represents an atypical form from a complex of species whose delimitation is problematic. However, it is quite common to find specimens of what appear to be undescribed new species.

In an ideal world, the researcher would set out to find living material of these putative new species. These efforts are sometimes successful, as in the case of the plant first collected by Jim Solomon in 1985, then recollected, sequenced and described as *I. lactifera* J.R.I. Wood & Scotland after rediscovery in 2014 (Wood et al 2015). More common is the first author's experience of a frustrating day trying to refind *I. gypsophila* J.R.I. Wood & Scotland in the field near Tarija, in Bolivia, after "discovering" it in the Lillo herbarium (LIL) in Tucuman, Argentina (Wood et al. 2015: 61). There are many factors which make efforts at rediscovery by a single researcher impractical if not impossible, including time, budgetary considerations, the complexities of getting collecting permits, the imprecision, inaccessibility or destruction of the original collection locality and so on. However, once a species is formally described and recognised, there exists a specific biological entity, which can constitute the target of efforts at rediscovery. The experience of the first author in different regions of the world from the Himalayas and Arabia to South America is that many long-lost species can be refound after informed and focussed search, but the knowledge that the species exists is a prerequisite for success.

It should also be stressed that unless a species is formally described it does not exist as an entity to be considered for conservation. A nameless plant cannot be catalogued or red-listed. The threats to its existence cannot be assessed. It adds nothing to the conservation value of a particular habitat, locality or protected area. In contrast, the description in this paper of four new species endemic to the Chapada dos Veadeiros National Park augments the biological importance of this national park as a centre of endemism and a priority for conservation. Similarly, the description of two new species from isolated inselbergs in eastern Brazil draws attention to the importance of this type of habitat as a reservoir of rare endemic species.

If a putative new species cannot be immediately refound, a decision has to be made as to whether or not to go ahead with a description using only the herbarium specimen(s). The decision is, of course, made easier if more than a single specimen is known, especially if the specimens come from different localities. More collections provide greater certainty in diagnosing a new taxon. However, in many cases a single collection is all there is. A decision then has to be made based on whatever evidence is available. Sometimes analysis of DNA sequences can provide support for the description of a new species, if fresh or recently collected material is available as in the case of *I. kraholandica* described below. In other cases, a decision has to be made based entirely on morphological evidence, a decision that depends ultimately on the authors' knowledge of the group and the characters that are significant in species delimitation, characters that are often not constant throughout the genus but which may be specific to a particular clade, group or subgroup. To some extent, our comprehensive monographic studies and knowledge of species-level variation gives us confidence that our description of new species based on limited material is sound. However, there is a degree of subjectivity involved and only the perspective of time can show how reliable the taxonomist's judgement was. Amongst major neotropical taxonomists working on *Ipomoea*, the data would suggest that Choisy and Meisner's decisions were unreliable, House's were better, whereas O'Donell's were usually very sound (Wood 2017). Our own judgements will no doubt be evaluated over time based on how well they have accounted for the variation found in *Ipomoea*.

This paper describes twelve new species of *Ipomoea* from Brazil, one from Brazil and Peru and one each from Paraguay and Peru, all based on herbarium specimens, mostly found in Brazilian herbaria. There is little doubt that other species will be found as the American flora, the Brazilian in particular, is explored more intensively. The Checklist of the Brazilian Flora (Forzza et al. 2010) listed 118 species, but since its publication many further species have been added (Vasconcelos et al. 2016, Wood et al. 2015, 2016, 2017d, Wood and Scotland 2017a, 2017b) so that the total had reached about 150 by the middle of 2017. Similarly, 44 species of *Ipomoea* were listed for Paraguay in the Catálogo del Cono Sur (Austin 2008) but a recent checklist has raised this number to 61 (Wood et al. 2017e). Most of these species come from the Cerrado and Caatinga biomes, the rarity of new species in Amazonia being striking (Maps 1, 2). Here we add a further fifteen species to the list of novelties, mostly from these two biomes. This is far from being the total number of Brazilian plants which cannot be assigned to a recognised species so it is likely that further new species will be described in the future although at a diminishing rate.

Materials and methods

The species described in this paper are only known to the authors from herbarium specimens deposited at ARIZ, CEN, CUZ, E, FTG, K, MG, MICH, MO, MSM, NY, RB, SPF and UB. In every case we have examined herbarium specimens to prepare the descriptions but have sometimes cited duplicates based on digital images provided by various herbaria. Specimens have been examined using a binocular microscope but limited dissection has been carried because of the state of the material. When possible, we obtained DNA sequences from a few of these new species, specifically using standard Sanger sequencing to sequence the nuclear ribosomal Internal Transcribed Spacer (*ITS*), which had proved useful in *Ipomoea* before (Miller et al. 1999; Manos et al. 2001). This has helped us to confirm the relationships of some species. All cited specimens have been seen by the authors unless indicated otherwise. Barcodes have been added where known. Most species in this paper are too poorly known for a realistic conservation assessment following IUCN guidelines (2012) but it is likely that many are Black Star species according to the system elaborated by William Hawthorne (Hawthorne and Marshall 2016), which is in many ways more satisfactory at categorizing rare, poorly-known species such as those described in this present paper.

The descriptions that follow are based on limited material and, in most cases, very sparse field notes. Information about size, habit (and habitat) often has to be inferred. Rootstock, fruit and seeds are often missing and unknown. The range of variation in dimensions may not prove completely correct once a larger number of specimens becomes available. Dissection of flowers is often problematic as the specimen may have only one or two corollas pasted to the sheet and any attempt at dissection may result in the destruction of the flower, given the fragile nature of most *Ipomoea* corollas. Fortunately, diagnostic information is rarely provided by detailed study of the stamens or style; the filaments seem always to be unequal (two long, three short) with included anthers in species with a funnel-shaped corolla; they are nearly always hairy at the base only; the ovary is usually glabrous, 2-locular with 4 ovules and the stigma obscurely 2-lobed and subglobose in form. Exceptions are rare and mostly found in the well-marked clades such as *Quamoclit*, *Batatas* and *Pharbitis*, which are not represented among the species described below.

Table 1 has been provided to show the differences between three of the new species and *I. campestris* Meisn., with which they appear to be related. This table should be treated with caution as two of the species are only known from single collections and so the range of variation is not fully known. In general, we have tried to highlight so-called “conservative” or diagnostic characters in the notes which accompany each species description. Amongst characters which we regard as diagnostic are the shape, indumentum and relative sizes of the sepals, the shape and external indumentum of the corolla, the form of a well-developed inflorescence, the indumentum of the ovary and capsule and the indumentum of the seeds. We have relied on these “conservative” characters as far as possible.

Taxonomy

Ipomoea attenuata J.R.I.Wood & Scotland, sp. nov.

urn:lsid:ipni.org:names:77166175-1
Figure 1

Diagnosis. *Ipomoea attenuata* has been generally treated in herbaria as *I. campestris* because of the similar leaves and the pubescent exterior of the corolla, but is readily distinguished by the distinctive ovate sepals, 11–14 mm long, with truncate base and long attenuate apex. Additionally, the inflorescence is of elongate complex cymes, somewhat racemose in form and with distinctive persistent linear-lanceolate bracteoles. This contrasts with *I. campestris*, which has oblong-ovate, acute sepals 8–11 mm long, clearly narrowed to the base. The inflorescence of *I. campestris* is short, usually less than 5 cm long, and consists of shortly pedunculate cymes, these often reduced to single flowers, the bracteoles caducous (Table 1).

Type. BRAZIL. Distrito Federal, Loc. Gama, BR 60, ca. 8.2 km do Tevo, DF-180 SO, disturbed campo sujo, dispersed locally, 15.5756°S 48.1059°W, 1030 m, 26 Feb. 2015, *M. Mendoza, J.B.A. Brugel, A.A. Santos, T. Reis & T.K.M. Arquelão* 4802 (holotype UB, isotypes CEN, K).

Table 1. Differences between *Ipomoea campestris*, *I. attenuata*, *I. dolichopoda* and *I. ensiformis*.

	I. campestris	*I. attenuata*	*I. dolichopoda*	*I. ensiformis*
Habit	usually erect, sometimes decumbent	decumbent or climbing	decumbent	procumbent
Indumentum	pubescent	pubescent	pilose with long spreading white hairs	thinly pubescent, glabrescent
Leaf size	4–10 × 0.1–1 cm	4–10 × 0.3–0.7 cm	4–6.5 × 0.8–1.5 cm	2–6 × 0.3–1.6 cm
Inflorescence	simple axillary cymes of 1–2 flowers	elongate, complex cymes, racemose in form	axillary cymes with long secondary peduncles	simple axillary cymes of 1(–2) flowers
Peduncles	0.2–1.5 cm, relatively stout	2–7 cm	0.3–12 cm	1.4–3.2 cm
Bracteoles	Linear, 1–2 mm, caducous	Linear-lanceolate, 4–7 mm, persistent	filiform, 9–12 mm, tardily caducous	ovate, 3 mm, tardily caducous
Pedicels	3–9 mm	3–5 mm	8–15 mm	5–6 mm
Sepal length	8–11 mm	11–14 mm	10–14 mm	6–8 mm
Sepal shape	oblong-ovate, apex acute, base rounded	ovate, apex acuminate to attenuate, base truncate	ovate, apex acuminate and mucronate, base truncate	oblong-ovate, apex obtuse, base rounded
Corolla length	3.5–6 cm	4–5 cm	c. 5.5 cm	3–4 cm
Corolla indumentum (exterior)	pubescent	pubescent	glabrous	Sparsely pubescent

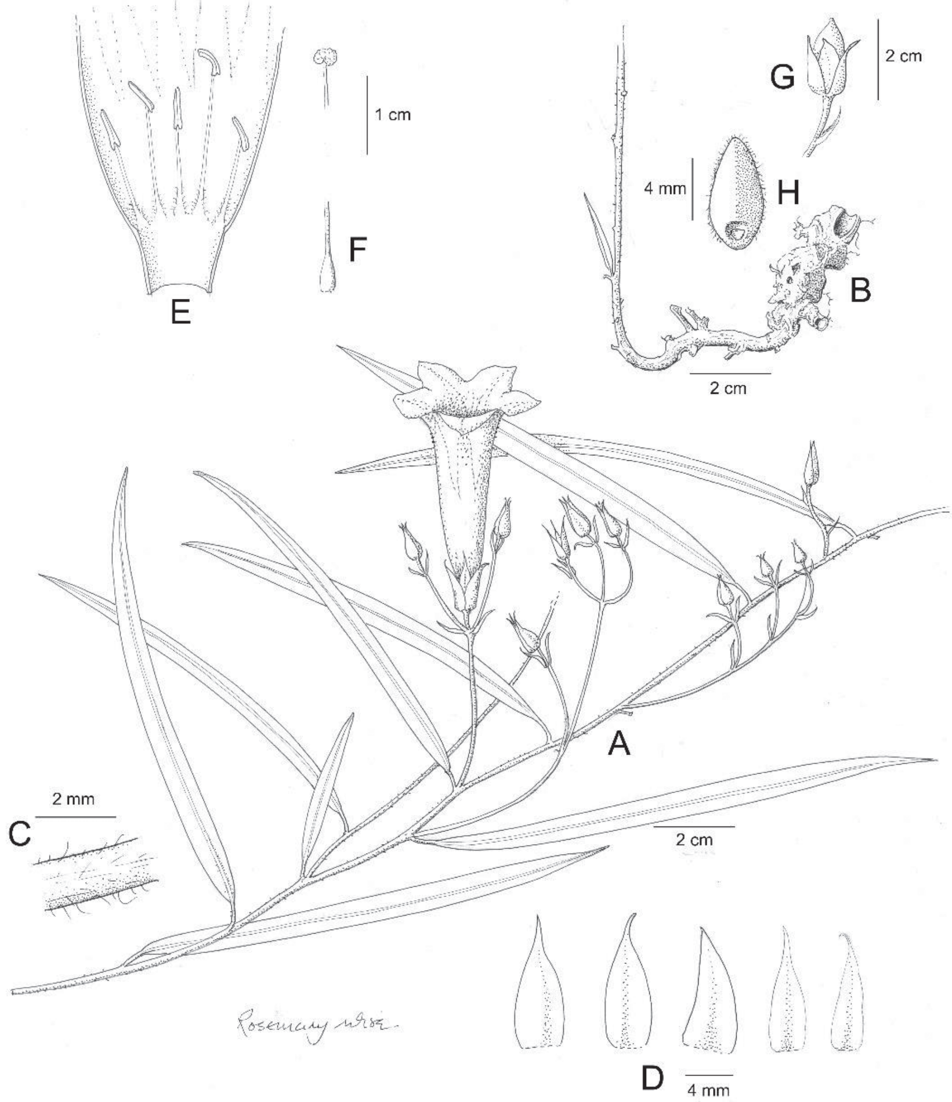

Figure 1. *Ipomoea attenuata* **A** habit **B** xylopodium **C** section of stem showing indumentum **D** sepals outermost (left) to innermost (right) **E** corolla opened out to show stamens **F** ovary and style **G** capsule **H** seed. Drawn by Rosemary Wise **A–E** from *H.S. Irwin et al.* 11019 **F–H** from *M. Mendoza et al.* 4802.

Description. Perennial herb; rootstock a woody xylopodium; stems up to 80 cm long, 2 mm diam., decumbent, weakly ascending or, fide field notes, climbing, pubescent with relatively long, often twisted, spreading and appressed hairs. Leaves shortly petiolate, 4–10 × 0.3–0.7 cm, narrowly oblong, entire, apex acute and shortly mucronate, base cuneate, both surfaces thinly pubescent but more densely so abaxi-

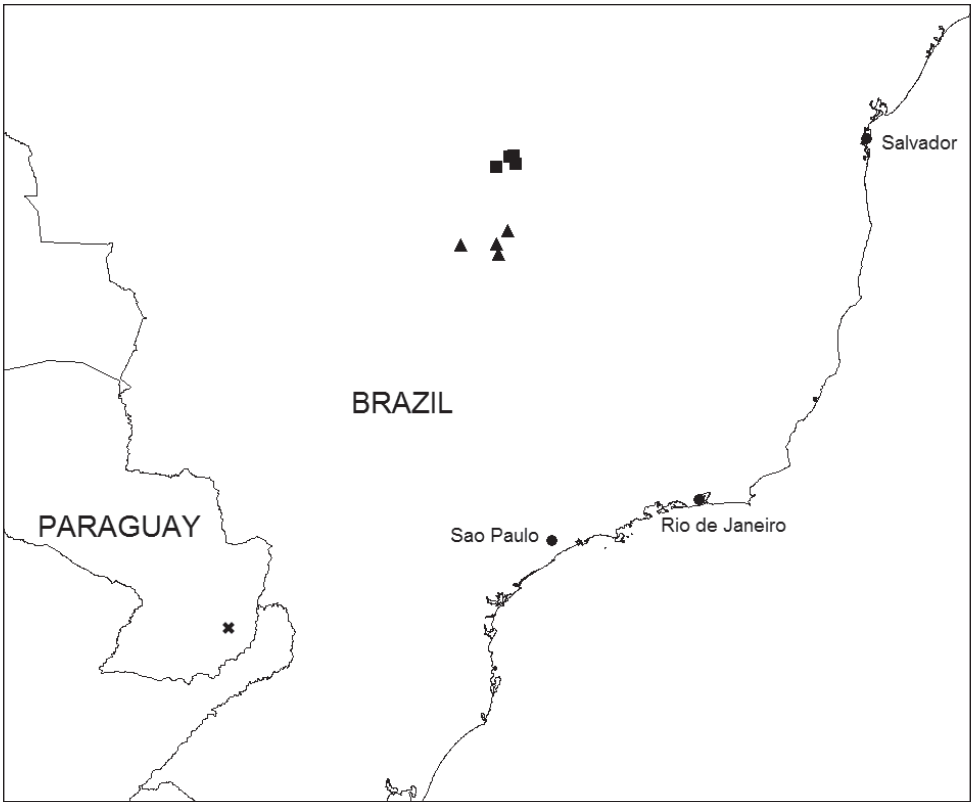

Figure 2. Map of Eastern Brazil and Paraguay showing distribution of *Ipomoea attenuata* (▲), *I. dasycarpa* (■) and *I. dolichopoda* (✖).

ally; petioles 3–7 mm long, pubescent. Inflorescence of lax, compounded axillary cymes from the middle and upper leaf axils; cymes up to 15 cm long, rather narrow, diminishing in size upwards, irregularly racemose in form; peduncle 2–7 cm long, often extending into a rhachis, pubescent; primary bracteoles foliose, 9–12 × 1–3 mm, linear, acuminate, persistent; secondary peduncles 0.5–2 cm long, thinly pubescent; ultimate bracteoles 4–7 × 0.5–1 mm, linear-lanceolate, finely acuminate to attenuate, persistent; pedicels very short, 3–5 mm long, a few scattered hairs present; calyx ovate in outline; sepals subequal, 11–14 × 4–5 mm, ovate with distinct truncate base and long-attenuated acuminate apex, glabrous, the inner sepals very slightly longer than outer; corolla funnel-shaped, pink or reddish-purple, 4–5 cm long, pubescent on the midpetaline bands, limb c. 2.5–3 cm diam., shallowly lobed; stamens glabrous except at the base, unequal, longer 1.7–1.8 cm, shorter c. 1 cm, anthers linear, c. 3 mm long; ovary bilocular, glabrous; style glabrous, stigma bilobed. Capsule 13–15 × 8 mm, ovoid, glabrous; seeds 7 × 3.5 mm, ellipsoid, blackish-brown, glabrous except for pubescence along the angles.

Distribution and habitat. BRAZIL. Endemic to the Distrito Federal and Goiás State, where it appears to be a rare species of cerrado. Figure 2.

Additional collections seen. Goiás: Samambaia, Rio Corumbá, *E.P. Heringer* 11283 (NY). Goiás: Mun. Luziania, Santo Antonio do Descoberto, *R.C. Mendonça* 93 (IBGE, NY). Goiás: Serra dos Pireneus, c. 20 km S of Corumbá de Goiás, *H.S. Irwin et al.* 11019 (NY).

Conservation status. This species has been found in four separate locations. Two of the four collections are of apparent unicates and the only collection for which any details are available is the type. The field notes of this collection describe the plant as dispersed in campo sujo. *Ipomoea attenuata* is, therefore, apparently rare but relatively widely distributed. (Fig. 2). It has an area of occupancy of approximately 16.000 km^2, thus indicating Endangered status (EN) within IUCN guidelines (2012) but should probably be treated as Data Deficient (DD) until the populations of this species can be carefully evaluated.

Etymology. The epithet "*attenuata*" refers to the attenuate tips of the sepals and bracteoles.

Notes. Although we have not been able to sequence this species, *I. attenuata* probably belongs to a large clade of around 70 species almost restricted to South America, which is characterised morphologically by the pubescent exterior of the corolla and the subequal, pubescent, ovate herbaceous sepals. However, the attenuate sepal tips raise doubts about this tentative placement as this shape is atypical of species in this clade.

The form of the inflorescence (axillary cymes) combined with the oblong leaf shape strongly suggests this is essentially a decumbent species even though this is not indicated in field notes.

Ipomoea cuscoensis J.R.I.Wood & P.Muñoz, sp. nov.

urn:lsid:ipni.org:names:77166176-1
Figures 3–4

Diagnosis. *Ipomoea cuscoensis* is a distinct species because of its glabrous indumentum, 3–5-lobed leaves, large ovate-elliptic scarious-margined sepals and striking purple corolla. It is most likely to be confused with *I. peruviana* O'Donell and *I. clavata* (G. Don) Ooststr. ex J.F. Macbr., but differs from both in the purple corolla, c. 6.5 cm long, and in having all leaves 3–5-lobed. *I. peruviana* differs additionally in its much larger (10–11 cm long), very pale blue corolla and mostly entire leaves while *I. clavata* differs in its solitary blue flowers and pilose stems.

Type. PERU. Cusco: Anta, Sisal, Limatambo, 2300 m, 15 March 1963, *C. Vargas* 14325 (holotype CUZ, isotype US).

Description. Twining perennial of unknown height; stems glabrous. Leaves petiolate, 3–6 × 3–6.5 cm, 3–5-lobed, the terminal lobe larger, lobes elliptic in outline, apex acuminate to an obtuse mucronate tip, base shallowly cordate, margin weakly crenate, both surfaces glabrous, abaxially paler with prominent whitish veins; petioles 1.3–3 cm. Inflorescence of pedunculate axillary cymes with up to 7 flowers; peduncles

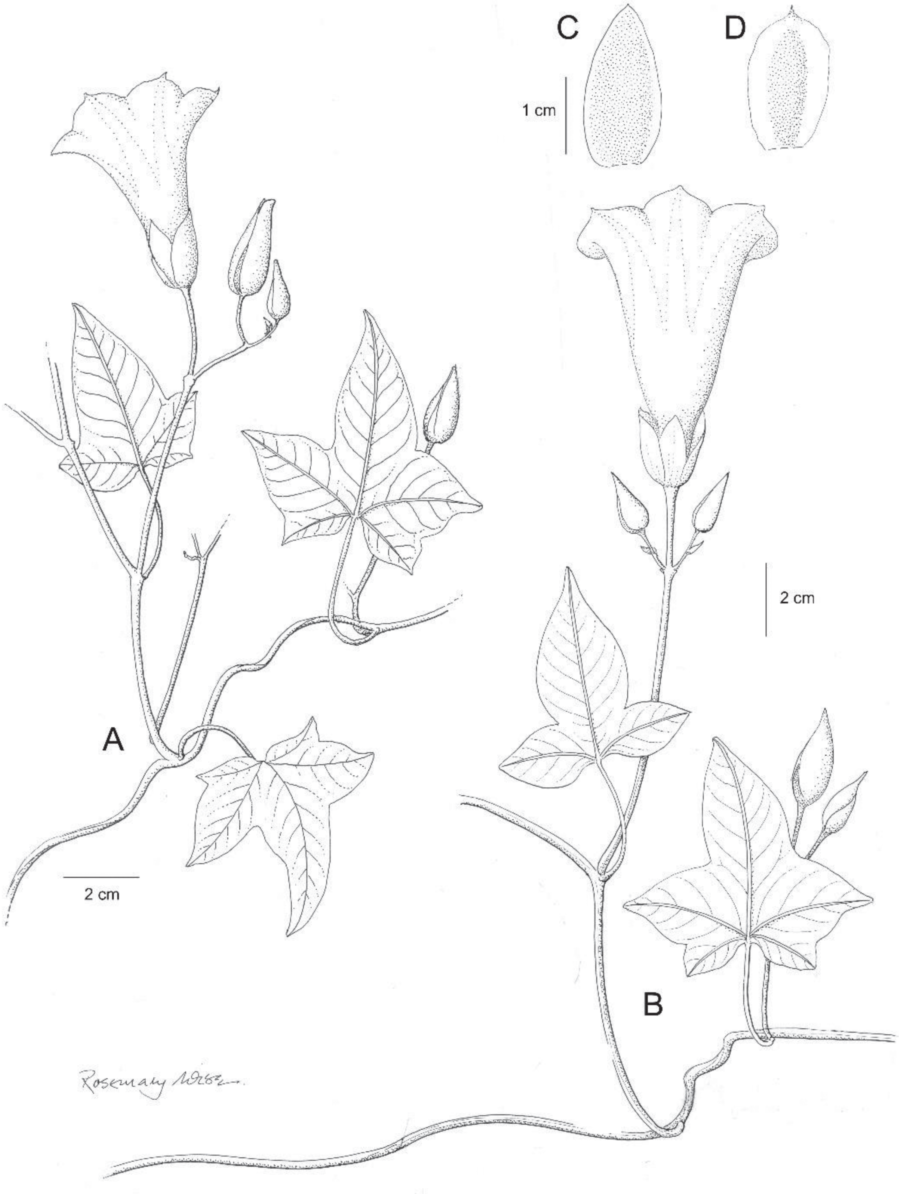

Figure 3. *Ipomoea cuscoensis*. **A** habit **B** habit; **C** outer sepal; **D** inner sepal. Drawn by Rosemary Wise from *Galiano et al.* 5146.

4–6 cm, glabrous; bracteoles caducous, not seen; pedicels 8–20 mm, glabrous; calyx narrowly ovoid, sepals somewhat unequal, outer sepals 20–22 × 10 mm, ovate to ovate-elliptic, shortly mucronate, glabrous, margins scarious; inner sepals 15 × 8 mm, ellipsoid, mucronate, the scarious margins broad; corolla 6.5 cm long, campanulate, glabrous, deep pink, limb 3–4 cm diameter. Capsule and seeds unknown.

Figure 4. Image of *Vargas* 22075 showing the distinctive purple flowers of *Ipomoea cuscoensis.*

Distribution and habitat. Endemic to dry forest and scrub at 2100–2700 m in Southern PERU. Figure 5.

Additional collections seen. Apurimac: Abancay, Cachora, 2700 m, 17 Jan 1950, *C. Vargas* 9083 (CUZ); Grau, bajando a Kai Ranka, 2400 m, 9 March 1946, *C. Vargas*

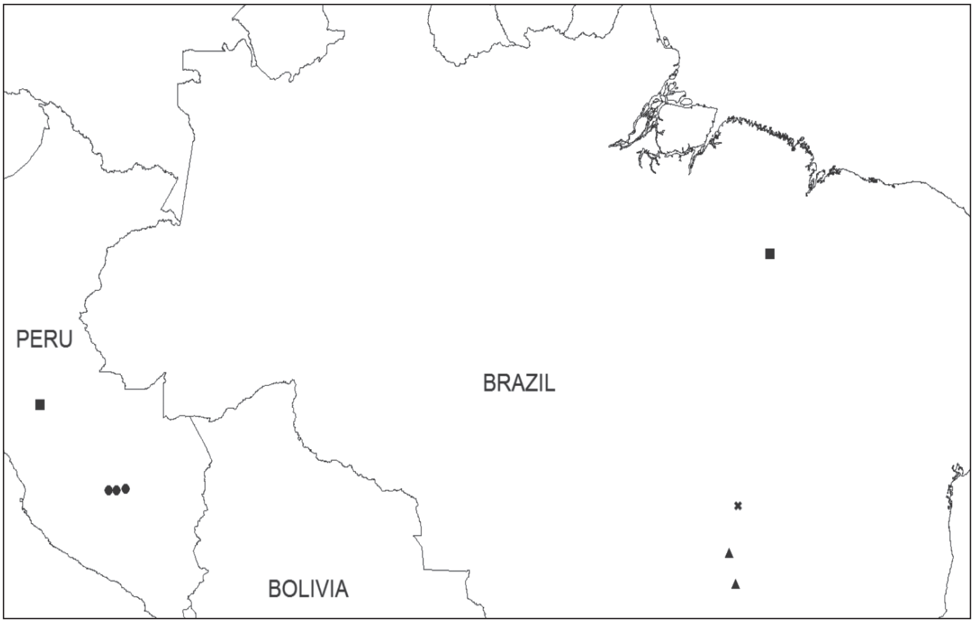

Figure 5. Map of equatorial South America showing the distribution of *Ipomoea cuscoensis* (●), *I. graminifolia* (✖), *I. uninervis* (▲) and *I. velutinifolia* (■).

5826 (CUZ). Cusco: Anta, Río Blanco, 2100 m, 22 March 1971, *C. Vargas* 22075 (CUZ); Mollepata, 2710 m, 3 May 2003, *W. Galiano et al.* 5146 (MO).

Conservation status. Although we have seen five separate collections of this species, they all come from a restricted area of Peru and the labels provide no information about the plant's frequency. It should probably be treated as a "black star" species within the classification of Hawthorne and Marshall (2016) and be classified as Endangered (EN) within IUCN (2012) guidelines because of an area of occupancy of < 12, 000 km², based on an analysis using GEOCAT. However, these classifications should be treated as provisional until a full field evaluation is carried out.

Etymology. The epithet "*cuscoensis*" refers to the Cusco region to which this species is endemic.

Notes. Phylogenetic analysis using *ITS* sequences (unpublished data) indicates that this species belongs to a small clade, which includes *I. lindenii* M Martens & Galeotti, *I. corymbosa* (L.) Roth ex Roem. & Schult. and *I. clavata*, all of which are characterised by their relatively large sepals. It has been confused with *I. peruviana* both in the herbarium and also by Wood and Scotland (2017b), partly because *I. peruviana* is poorly known and partly because images of *I. cuscoensis* have only recently become available to us after Muñoz's visit to CUZ in April 2017. These make clear the very distinctive flowers of the new species and confirm that it grows at the relatively high altitude of 2100 to 2710 m, at a much higher elevation than the lowland *I. peruviana*.

Ipomoea dasycarpa J.R.I.Wood & Scotland, sp. nov.

urn:lsid:ipni.org:names:77166177-1
Figure 6

Diagnosis. *Ipomoea dasycarpa* is close to *I. verbasciformis* (Meisn.) O'Donell but is distinguished by the larger dimensions of the leaves (2.5–11 × 1–3.5 cm, not 3–5.5 × 1–2.5 cm), bracteoles (15–20, not 5–12 mm long) and sepals (14–18 × 5–8, not 10–12 × 5 mm), by the strongly mucronate leaves, acuminate, submucronate (not obtuse) sepals and the comose (not glabrous) ovary.

Type. BRAZIL. Goiás, P.N. Chapada dos Veadeiros, ca. 1100 m, perto da sede do parque, *J.R. Pirani, R.M. Harley, B.L. Stannard, A. Furlan & C. Kameyama* 1715 (holotype SPF, isotype K000944456).

Description. Erect perennial subshrub to 1 m, rootstock unknown, presumably a xylopodium, stem densely tomentose with white hairs. Leaves very shortly petiolate, 2.5–11 × 1–3.5 cm, oblong to narrowly-oblong-elliptic, margin entire, base cuneate, apex acute, mucronate, the mucro 1.5–2 mm long, often bent, adaxially green, tomentose, abaxially whitish, tomentose, veins prominent; petioles 2–5 mm, tomentose. Inflorescence terminal formed of shortly pedunculate, 3-flowered cymes arising in the axils of the reduced uppermost leaves; peduncles 1–5.5 cm, grey-tomentose; lower bracteoles 15–20 × 4–7 mm, foliose, elliptic, acuminate to a fine point and ±mucronate, tomentose, persistent; upper bracteoles similar, but slightly smaller; pedicels 0–11 mm, tomentose; sepals subequal, outer 15–18 × 6–8 mm, ovate, acuminate, submucronate, tomentose, inner 14–15 × 5–7 mm, tomentose with broad glabrous margins; corolla 4.5–5 cm, funnel-shaped, pink, tomentose in bud, limb c. 4 cm diameter, entire. Capsule 9 × 5 mm, ovoid, muticous, comose with shaggy, somewhat deciduous hairs; seeds 6 × 3 mm, glabrous apart from the fine white marginal hairs c. 5–6 mm long.

Distribution and habitat. BRAZIL. Endemic to relatively high altitudes between 1000 and 1250 m in the Chapada dos Veadeiros in Goiás, apparently growing in rocky cerrado. Figure 2.

Additional collections seen. Goiás: Chapada dos Veadeiros, c. 20 km W of Veadeiros, *H.S. Irwin et al.* 12407 (FTG114226); 10 km S of Alto do Paraíso, *H.S. Irwin et al.* 24946a (FTG114228); 18 km N of Alto do Paraíso, *H.S. Irwin et al.* 32875 (FTG114227); Fazenda de Sao Bento, *Glaziou* 21786 (P).

Conservation status. This species has only been found on five occasions, all in the Chapada dos Veadeiros region, indicating this species is very localised in its distribution. Apparently there are duplicates of only one of these collections, suggesting the species is not common in any of the places where it has been found. Field notes are minimally informative. It should probably be treated as Data Deficient (DD) within IUCN (2012) guidelines until the populations can be carefully evaluated. All recorded locations apparently lie within the Chapada dos Veadeiros National Park, which enjoys legal protection.

Etymology. The epithet "*dasycarpa*" refers to the comose ovary and capsule.

Notes. Molecular sequencing using *ITS* (unpublished data) shows that *I. dasycarpa* belongs to a large clade of around 70 species almost restricted to South America, which is characterised morphologically by the pubescent exterior of the corolla and the

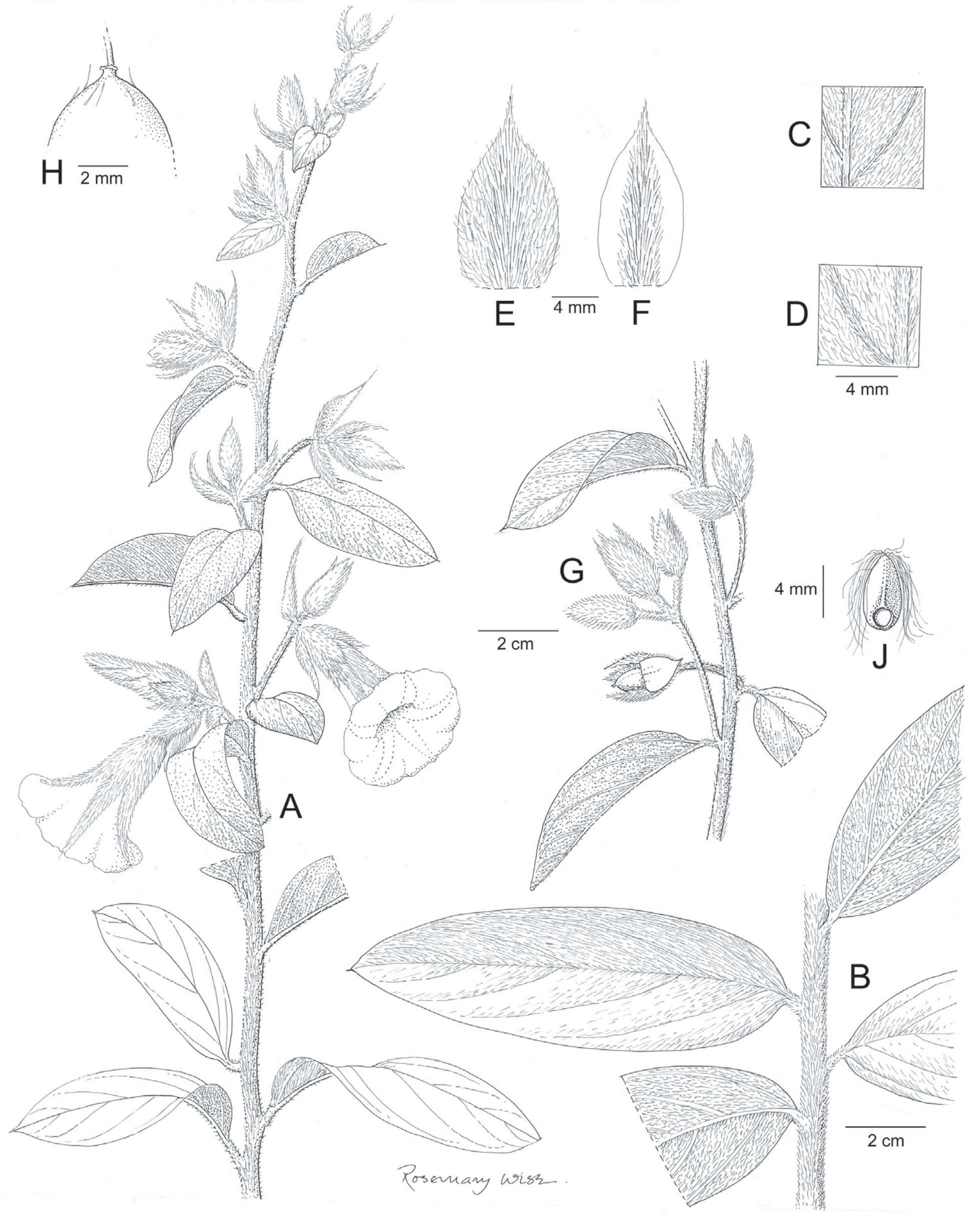

Figure 6. *Ipomoea dasycarpa.* **A** habit **B** leaves and stem **C** adaxial leaf surface **D** abaxial leaf surface **E** outer sepal **F** inner sepal **G** fruiting inflorescence with fallen bracteoles **H** apex of capsule **J** seed. Drawn by Rosemary Wise: **A–D** from *J.R. Pirani et al.* 1715, **E–F, H, J** from *H.S. Irwin et al.* 32875, **G** from *H.S. Irwin et al.* 24946.

subequal, pubescent, ovate herbaceous sepals. The comose (not glabrous) ovary is an especially interesting character as hirsute capsules are rare in *Ipomoea* and found outside the Batatas clade in only a few species such as *I. sidifolia* Schrad. and *I. velutinifolia* described below. None of these appear to be related to or resemble *I. dasycarpa*.

Ipomoea dolichopoda J.R.I.Wood & R.Degen, sp. nov.

urn:lsid:ipni.org:names:77166178-1
Figure 7

Diagnosis. *Ipomoea dolichopoda* resembles *I. attenuata* in the oblong, shortly petiolate leaves, persistent bracteoles and ovate sepals with a distinct truncate base and attenuate apex but differs in the long, stiff white hairs, 1–2 mm in length, which are scattered over all vegetative parts, the very short primary peduncles combined with very long secondary peduncles, the pilose outer sepals and the glabrous exterior of the corolla. Table 1.

Type. PARAGUAY. Caazapá, Castor Cue, 26°10'S, 55°20'W, *I. Basualdo* 002775 (holotype FCQ, isotype MO).

Description. Trailing herb, probably perennial; stems thinly pilose with white hairs. Leaves petiolate, 4–6.5 × 0.8–1.5 cm, slightly oblique, oblong, base cuneate, apex obtuse and mucronate, margins ciliate, adaxially glabrous, punctate, abaxially pilose on the veins; petioles 7–8 mm, thinly pilose. Inflorescence of pedunculate axillary cymes with 1–4 flowers borne on long secondary peduncles; primary peduncles 0.3–1.2 cm; secondary peduncles 7–12 cm, thinly pilose; bracteoles 9–12 × 1 mm, filiform, persistent till anthesis; pedicels 8–15 mm, pilose; sepals 10–14 × 3–4 mm, ovate, finely acuminate to a mucronate apex, base rounded to truncate, outer sepals pilose except at margins, inner sepals slightly shorter with glabrous, scarious margins; corolla c. 5.5 cm long, broadly funnel-shaped, glabrous even in bud, pink, limb c. 3.5 cm diam.; stamens unequal, filaments, glabrous except at base, longer pair c. 1.8 cm, shorter c. 1 cm, anthers linear, 4 mm, included; ovary presumably bilocular; stigma bi-globose. Capsule and seeds unknown.

Distribution and habitat. PARAGUAY. Only known from the type collection which was found in "praderas," presumably some kind of cerrado grassland in eastern Paraguay. Figure 2.

Conservation status. Field notes give no data about the frequency of this species and in the absence of other collections or any information about threats to its habitat, it can only be classified as Data Deficient (DD) within IUCN guidelines. It would be treated as a "black star" species within the classification of Hawthorne and Marshall (2016), but again this must be considered a provisional classification as no systematic search has been made for the species at the type locality or in other suitable habitats, although it must be presumed to be rare.

Etymology. The epithet *dolichopoda* meaning "long-stalked" refers to the exceptionally long secondary peduncles of the inflorescence.

Notes. This species has a strong superficial resemblance to *I. attenuata*, described above. Both species have somewhat similar oblong, shortly petiolate leaves and ovate sepals with a distinct truncate base and acuminate apex. The persistent bracteoles are also somewhat similar. *Ipomoea dolichopoda*, however, can be distinguished at first glance by the long white hairs which are scattered over all vegetative parts including the pedicels and sepals. It is also distinct in the very short primary peduncles combined with the very long secondary peduncles, a combination that in our experience is unique

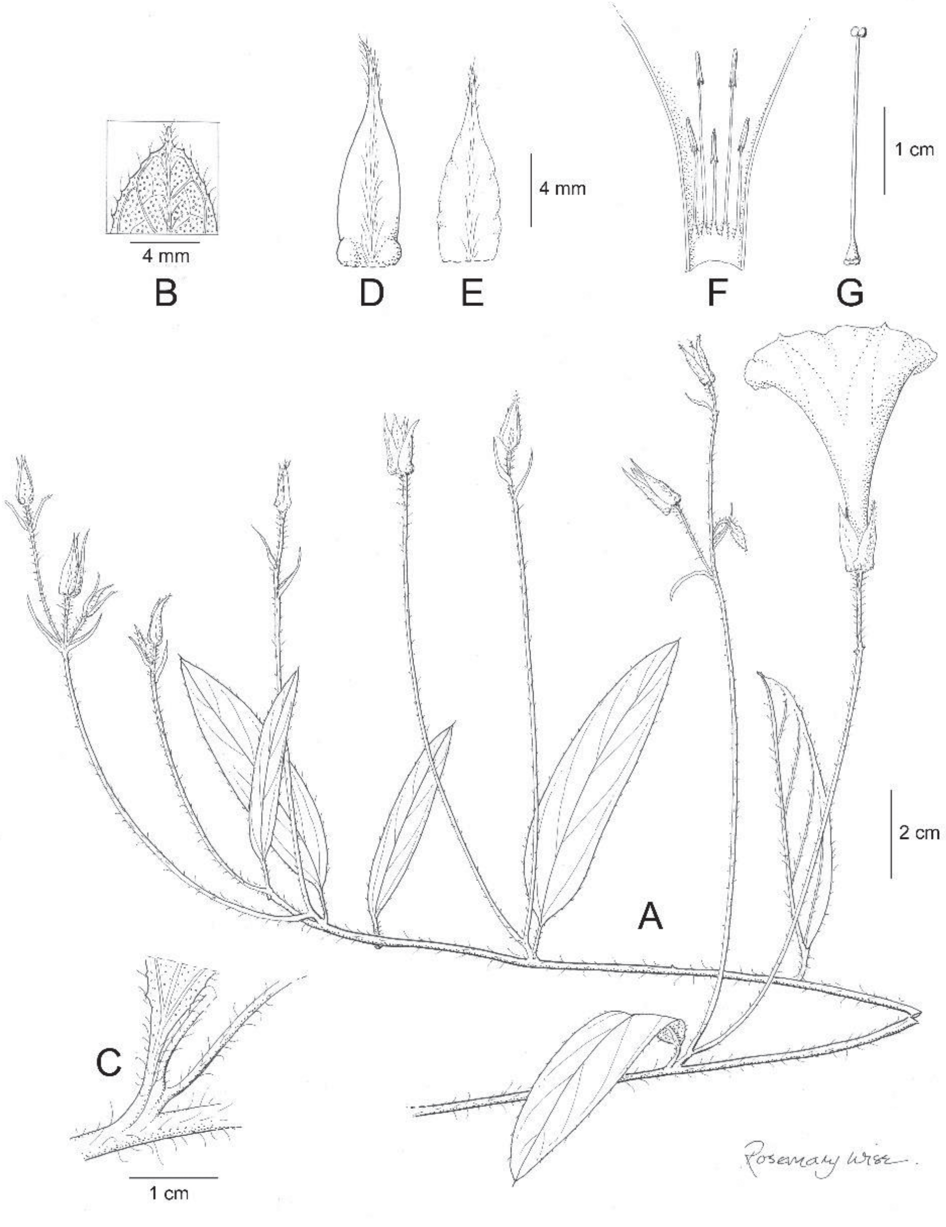

Figure 7. *Ipomoea dolichopoda*. **A** habit **B** leaf apex **C** leaf base, showing peduncle and inflorescence **D** Outer sepal **E** inner sepal **F** corolla opened out to show stamens **G** ovary and style. Drawn by Rosemary Wise from *I. Basualdo* 002775.

in *Ipomoea*. The glabrous exterior of the corolla is another distinguishing feature which raises doubts about the relationship of the two species and serves to distinguish it from *I. delphinioides* Choisy, with which it has been identified.

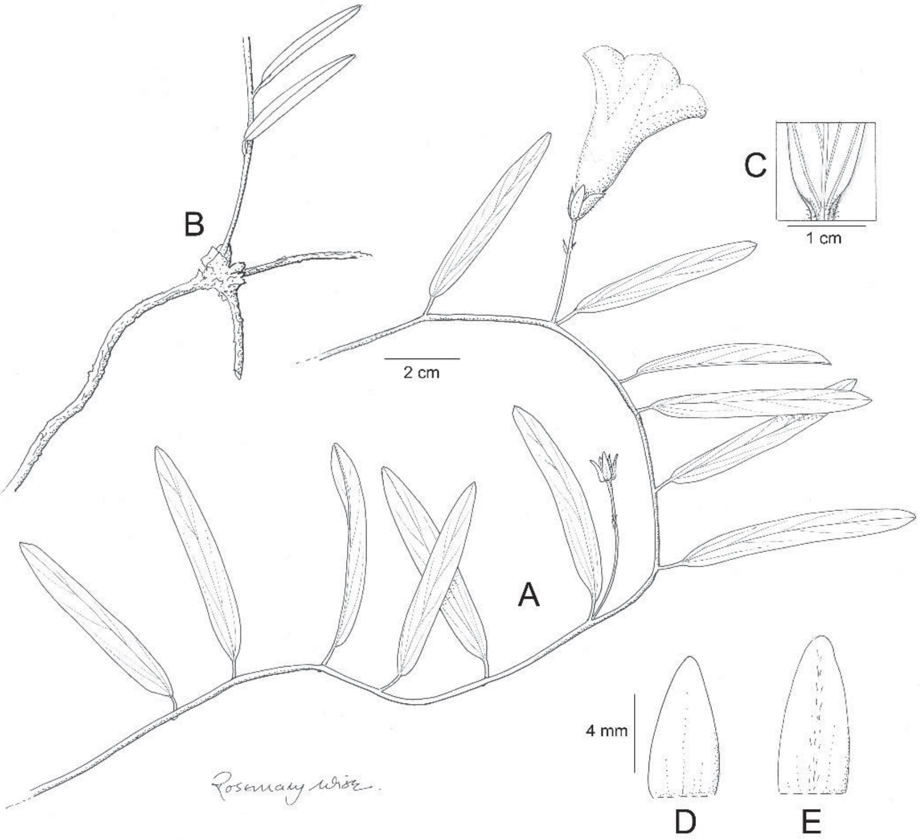

Figure 8. *Ipomoea ensiformis.* **A** habit **B** rootstock **C** base of young leaves showing indumentum **D** Outer sepal **E** inner sepal. Drawn by Rosemary Wise from *Gates & Estabrook* 4.

Ipomoea ensiformis J.R.I.Wood & Scotland, sp.nov.

urn:lsid:ipni.org:names:77166179-1
Figure 8

Diagnosis. *Ipomoea ensiformis* somewhat resembling *I. campestris* but differs in a range of characters. It is a prostrate, glabrescent (pubescent only on young parts) plant, the leaves distinctly petiolate and terminating in an obtuse apex. The sepals are glabrous, < 8 mm long and the corolla is smaller at 3–4 cm long and relatively widely funnel-shaped. In contrast, *I. campestris* is usually erect, pubescent to pilose in all vegetative parts and the leaves are subsessile, acute and mucronate. The sepals are 8–11 mm long, the exterior pubescent while the corolla is about 5.5 to 6 cm in length. Table 1.

Type. Brazil, Goias, 5 km Alto Paraiso, Chapada dos Veadeiros, 1450 m, 24 Jan 1979, *Gates & Estabrook* 4 (holotype UB62303, isotypes MICH, RB00263006).

Description. Procumbent perennial herb, stems thinly pubescent, to 50 cm; rootstock a knotted woody xylopodium. Leaves shortly petiolate, 2–6 × 0.3–1.2 cm, ob-

Figure 9. Map of Eastern Brazil showing distribution of *I. ensiformis*, *I. fasciculata*, *I. kraholandica*, *I. longirostra*, *I. revoluta*, *I. scopulina*, *I. veadeirosii*, and *I. walteri*.

long to oblong-lanceolate, base rounded, apex subacute to obtuse, very shortly mucronate, margin entire to undulate, glabrescent, the very young leaves pubescent; petioles 1–4 mm, puberulent. Inflorescence of solitary (rarely paired), axillary flowers borne on slender peduncles; peduncles 1.4–3.2 cm, slender, puberulent; bracteoles 3 × 1 mm, ovate, acuminate, relatively persistent; pedicels 5–6 mm, thinly puberulent; sepals subequal, outer 6–7 × 2.5–3 mm, oblong-ovate, obtuse, glabrous, inner similar but narrowly oblong-ovate, 7–8 mm long, abaxial surface sparsely pubescent centrally; corolla 3–4 cm, pink, very sparsely pubescent on midpetaline bands, funnel-shaped, limb 3.5 cm diameter. Capsule and seeds not seen.

Distribution and habitat. BRAZIL. Endemic to Goiás State where it is only known from the type collection. It is one of several *Ipomoea* species which are apparently restricted to the Chapada dos Veadeiros and, like *I. graminifolia*, was found at 1450 m, an exceptionally high altitude in the Brazilian planalto. Figure 9.

Conservation status. In the absence of other collections or any information about its frequency, the status of this species can only be classified as Data Deficient (DD) within IUCN (2012) guidelines. It would be treated as a "black star" species within the classification of Hawthorne and Marshall (2016), but again this must be considered as a provisional classification as no systematic search has been made for the species at the type locality or in other similar habitats in the area.

Etymology. The epithet *ensiformis* refers to the shape of the leaves, which resemble small swords.

Notes. This has the appearance of a nearly glabrous prostrate form of *Ipomoea campestris*. *I. campestris* is quite variable in leaf shape but is always readily distinguished by the longer, narrower corolla, which reaches 6 cm, and the conspicuous pubescent indumentum.

Ipomoea fasciculata J.R.I.Wood & Scotland, sp. nov.

urn:lsid:ipni.org:names:77166180-1

Figure 10

Diagnosis. *Ipomoea fasciculata* is a very distinct species with no obvious affinities, distinguished by the clustered flowers forming a subcapitate inflorescence, the small, prominently mucronate, scarious glabrous sepals and the small, rostrate capsule.

Type. BRAZIL, Pernambuco, Agrestina, Inselberg Pedra Cabeça de Velho, 8°23'29.7"S 36°00'37.6"W, 832 m, 22 Oct. 2007, *P. Gomes, M. Alves & B. Maciel* 658 (holotype RB00601358, isotype UFP, n.v.).

Description. Climbing perennial, stem minutely puberulent, glabrescent. Leaves petiolate, 2.5–5.5 × 2.4–5 cm, ovate, cordate with rounded auricles, apex acute, margin obscurely undulate, both surfaces shortly puberulent, abaxially paler; petioles 1–4.5 cm, thinly puberulent. Inflorescence of pedunculate axillary cymes reduced to pedunculate clusters or fascicles; peduncles 3.5–5.5 cm, puberulent; bracteoles 5 × 1.5 mm, lanceolate, acuminate, scarious; pedicels 1–3 mm, pubescent; sepals slightly unequal, glabrous, outer 5–6 × 3 mm, ovate, mucronate, abaxially slightly muricate, margin scarious, inner 6–8 × 4–6 mm, oblong-elliptic, rounded and mucronate, entirely scarious except central area; corolla c. 5 cm long, pink, funnel-shaped, glabrous, limb 3 cm diameter; stamens included; longer filaments 12–15 mm, shorter c. 10 mm; ovary bilocular, style c. 2.5 cm, glabrous, stigma bi-globose. Capsule (immature) ovoid, rostrate, 5 × 3 mm, glabrous; seeds not seen.

Distribution and habitat. BRAZIL. Endemic to Pernambuco State in NE Brazil and only known from the type collection. It was found growing on the Inselberg Pedra Cabeça de Velho at 832 m, presumably on granite rock. The vegetation is described in more detail by Gomes and Alves (2010), who report that, as in Bolivia (Wood 2009), plant families such as Bromeliaceae, Leguminosae and Asteraceae are common, genera such as *Croton* L. and *Chamaecrista* Moench being especially characteristic. Figure 9.

Conservation status. In the absence of other collections or any information about threats to its habitat, the status of this species can only be classified as Data Deficient (DD) within IUCN (2012) guidelines. It would be treated as a "black

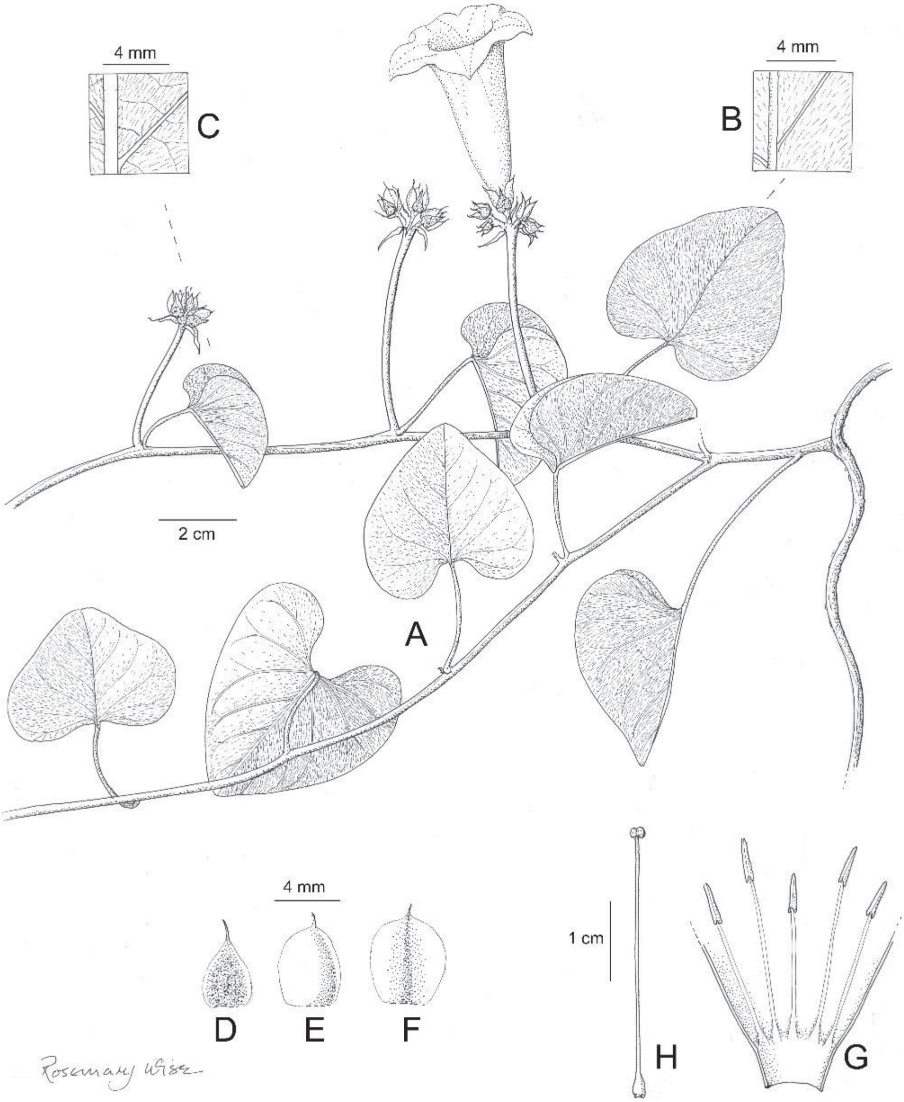

Figure 10. *Ipomoea fasciculata*. **A** habit **B** adaxial leaf surface **C** abaxial leaf surface **D** outer sepal **E** middle sepal **F** inner sepal **G** corolla opened out to show stamens **H** ovary, style and stigma. Drawn by Rosemary Wise from *P. Gomes et al.* 658.

star" species within the classification of Hawthorne and Marshall (2016), but again this must be considered a provisional classification as no systematic search has been made for the species at the type locality or in other similar habitats. Given the highly dispersed distribution of other inselberg species, it might be expected to occur in other isolated locations.

Etymology. The epithet *fasciculata* refers to the clustered or bunched inflorescence, which is a salient characteristic of this species.

Note. We have not been able to sequence this species and its relationships are not clear. It is very distinct because of the subcapitate inflorescence, the small, prominently mucronate, scarious glabrous sepals and the small, rostrate capsule.

Within the context of this paper this species is unique not only for the form of its inflorescence but also for having been found on a dome mountain within the Caatinga biome. Similar granite or crystalline domes are fairly common in parts of eastern Brazil but are less common in the Cerrado biome, although they are found in Mato Grosso and parts of Eastern Bolivia. Several species of *Ipomoea* have been described from these domes, notably *I. graniticola* J.R.I. Wood & Scotland and *I. chiquitensis* J.R.I. Wood & Scotland from Bolivia (Wood et al 2015), both of which were thought originally to have been pin-point endemics, but the former has been subsequently found in similar habitats in both Paraguay and Brazil, while the latter has been found in NE Brazil. It is to be hoped that *I. fasciculata* will be found on other inselbergs, perhaps at a considerable distance from the type locality.

Ipomoea graminifolia J.R.I.Wood & Scotland, sp. nov.

urn:lsid:ipni.org:names:77166181-1
Figure 11

Diagnosis. *Ipomoea graminifolia* resembles and is probably related to *I. procumbens* Mart. ex Choisy and *I. aequiloba* J.R.I. Wood & Scotland, being completely glabrous and having solitary flowers and subequal, lanceolate to ovate sepals. From *I. procumbens* it is distinguished by the much smaller calyx (the inner sepals oblong-lanceolate, only 7–9 × 2 mm , not 12–15 × 4–6 mm) and corolla (< 3.5 cm long, not >5.5cm long), the wiry stems, and the sessile, filiform leaves. In these dimensions and habit it is closer to *I. aequiloba* but is immediately distinguished by the simple, nor subequally 3-lobed leaves.

Type. BRAZIL. Goiás, Fazenda Agua Fria, Alto Paraiso de Goiás, cerca 10 km en direção a Teresina de Goiás, 14°04'217"S, 47°30'336" W, 1448 m, 20 Feb. 2001, *C. Munhoz, N. Rodrigues & K.M.O. Ramos* 2567 (holotype MO-5948847, isotypes not found).

Description. Completely glabrous, slender, probably clambering perennial herb, stems thin, wiry, slightly woody. Leaves sessile, 2.5–5.5 × 0.05–0.1 cm. linear-filiform, acute, minutely apiculate. Inflorescence of solitary axillary flowers; peduncles 8–18 mm; bracteoles deltoid, 1 mm long, caducous; pedicels 6–8 mm, thickened upwards; sepals unequal, outer 5–6 × 2 mm, broadly lanceolate, acute and mucronate, margin narrow, scarious; inner 7–9 × 2 mm, oblong-lanceolate, acute, margins broad, scarious; corolla 3–3.5 cm long, funnel-shaped, pink, glabrous, limb 2.5–3 cm diameter, undulate, the midpetaline bands ending in acute points; stamens included; style very short, c. 1.2 cm, stigma bi-globose. Capsule and seeds unknown.

Habitat and Distribution. BRAZIL. High altitude endemic of campo limpo úmido, only known from the type collection in Goiás, where it was collected in or near

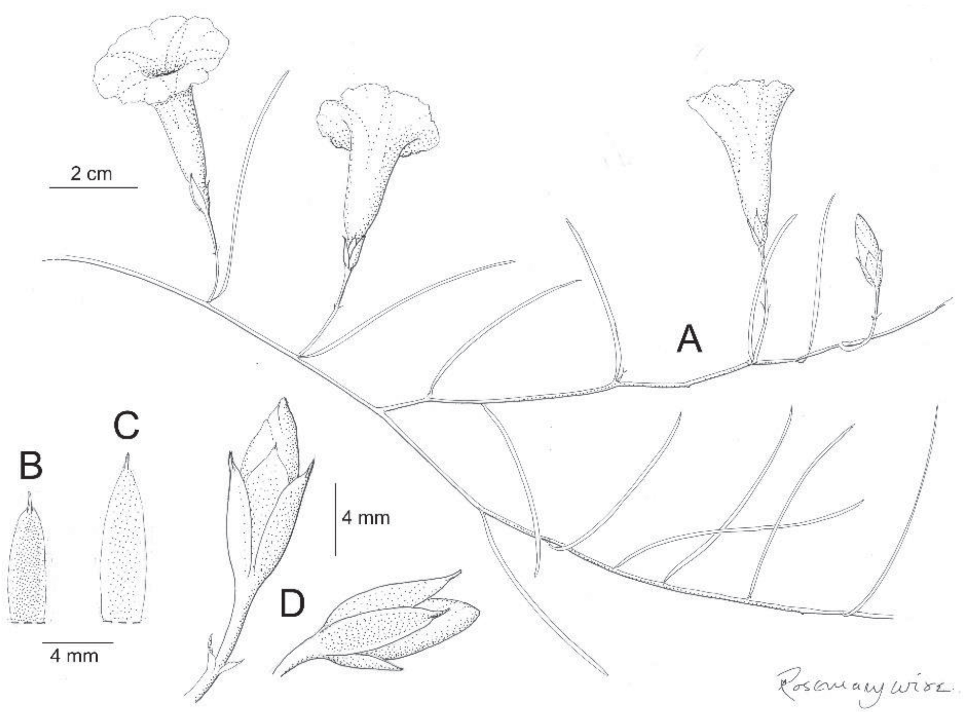

Figure 11. *Ipomoea graminifolia.* **A** habit **B** outer sepal **C** inner sepal **D** buds showing calyx. Drawn by Rosemary Wise from *C. Munhoz et al.* 2567.

the Chapada dos Veadeiros National Park. The recorded altitude of 1400 m is unusually high for an *Ipomoea* species in Brazil. Figure 5.

Etymology. The epithet *graminifolia* refers to the characteristic grass-like leaves of this species.

Conservation status. In the absence of other collections or any information about threats to its habitat, the status of this species can only be classified as Data Deficient (DD) within IUCN guidelines. It would be treated as a "black star" species within the classification of Hawthorne and Marshall (2016), but again this must be considered as a provisional classification as no systematic search has been made for the species at the type locality or in other suitable habitats, although it must be presumed to be rare.

Ipomoea kraholandica J.R.I.Wood & Scotland, sp. nov.

urn:lsid:ipni.org:names:77166182-1
Figure 12

Diagnosis. *Ipomoea kraholandica* is a very distinct species unlike any other known to us because of the solitary flowers with suppressed peduncles, the narrowly lanceolate, pubescent sepals and the apparently unique lamina, which is essentially 3-lobed, the middle lobe

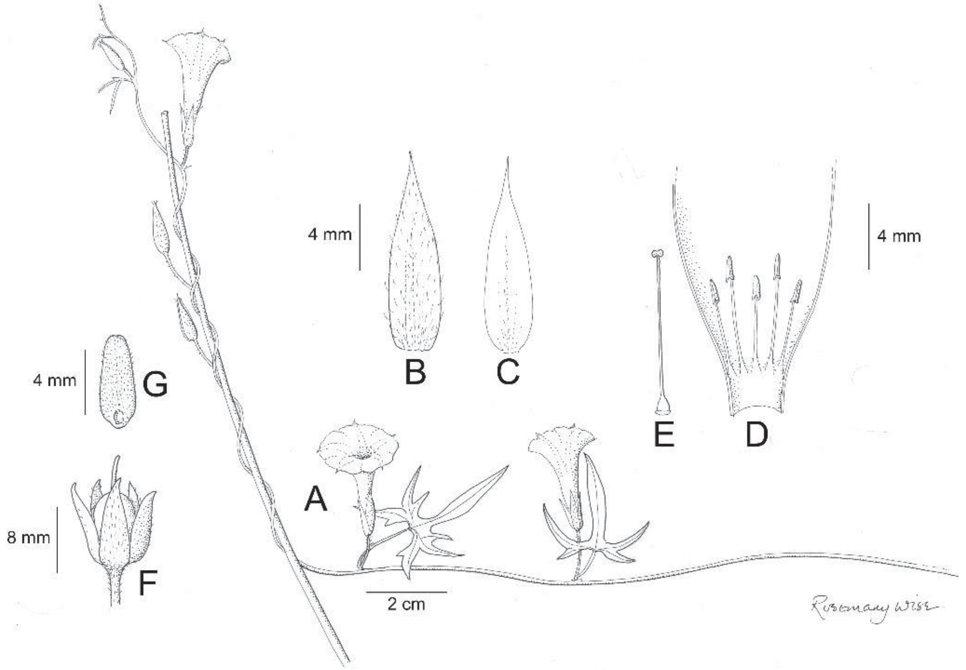

Figure 12. *Ipomoea kraholandica*. **A** habit **B** outer sepal **C** inner sepal **D** corolla opened out to show stamens **E** ovary and style **F** capsule and calyx **G** seed. Drawn by Rosemary Wise from *A.A. Santos et al* 719.

lanceolate to oblong-lanceolate, the two laterals bifurcate or trifurcate with the lower lobe curved backwards whereas the upper and middle lobes (when present) are bent forward.

Type. BRAZIL. Tocantins, Mun. Itacajá, Reserva Indígena Krahó, Aldea Pedra Branca, 9 May 2000, *A.A. Santos, A. Reatto, E. de Souza Martins, L. Rovênia, M. de Andrade & L. Moreira Rodrigues* 719 (holotype CEN).

Description. Slender twining herb of unknown height; stems glabrous. Leaves petiolate, 2–3.5 × 1–3 cm, 3-lobed with the central lobe lanceolate, entire, the lateral lobes 2–3-lobed, the first and second lobes bent forwards and the third lobe bent backwards, base truncate, apex finely acuminate, both surfaces glabrous; petioles 0.7–2 cm. Inflorescence of solitary, axillary flowers; peduncles very short, 0–3 mm, thinly pubescent; bracteoles 1–3 mm, relatively persistent, thinly ciliate; pedicels 6–12 mm, thickened upwards, pubescent; sepals subequal, 11–12 × 1.5–2.5 mm, narrowly lanceolate, finely acuminate, mucronate, outer pubescent, inner pubescent with broad glabrous margins; corolla c. 2.5 cm long, funnel-shaped, pink, glabrous, midpetaline bands terminating in a prominent tooth, limb c. 2.5 cm diameter; filaments glabrous except for glandular-pilose base, longer pair 7–8 mm, shorter 4–5 mm; ovary bilocular, glabrous; style 8 mm, glabrous; stigma bi-globose. Capsule 10 × 5 mm, ovoid, glabrous; seeds 4, 5 × 2 mm, dark grey, minutely tomentellous.

Distribution. BRAZIL. Only known from the type locality in Tocantins. Locally abundant in disturbed ground on sand. Figure 9.

Conservation status. Field notes record this plant as “locally abundant” but in the absence of other collections or any information about threats to its habitat, it can only be classified as Data Deficient (DD) within IUCN (2012) guidelines. It would be treated as a “black star” species within the classification of Hawthorne and Marshall (2016), but again this must be considered a provisional classification as no systematic search has been made for the species at the type locality or in other suitable habitats, although it must be presumed to be rare.

Etymology. The epithet *kraholandica* refers to Reserva Indígena Krahó, where this species was found.

Note. Molecular studies using *ITS* (unpublished data) place this species in a well-supported clade of mainly Brazilian species with *I. bahiensis* Willd. ex Roem. & Schult., *I. squamosa* Choisy, *I. eriocalyx* (Choisy) Meisn. and *I. acanthocarpa* (Choisy) Aschers. & Schweinf., and more distantly with *I. imperati* (Vahl) Griseb. and *I. longeramosa* Choisy. It does not, however, resemble any of these species except perhaps *I. longeramosa*, which differs in its cream-coloured flowers, longer peduncles 2–5 cm in length and quite different leaf shape. The leaf shape of *I. kraholandica* is especially unusual. The lamina is essentially 3-lobed, the middle lobe lanceolate to oblong-lanceolate, the two laterals bifurcate or trifurcate, the lower lobe curved backwards whereas the upper and middle (when present) lobes are bent forward (Figure 12). The seeds are shortly hirsute, best described as tomentellous.

Ipomoea longirostra J.R.I.Wood & Scotland sp. nov.

urn:lsid:ipni.org:names:77166183-1
Figure 13

Diagnosis. *Ipomoea longirostra* is probably related to and certainly resembles *I. procumbens* Mart. ex Choisy in being completely glabrous and with solitary flowers but is distinguished by its ovate-deltoid, basally truncate leaves borne on slender pedicels, and the ovate-elliptic, obtuse to rounded, not lanceolate to ovate, acute to acuminate sepals. The strongly rostrate capsule is also distinct.

Type. BRAZIL. Minas Gerais, Lima Duarte, P.N. Estadual do Ibitipoca, prov. Rio do Salto, 21°42'80"S, [43°47'W] (longitude missing from label), 1200 m, 9 March 2003, fl., fr., *R.C. Forzza, L.C.S. Assis. J.G. Jardim, R. Lima, L. Menini Neto, E. Lucas, B.R. Silva, S. Edwards & D. Zappi* 3031 (holotype RB00552260; isotypes K, NY)

Description. Twining perennial of unknown height, glabrous in all vegetative parts. Leaves petiolate, 3–4 × 1.3–2.2 cm, deltoid, finely acuminate, shortly mucronate, base truncate to cordate with rounded auricles, margin denticulate, abaxially paler with prominent veins; petioles very slender, curved, 9–17 mm. Inflorescence of solitary, pedunculate, axillary flowers; peduncles 10–15 mm; bracteoles caducous, not seen; pedicels noticeably stouter than peduncles 12–15 mm; sepals subequal, elliptic, glabrous, margins scarious, outer 8–11 × 4–6 mm, obtuse, inner 9–12 × 6–7 mm, rounded, usually c. 0.5 mm longer and 1 mm wider than outer sepals; corolla 5.5 cm

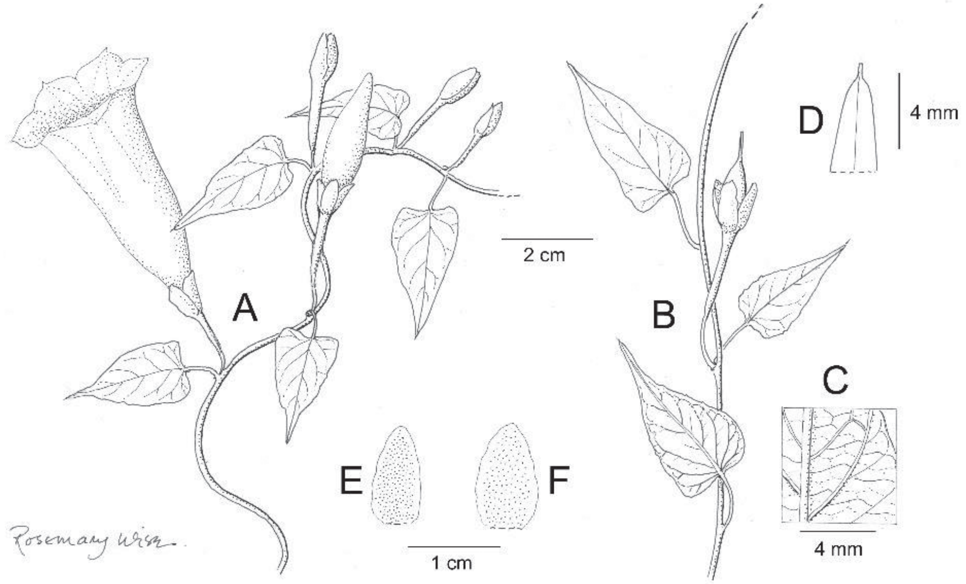

Figure 13. *Ipomoea longirostra*. **A** habit showing inflorescence **B** habit showing rostrate capsule **C** abaxial leaf surface **D** leaf apex **E** outer sepal **F** inner sepal. Drawn by Rosemary Wise from *R.C. Forzza et al.* 303.

long, pink, glabrous, funnel-shaped, limb 3–3.5 cm diameter. Capsule 13 × 6–7 mm, conical, glabrous, strongly rostrate, the apex 4–5 mm long, persistent; seeds unknown.

Distribution. BRAZIL. Endemic to the area of the type locality in the Parque Nacional Estadual do Ibitipoca in Minas Gerais. Figure 9

Additional collections seen. Minas Gerais, Lima Duarte, P.N. Estadual do Ibitipoca, casa da polícia florestal, 21°42'33"S, 43°53'46"W, *R.C. Forzza et al.* 2638 (RB0055171); ibid., Cachoeira dos Macacos 6 Feb. 2004, fl., *R.C. Forzza et al.* 2692 (RB00551680); ibid., prov. Rio do Salto, campo ao lado do alojamento, Nov. 2006, fl., *R.C. Forzza et al.* 4362 (NY01018831, RB00552445).

Conservation status. The four collections were made at different dates from the near vicinity of each other. Field notes do not indicate the plant's frequency and in the absence of other collections or any information about threats to its habitat, it can only be classified as Data Deficient (DD) within IUCN (2012) guidelines. It would be treated as a "black star" species within the classification of Hawthorne and Marshall (2016), but again this must be considered a provisional classification as no systematic search has been made for the species at the type locality or in other suitable habitats, although it must be presumed to be rare.

Etymology. The epithet *longirostra* refers to the prominently beaked capsule.

Notes. We have not been able to sequence material of this species but it is almost certainly related to *I. procumbens* under which name it was provisionally identified at Kew. Although *I. procumbens* is a quite variable species, it never has the finely petiolate, truncate leaves of *I. longirostra*. The strongly rostrate capsule of the new species is also very striking.

Ipomoea revoluta J.R.I.Wood & Scotland, sp. nov.

urn:lsid:ipni.org:names:77166184-1
Figure 14

Diagnosis. *Ipomoea revoluta* is almost certainly related to *I. malvaeoides* Meisn. and its allies but is distinguished from all of these by its twining (not erect) habit and distinctly petiolate leaves. Related species in which the leaves are furnished with linear leaflets, such as *I. fiebrigii* O'Donell, *I. itapuaensis* J.R.I. Wood & R. Degen and *I. theodori* O'Donell, are erect herbs with sessile or near sessile leaves.

Type. BRAZIL. Mato Grosso do Sul, Serra de Maracaju, 17 Feb. 1970, *G. Hatschbach* 23761 (holotype MBM, isotypes CTES, F, MICH, S).

Description. Slender twining liana of unknown height; stem woody, c. 2–3 mm thick, pale brown, shortly pubescent. Leaves petiolate, digitately divided into 5–7 free leaflets; leaflets 5–9 × 0.15–0.4 cm, linear, attenuate to a mucronate apex, basally tapered, margin revolute; adaxially glabrous, midvein strongly impressed; abaxially white-tomentose, the midvein prominent, nearly glabrous; petioles 8–13 mm, thinly pubescent. Inflorescence of 1–3-flowered axillary cymes; peduncles 7–9 mm, very thinly pubescent with scattered hairs; bracteoles c. 1 mm long, scale-like, caducous; pedicels 8–10 mm long, very thinly pubescent with scattered hairs; sepals subequal, 8–10 × 6–7 mm, ovate to elliptic, acute to shortly mucronate, sericeous with narrow, scarious, glabrous margins, inner sepals white-sericeous with wider scarious margins; corolla 5–6 cm long, pink, sericeous in bud, funnel shaped from a short basal cylindrical tube, limb c. 2 cm diameter, lobes rounded; stamens unequal, filaments pilose at base only, the two longer c. 20 mm, the shorter c. 12 mm; anthers included; ovary bilocular, glabrous; style c. 20 mm, stigma bi-globose. Capsule ovoid, apiculate, c. 10 mm long (immature), glabrous, ±enclosed by the sepals.

Distribution. BRAZIL. Apparently endemic to the Serra de Maracaju in Mato Grosso do Sul, where it grows on arenite outcrops. Figure 9

Additional collection seen. Mato Grosso do Sul, *G.M. Hatschbach & J.M. Silva* 60724 (MBM).

Conservation status. The two collections were made at different dates from the near vicinity of each other. Field notes do not indicate the plant's frequency and in the absence of other collections or any information about threats to its habitat, it can only be classified as Data Deficient (DD) within IUCN guidelines. It would be treated as a "black star" species within the classification of Hawthorne and Marshall (2016), but again this must be considered a provisional classification as no systematic search has been made for the species at the type locality or in other suitable habitats, although it must be presumed to be rare.

Etymology. The epithet *revoluta* refers to the revolute margins of the leaflets.

Note. We have not been able to sequence material of this species but it is almost certainly related to *I. malvaeoides* and its allies, which are part of a large clade of around 70 species almost restricted to South America. Species in the clade are characterised morphologically by the pubescent exterior of the corolla and the subequal, sericeous

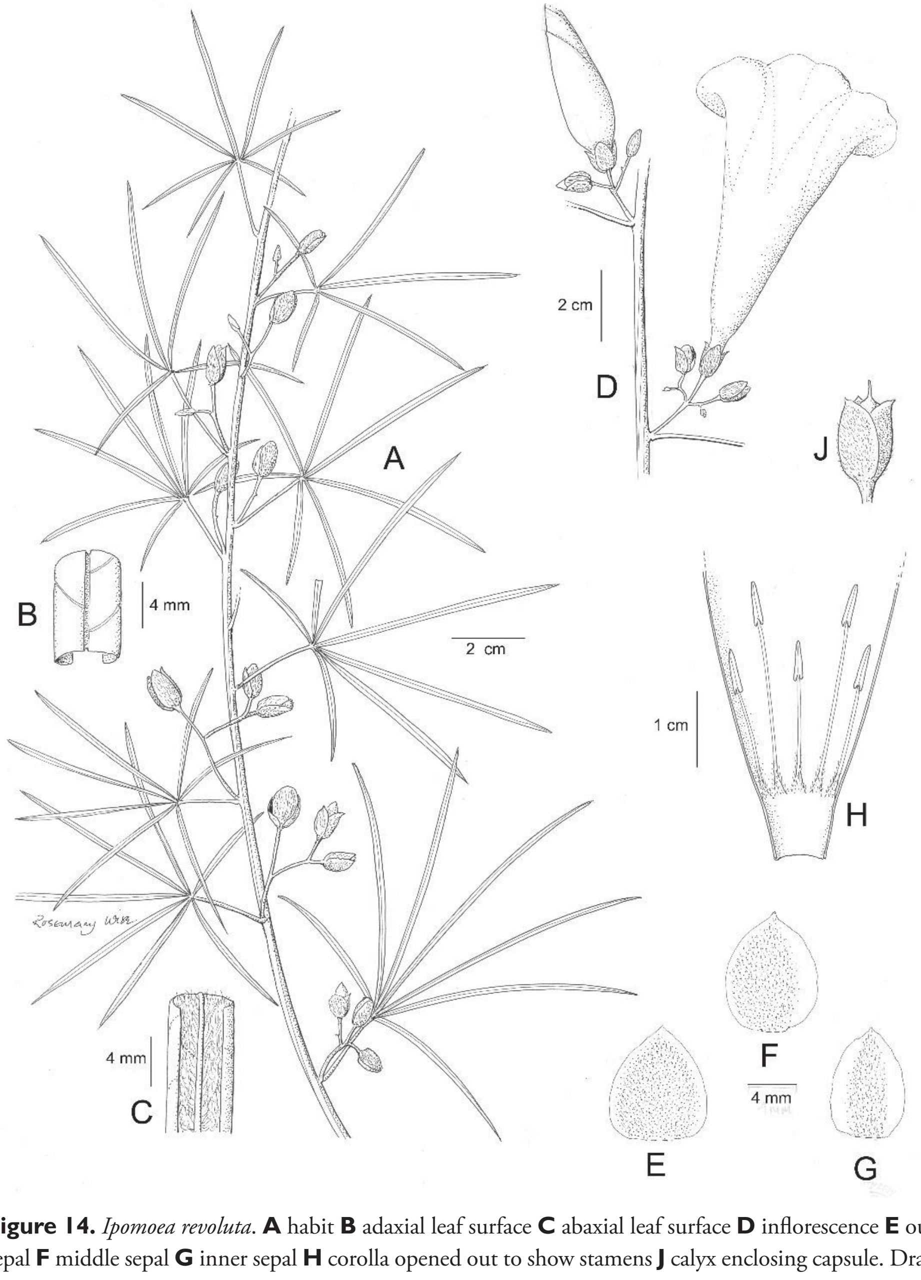

Figure 14. *Ipomoea revoluta*. **A** habit **B** adaxial leaf surface **C** abaxial leaf surface **D** inflorescence **E** outer sepal **F** middle sepal **G** inner sepal **H** corolla opened out to show stamens **J** calyx enclosing capsule. Drawn by Rosemary Wise from *G. Hatschbach* 23761.

or pubescent, ovate herbaceous sepals. The linear leaflets of *I. revoluta* recall those of the unrelated *I. subrevoluta* Choisy, with which it has been wrongly identified in many herbaria. It is easily distinguished from that species by the sericeous exterior of the corolla and the larger, abaxially pubescent sepals.

Ipomoea scopulina **J.R.I.Wood & Scotland, sp. nov.**

urn:lsid:ipni.org:names:77166185-1
Figure 15

Diagnosis. Amongst Brazilian species of *Ipomoea*, *I. scopulina* resembles only *I. longistaminea* O'Donell and *I. ana-mariae* L.V.Vasconcelos & Sim.-Bianch in having a cylindrical suburceolate corolla but is distinguished from both of these by the broadly lanceolate subacute (not oblong-elliptic, coriaceous, somewhat concave) sepals.

Type. BRAZIL. Espirito Santo, Pancas, Pedra da Colina, 19°13'51"S 40°52'35"W, 700 m, *D.P. Saraiva, J. Silva, K.V. Hmeljeviski & R.C. Forzza* 47 (holotype RB 00591205).

Description. Liana of unknown height; stems woody, pale grey, glabrous. Leaves petiolate, 4–7 × 3–5 cm, ovate, shortly acuminate, base cordate with rounded auricles, margin undulate, adaxially glabrous, abaxially paler, somewhat reticulate, the main veins obscurely puberulent; petioles 1.5–2.5 cm, glabrous or obscurely puberulent upwards. Inflorescence borne on woody branchlets, the axillary cymes subracemose in form, apparently arising after the leaves have fallen; peduncles 6–7 mm long, somewhat woody, glabrous apart from a few scattered hairs; bracteoles deltoid, c. 1 mm long, glabrous, caducous; secondary peduncles 2–7 mm long; pedicels 6–10 mm long, glabrous; sepals slightly unequal, outer 6–7 × 3–3.5 mm, broadly lanceolate, subacute, glabrous, margin scarious, inner similar but obtuse and with broader scarious margins; corolla suburceolate, glabrous, reported to be "white", 3.5–4 cm long, tube subcylindrical, c. 4 mm wide at base, widened to 10 mm in the middle, constricted upwards, c. 6 mm wide at mouth, lobes broadly ovate, c. 2 × 3.5 mm; filaments 1–1.5 cm long, glabrous except for pilose base, anthers linear, c. 2.5 mm, included; ovary presumably bilocular, glabrous, style c. 2.2 cm, stigma bi-globose. Capsule and seeds not seen.

Distribution and habitat. BRAZIL. Endemic to Espírito Santo state and only known from the type collection. It was found growing in deciduous forest amongst rock outcrops on the Pedra de Colina granite "sugarloaf" inselberg which is a feature of the country around Pancas. Like *I. fasciculata* described elsewhere in this paper, this is one of a number of *Ipomoea* species described from Bolivia and Brazil from granite inselbergs. It is to be hoped that *I. scopulina* will be found elsewhere in the same region or in similar habitats, perhaps at a considerable distance from the type locality. Figure 9

Conservation status. In the absence of other collections or any information about its frequency the status of this species can only be classified as Data Deficient (DD) within IUCN (2012) guidelines. It would be treated as a "black star" species within the classification of Hawthorne and Marshall (2016), but again this must be considered as a provisional classification as no systematic search has been made for the species at the type locality or in other similar habitats in the area.

Etymology. The epithet *scopulina* refers to the cliff-like sides of the granite mountain on which this species was found.

Notes. The relationships of this species are not obvious but species of *Ipomoea* with tubular suburceolate corollas are generally rare in the genus and especially so in Brazil. The only two comparable Brazilian species are *I. longistaminea* and *I. ana-mariae*.

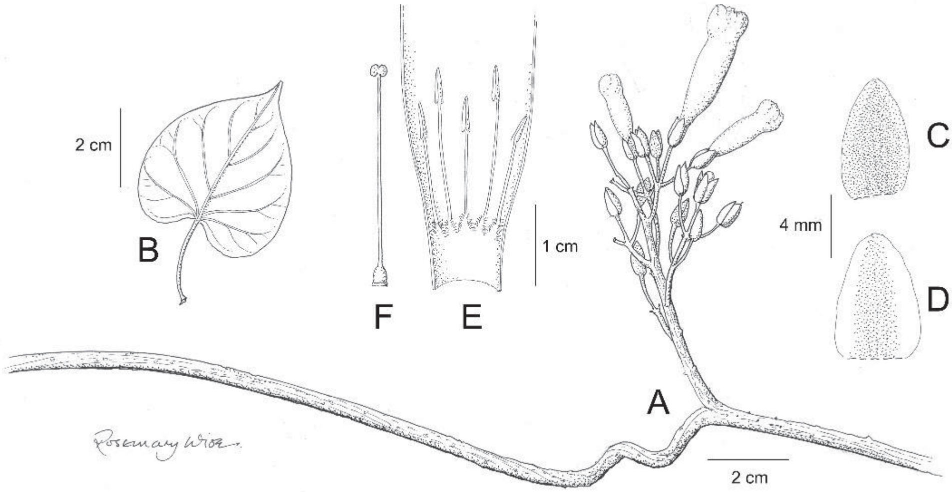

Figure 15. *Ipomoea scopulina*. **A** habit **B** leaf **C** outer sepal **D** inner sepal **E** corolla opened out to show stamens **F** ovary and style. Drawn by Rosemary Wise from *D.P. Saraiva et al.* 47

Both have oblong-elliptic, coriaceous, somewhat concave sepals very different from the broadly lanceolate subacute sepals of *I. scopulina*, almost certainly indicating they belong to different clades. Additionally, *I. longistaminea* differs in its strongly exserted stamens, truncate-based, tomentellous leaves while *I. ana-mariae* differs in its oblong-elliptic cuneate-based (not ovate, cordate) leaves.

Like *I. longistaminea*, *I. scopulina* appears to be partially deciduous at anthesis. This may be significant as several species with a subcylindrical corolla from Cuba (*I. praecox* Wright) and Mexico (*I. tehuantepecensis* L. Torres, R. Torres, M.P. Ramírez & J.A. McDonald, *I. concolora* Matuda) are often leafless at anthesis.

Ipomoea uninervis J.R.I.Wood & Scotland, sp. nov.

urn:lsid:ipni.org:names:77166186-1
Figure 16

Diagnosis. *Ipomoea uninervis* can be confused with *I. aprica* House but differs in the grey-tomentellous, oblong outer sepals 7.5–8 mm long (these are green-tomentose, broadly ovate to suborbicular and 5–6 mm long in *I. aprica*) and the elongate inflorescence with deciduous bracts so appearing naked (not leafy with persistent bracts). It is also close to *I. oblongifolia* (Hassl.) O'Donell but differs in the 1-veined leaves (not with 3–5 prominent longitudinal veins) and oblong, not elliptic bracts, and relatively long inflorescence

Type. BRAZIL. Distrito Federal, próximo ao posto Colorado, Chácara FTRC, Centro Oeste, 15°41'S, 47°52'W, 6 Feb. 1999, *C. Proença, R.S. Oliveira, C.M. Clemente, J.F. Ribeiro* 2074 (holotype UB8208-2, isotype E00202955).

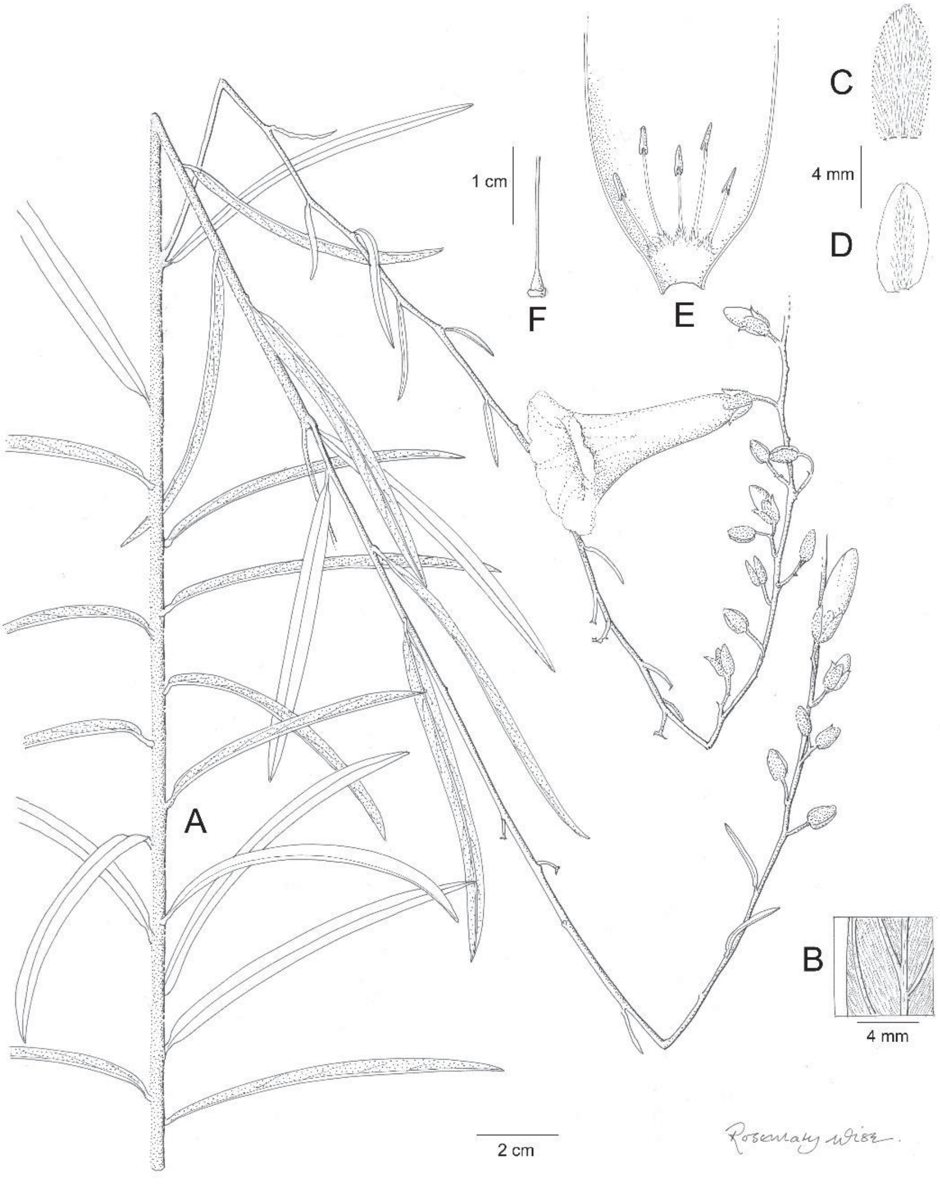

Figure 16. *Ipomoea uninervis*. **A** habit **B** abaxial leaf **C** outer sepal **D** inner sepal **E** corolla opened out to show stamens **F** ovary and base of style. Drawn by Rosemary Wise from *C. Proença et al.* 2074.

Description. Perennial undershrub; stems erect, to 1.2 m, sparingly branched, grey-puberulent to subsericeous. Leaves subsessile, 4–12 × 0.1–0.5 cm, linear to narrowly oblong, obtuse, shortly mucronate, both surfaces grey-puberulent to subsericeous, abaxaially paler with a single prominent longitudinal vein; petioles 0–3 mm, tomentellous. Inflorescence of few-flowered cymes from the upper leaf-axils, forming a terminal, usually elongate inflorescence up to 15 cm in length; bracts formed of reduced leaves, caducous so inflorescence appearing naked; peduncles 1–4 mm, grey-tomentellous; bracteoles 1.5 mm, linear, tomentellous, caducous; pedicels 3–7 mm, grey-tomentellous; sepals subequal, 7.5–8 × 3–4 mm, broadly oblong, obtuse to rounded, grey-tomentose, the inner with broad glabrous, scarious margins; corolla 4.5 cm long, pink, pubescent, funnel-shaped; limb c. 4 cm diameter; filaments unequal, shorter 7–10 mm, longer 12–20 mm, glabrous except for basal hairs; anthers 3.5 mm, narrow; ovary bilocular, conical, glabrous; style 15–22 mm, glabrous; stigma bilobed. Capsule and seeds not seen.

Distribution and habitat. BRAZIL. Endemic to the Distrito Federal and Goiás State, where it appears to be a rare species of cerrado. Figure 5.

Additional collection seen. BRAZIL. Goiás: Cristalina, 5 km along estrada para Paracatu, 16°46'S, 47°37'W, 1050 m, *J.R. Pirani et al.* 1560 (SPF60276, K000944736).

Conservation status. This species has been found in two quite separate locations and so might be expected elsewhere. However, field notes give no information about its frequency so it should be treated as Data Deficient (DD) within IUCN guidelines until the populations of this species can be carefully evaluated.

Etymology. The epithet *univervis* refers to the 1-veined leaves, the principal character separating it from *I. oblongifolia*.

Note. Molecular studies using *ITS* (unpublished data) place this species in a large well-supported clade of around 70 species almost restricted to South America, which is characterised morphologically by the pubescent exterior of the corolla and the subequal, pubescent, ovate herbaceous sepals. The caducous bracts of *I. uninervis* result in a near naked inflorescence rather different from that of *I. aprica* with which it is most likely to be confused. It is probably closest to the Paraguay endemic *I. oblongifolia* from Amambay, but differs most significantly in the 1-veined leaves. *I. oblongifolia* has prominently 3–5-veined leaves.

Ipomoea veadeirosii J.R.I.Wood & Scotland, sp. nov.

urn:lsid:ipni.org:names:77166187-1
Figure 17

Diagnosis. *Ipomoea veadeirosii* is a densely tomentose woody liana that appears closest to *I. calyptrata* Dammer because of the persistent bracteoles which are appressed to the calyx with the pedicel supressed. It differs most obviously in the glabrous corolla, near glabrous sepals and the roughly tomentose indumentum of the leaves and stem, which differs from the white tomentellous indumentum of the stem, leaves, bracteoles, sepals and corolla exterior of *I. calyptrata*.

Type. BRAZIL. Goiás, Chapada dos Veadeiros, 42 km N. of Alto do Paraíso, *H.S. Irwin, R.M. Harley & G.L. Smith* 33148 (holotype FTG114415, isotype ?NY, n.v.).

Description. Twining liana to c. 3 m; stem stout, somewhat woody, densely tomentose. Leaves petiolate, 5–11 × 4–9 cm, ovate, shallowly cordate to subtruncate with rounded auricles, margin undulate, apex obtuse and shortly mucronate, the mu-

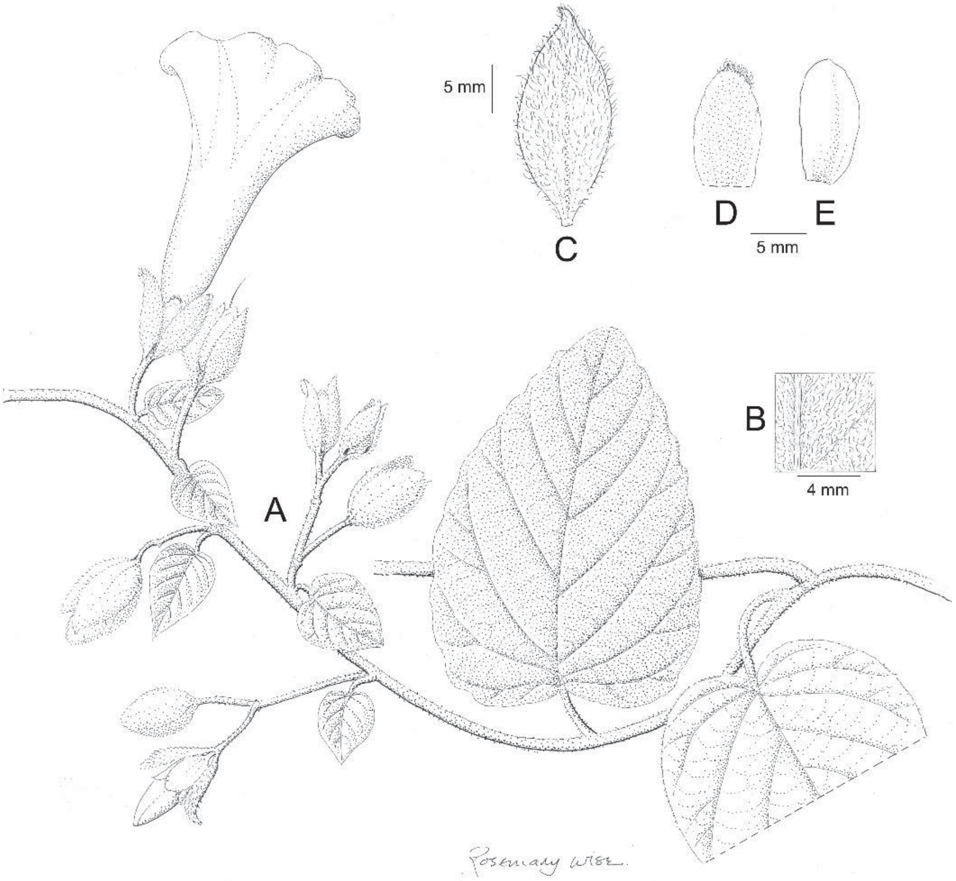

Figure 17. *Ipomoea veadeirosii*. **A** habit **B** abaxial leaf surface **C** bracteole **D** outer sepal **E** inner sepal. Drawn by Rosemary Wise: **A–B** from *H.S. Irwin et al.* 33148, **C–E** from *W.R. Anderson et al.* 6691.

cro rather stout, adaxially yellow-green, tomentose, glabrescent when old, abaxially grey-tomentose, the veins highlighted; petioles 0.5–4 cm, tomentose. Inflorescence of flowers borne on axillary bracteate branchlets; bracts 2–2.5 × 1–1.7 cm, ovate, tomentose; cymes 1–2-flowered; peduncles 1–6 cm, tomentose; secondary peduncles pedicel-like, 0.8–1.7 cm, pubescent, more slender than primary peduncles; bracteoles 2–2.3 × 0.8–1.4 cm, narrowly elliptic, obtuse, somewhat boat-shaped, tomentose, persistent and ± clasping the calyx; pedicels 1–4 mm, glabrous; sepals subequal, 11–13 × 5–7 mm, elliptic, obtuse to rounded, outer glabrous, margins scarious; corolla 6–7 cm, narrowly funnel-shaped, glabrous, deep pink.

Distribution and habitat. BRAZIL. Endemic to rocky cerrado (campo rupestre?) at 1250–1700 m in the Chapada dos Veadeiros National Park. Figure 9.

Additional collection seen. Goiás: Chapada dos Veadeiros, 25 km N of Alto Paraíso, 1700 m, *W.R. Anderson et al.* 6691 (FTG114414, ?NY, n.v.)

Conservation status. The two collections were made on different dates from two nearby locations. Field notes do not indicate the plant's frequency and in the absence of other collections or any information about threats to its habitat, it can only be classified as Data Deficient (DD) within IUCN (2012) guidelines. It would be treated as a "black star" species within the classification of Hawthorne and Marshall (2016), but again this must be considered a provisional classification as no systematic search has been made for the species at the type locality or in other suitable habitats, although it must be presumed to be rare. Both recorded locations lie within the Chapada dos Veadeiros National Park and enjoy legal protection.

Etymology. This species is named after the Chapada dos Veadeiros National Park in Goiás State. It is one of the biologically richest and most important protected areas of the cerrado biome and four species described in this paper are endemic to this National Park.

Note. Although we have not been able to sequence this species, *I. veadeirosii* appears to belong to a small clade consisting of *I. descolei* O'Donell, *I. marcellia* Meisn. and *I. calyptrata*. All these species are somewhat woody and liana-like and share a densely tomentose indumentum. The inflorescence structure, with a tendency for the inflorescence to develop on foliose branchlets, is found in a number of woody species, notably in the *Arborescens* clade. *Ipomoea veadeirosii* appears closest to *I. calyptrata* because of the persistent bracteoles which are appressed to the calyx with the pedicel supressed but is readily distinguished from all these species by the glabrous exterior of the corolla.

Ipomoea velutinifolia J.R.I.Wood & Scotland

Figure 18

Diagnosis. *Ipomoea velutinifolia* is apparently related to *I. sericosepala* J.R.I. Wood & Scotland because of the compound inflorescence and the distribution of the indumentum on the corolla and almost all vegetative parts but differs in the distinctive velvety grey indumentum and in the shape and size of the sepals which are subequal, ovate to suborbicular, 7–8 × 6–8 mm, not unequal, elliptic-obovate, the outer oblong 8–10 × 3–4 mm and the inner 11–14 × 6 mm. The pubescent ovary is a very unusual character in *Ipomoea*.

Type. BRAZIL. Maranhão: Mun. Grajau, 4 km W of Mondelandia on path to Rio Grajaú, 23 April 1983, *E.L. Taylor, C.S. Rosario & J.B.F. Silva* 1326 (holotype MG114153, isotype ARIZ421888).

Description. Perennial climber, stems relatively stout, silky-velutinous. Leaves petiolate, 5–9 × 4–8 cm, ovate, apex acute, mucronate, base very broadly cuneate to subtruncate with rounded auricles, margin undulate, adaxially softly and densely pubescent, abaxially velvety-grey; petioles 2.5–4.5 cm, velvety-grey. Inflorescence of compound axillary cymes, these often racemose in form and sometimes distinctly leafy; peduncles 2.5–5 cm, velvety-grey, often extended as a rhachis and reaching 15 cm;

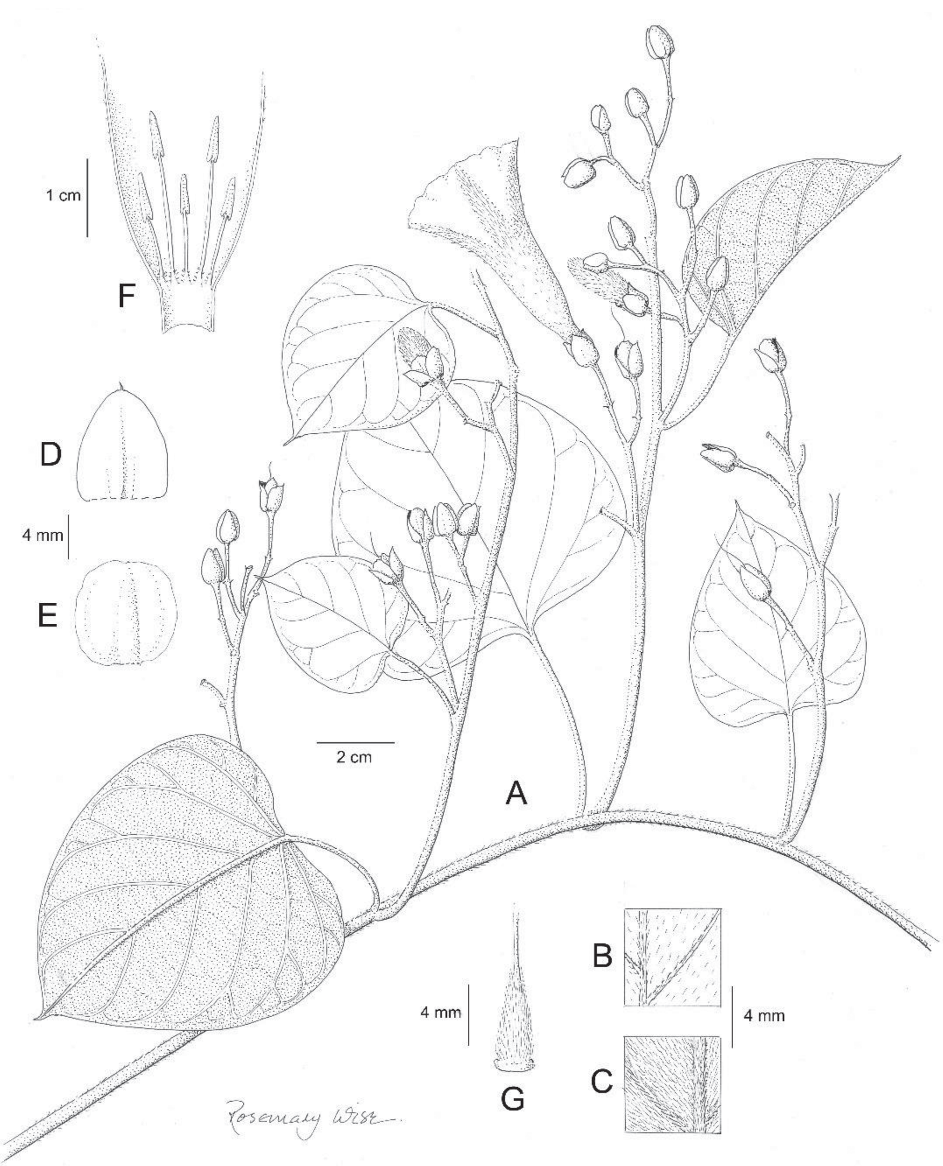

Figure 18. *Ipomoea velutinifolia.* **A** habit **B** adaxial leaf surface **C** abaxial leaf surface **D** outer sepal **E** inner sepal **F** corolla opened out to show stamens **G** ovary. Drawn by Rosemary Wise from *E.L. Taylor, et al.* 1326.

secondary peduncles 0.5–2 cm, velvety-grey; bracteoles caducous, not seen; pedicels 10–12 mm, puberulent; sepals subequal, 7–8 × 6–8 mm, outer ovate, obtuse, inner suborbicular, rounded, abaxially velvety-grey, adaxially glabrous; corolla 4.5–6 cm long, sericeous, funnel-shaped, exterior white, interior pale pink; stamens unequal, included, longer c. 2.5 cm, shorter c. 1.2 cm, anthers linear 5 mm; ovary pubescent; stigma not seen. Capsule and seeds unknown.

Distribution and Habitat. BRAZIL and PERU. Known from the type locality in Maranhão and a single locality at low altitudes in Pasco. Unlike most of the other species in this paper this is a forest species, found in Brazil in the only mature forest relic on a ridge and in Peru in primary forest on white sands. The forest in Brazil was reported to be relatively short with few emergent trees, an open understorey and the presence of many vines in areas where trees had fallen. The distribution (Figure 5) is very disjunct but suggests that this species might be found in other suitable habitats around the Amazon basin.

Additional collection. PERU. Pasco: Oxapampa, Palcazu Dist, San Cristobal, 323 m, 29 May 2008, *R. Vásquez et al.* 34378 (MO, USM); ibid., Comunidad Nativa Buenos Aires, *R. Vásquez et al.* 37328 (MO, OXF).

Conservation status. The two widely separated locations for this species combined with the relatively recent collection dates suggest this species may have been overlooked. No information is available to indicate the plant's frequency but field notes accompanying the type collection indicate that its forest habitat is threatened. It would be treated as a "black star" species in both Brazil and Peru within the classification of Hawthorne and Marshall (2016), but within IUCN (2012) guidelines it can only be classified as Data Deficient (DD). However, this must be considered only a provisional classification until the populations can be assessed.

Etymology. The epithet *velutinifolia* refers to the softly velvety indumentum of the leaves.

Note. This species appears to be related to *I. sericosepala* but differs in the subequal sepals and the grey-green velutinous indumentum. It might be interpreted as being related to *I. megapotamica* Choisy or *I. sericophylla* but differs from both in the form of the inflorescence and indumentum. From all these species and most others known from South America it also differs in the densely pubescent ovary.

Ipomoea walteri J.R.I.Wood & Scotland, sp. nov.

urn:lsid:ipni.org:names:77166188-1

Figure 19

Diagnosis. *Ipomoea walteri* is close to *I. sericophylla* but distinct because of the long-pedunculate lax inflorescence, adaxially nearly glabrous leaves and unequal sepals, the inner noticeably shorter than the outer. Particularly distinct are the strongly cuspidate leaves with a distinct apical mucro c. 3 mm long which is only matched in a few very different species, such as *I. daturiflora* Meisn.

Type. BRAZIL. Goiás: Colinas do Sul, arredores da Serra de Jipe, 500 m, *B.M.T. Walter, E. Gomes, G. Pereira-Silva & S. Pereira de Souza* 4734 (CEN58673).

Description. Liana of unknown height, stems thinly pubescent; leaves petiolate, 3–5 × 3.5–5.5 cm, ovate, apex obtuse and long-cuspidate (mucro c. 3–4 mm),

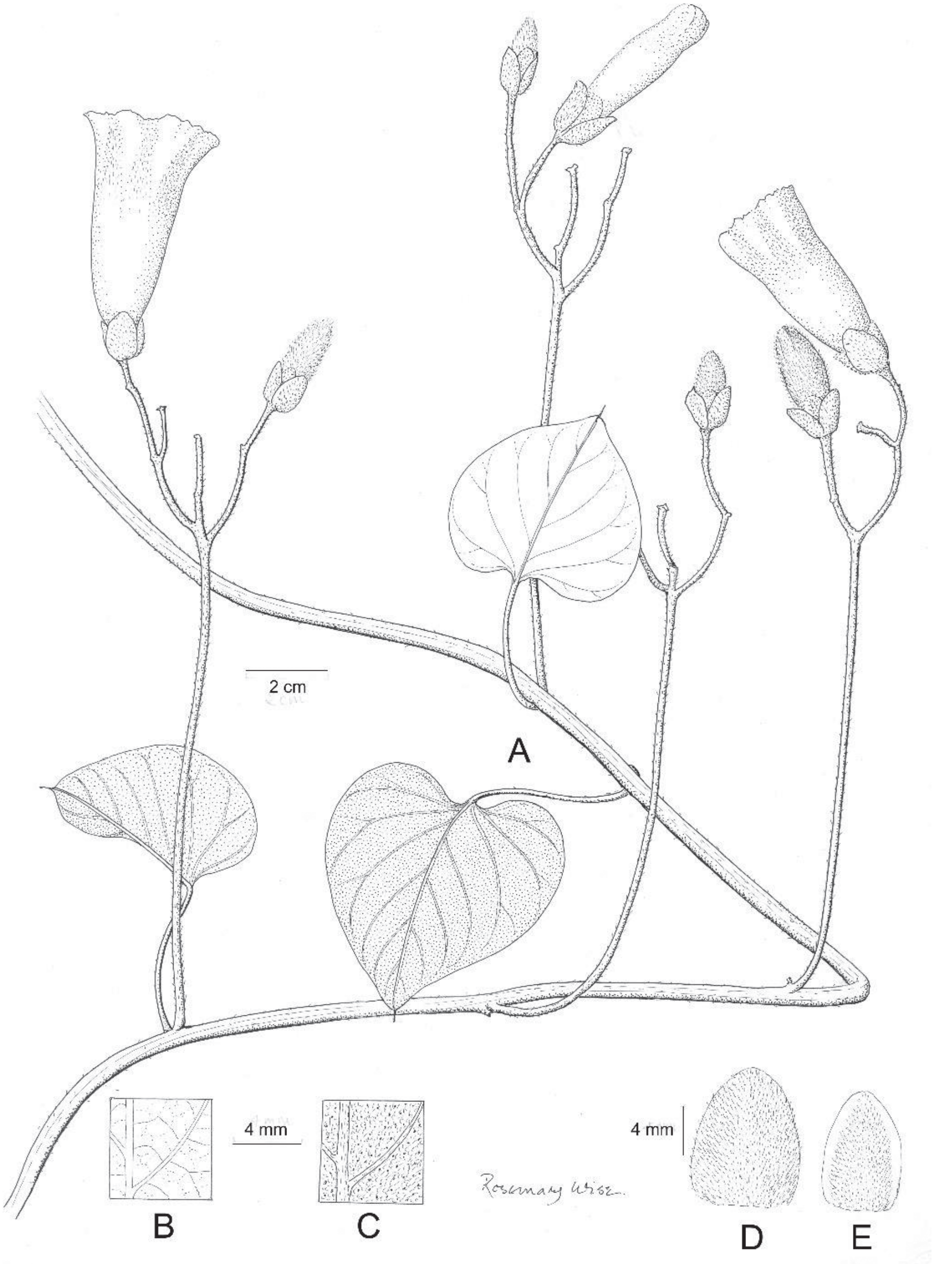

Figure 19. *Ipomoea walteri*. **A** habit **B** adaxial leaf surface **C** abaxial leaf surface **D** outer sepal **E** inner sepal. Drawn by Rosemary Wise from *B.M.T. Walter et al.* 4734.

base cordate with rounded auricles, adaxially very sparsely pubescent to subglabrous, abaxially grey tomentose, gland-dotted; petioles 2.5–3.5 cm. Inflorescence of long-pedunculate lax axillary cymes; peduncles 7–11 cm; bracteoles caducous, not seen, secondary peduncles 0.3–2.2 cm; tertiary peduncles c. 10 mm; pedicels 4–5 mm; sepals unequal, outer 11–12 × 8–9 mm, obovate-elliptic, rounded, thinly tomentellous; inner 8–9 × 6 mm, the central part densely tomentose, margins broad, glabrous, scarious; corolla 5.5 cm long, appearing broadly tubular but not fully open, probably funnel-shaped when open, pale pink; stamens unequal, longer c. 1.5–1.8 cm, shorter c. 1–1.2 cm; anthers 3 mm, included; style 2–2.3 cm, stigma bi-globose.

Distribution and habitat. BRAZIL. Goiás. Known only from the type collection. It was recorded as growing in gallery forest. Figure 9.

Conservation status. Field notes give no data about the frequency of this species and in the absence of other collections or any information about threats to its habitat, it can only be classified as Data Deficient (DD) within IUCN guidelines. It would be treated as a "black star" species within the classification of Hawthorne and Marshall (2016), but again this must be considered a provisional classification as no systematic search has been made for the species at the type locality or in other suitable habitats, although it must be presumed to be rare.

Etymology. This species is named after the collector Bruno Walter, who is a leading research worker for Embrapa at the Cenargen Herbarium in Brasilia and a specialist in the Flora of the Cerrado.

Note. Although we have not been able to sequence this species, *I. walteri* clearly belongs to the large clade of around 70 species almost restricted to South America, which is characterised morphologically by the pubescent exterior of the corolla and the subequal, pubescent, ovate herbaceous sepals. The strongly cuspidate leaves with a distinct apical mucro are particularly distinctive.

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Epilithic diatom communities of selected streams from the Lerma-Chapala Basin, Central Mexico, with the description of two new species

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Abstract

The Lerma-Chapala Basin, in Central Mexico, is geologically heterogeneous, climatically diverse and boasts high biodiversity, lying within two Biodiversity Hotspots, namely Mesoamerica and the Madrean Pine–Oak Woodlands. Epilithon and water samples were collected in the basin from 14 sampling sites three times each, two sampling campaigns during the rainy season and one in the dry season. A total of 274 infrageneric taxa in 48 genera were recorded. The taxonomic composition observed was dominated by taxa from the genera *Nitzschia*, *Gomphonema*, *Pinnularia*, *Navicula*, *Sellaphora* and *Eunotia*. About a third of the taxa found could not be identified to the species level. From those unidentified morphodemes, two are described as new species, namely *Brachysira altepetlensis* and *Sellaphora queretana*. Furthermore, *Eolimna rhombica* is transferred to *Sellaphora*. Canonical Correspondence Analysis (CCA) revealed that specific conductivity and pH were the main environmental factors driving the community composition observed. Three groups of samples were identified after the CCA: 1) characterized by acidic waters and low conductivity; 2) with circumneutral waters, low specific conductivity and high temperature and phosphorous concentrations; and 3) characterized by circumneutral waters, high conductivity and low nitrogen concentrations. The indicator value method (IndVal), based on the relative abundance and relative frequency of the most abundant taxa was calculated based on the groups observed in the CCA, identifying the characteristic taxa for each of the three groups.

Keywords

Central Mexico, diatom communities, epilithon, indicator species, Lerma-Chapala Basin, mountain streams, new species

Introduction

Lotic environments, i.e. streams, are unidirectional flows of water. They are characterized by a broad spatial (i.e. substrate, slope, vegetation) and temporal (i.e. water velocity, light) heterogeneity, which determines the specialized biota that inhabit them (Giller and Malmqvist 1998, Allan and Castillo 2007). Stream diatoms have features that allow them to thrive in flowing waters, such as the morphological and physiological ability to adhere directly or by means of stalks or mucilage pads to different substrate types to avoid being dragged away by water. Apart from water velocity, physical and chemical variables of the water such as temperature, pH, specific conductivity and nutrient concentrations are determining factors for diatom composition and community structure (Bellinger and Sigee 2010, Stevenson et al. 2010).

Even though there is mounting evidence of the applied use of diatoms as indicators of environmental change in lotic environments (Kelly 1998, Potapova and Charles 2002, 2007, Smol and Stoermer 2010), diatom studies from Mexican streams are relatively scarce, despite the increasing pressure these environments are facing to satisfy human demand for clean water.

Diatom studies of lotic environments from Mexico have been mostly focused on the center of the country: Antigua River Basin (Vázquez et al. 2011); Balsas River Basin (Valadez-Cruz et al. 1996, Bojorge-García et al. 2010, 2014), Lerma-Chapala Basin (Abarca-Mejía 2010, Segura-García et al. 2010, 2012, 2016, Mora et al. 2015), Mexico Basin (Ramírez-Vázquez et al. 2001, Ramírez-Vázquez and Cantoral-Uriza 2003, Bojorge-García and Cantoral-Uriza 2007, Carmona-Jiménez et al. 2016); Pánuco River Basin (Cantoral-Uriza et al. 1997) and Papaloapan River Basin (Tavera et al. 1994). Most of these studies focused on the flora *per se* but also on community structure and bioindication. Despite the research done, the diatom diversity of the region seems to be low due to clustering of taxa into species complexes and force–fitting into already described taxa.

The studies conducted in the Lerma-Chapala Basin have been focused on the polluted Lerma River and some of its main tributaries (Abarca-Mejía 2010, Segura–García et al. 2010, 2012, 2016, Mora et al. 2015). But no study has been conducted so far on the headwater streams of the basin, which are important in the establishment of reference conditions for biological integrity evaluations based on regional characteristics of the streams and its associated diatom flora (Stoddard et al. 2006, Tornés et al. 2007).

In order to contribute to the studies done in the Lerma-Chapala Basin, one of the most important basins of the country regarding population and trade, the aims of this study are: to document the epilithic diatom diversity from selected headwater and midland streams from the Lerma-Chapala Basin, Central Mexico; to illustrate the most abundant taxa; and to identify the environmental factors that determine the variation observed in diatom composition.

Methods

Study area. The Lerma-Chapala Basin is located in Central Mexico, covering an area of 53,591.3 km^2 (Fig. 1). It is geologically heterogeneous, has a strong elevational gradient, is climatically diverse, has well defined rainy (June to October) and dry seasons (November to May) and boasts high biodiversity. It lies within two Biodiversity Hotspots, namely Mesoamerica and the Madrean Pine–Oak Woodlands (Cotler et al. 2006, CEPF 2017a, b).

This basin is one of the most important centers in the country for agriculture and industry, and has a population of more than 15 million inhabitants (Wester et al. 2005, Cotler et al. 2006). But the Lerma-Chapala Basin is also one of the most environmentally degraded basins in the country, facing serious water related issues because of overexploitation and pollution of surface and underground waters (Aparicio 2001, Wester et al. 2005).

The 14 sampling sites selected for this study are located in the north and central–east sections of the Lerma-Chapala Basin at elevations ranging from 2,000 to 2,400 meters above sea level. Of those 14 sites, one is a perennial spring–fed creek and 13 correspond to streams that have water during most part of the year (Fig. 1, Table 1). Sampling sites 1–8 are located at the foothills of the Sierra de Santa Rosa, an oak–forested mountain range of priority for the conservation of biodiversity in Mexico (Arriaga et al. 2000); the mean temperature of the area is 16.1 °C and the average rainfall is 642 mm (CNA 2017a). Sites 9 and 10 are in a flat area dominated by shrubland and subsistence agriculture; the mean air temperature is 18.8 °C and the average rainfall is 566 mm (CNA 2017b). Sites 11–14 are located at the foothills of a small mountainous area dominated by pine–oak forests and subsistence agriculture; the mean air temperature is 15.6 °C and the average rainfall is 774 mm (CNA 2017c).

Sampling. Water and epilithon samples were collected three times from each sampling site in: September/October 2013, rainy season (sampling campaign I); February 2014, dry season (sampling campaign II); and September 2014, rainy season (sampling campaign III); resulting in 42 water and epilithon samples. Each epilithon sample was collected from five cobbles across a transversal section of the stream, brushing with a disposable toothbrush ten square centimeters of epilithic growth from each of the five cobbles to make a composite sample, fixed in 70% alcohol. *In situ* measurements of pH, water temperature, specific conductivity and total dissolved solids were recorded using a Hanna multi–sensor (HI 991300, California, USA). Dissolved oxygen was recorded with an YSI–85 oxygen meter (YSI, Ohio, USA). Dissolved oxygen saturation percentages were calculated from dissolved oxygen data according to correcting

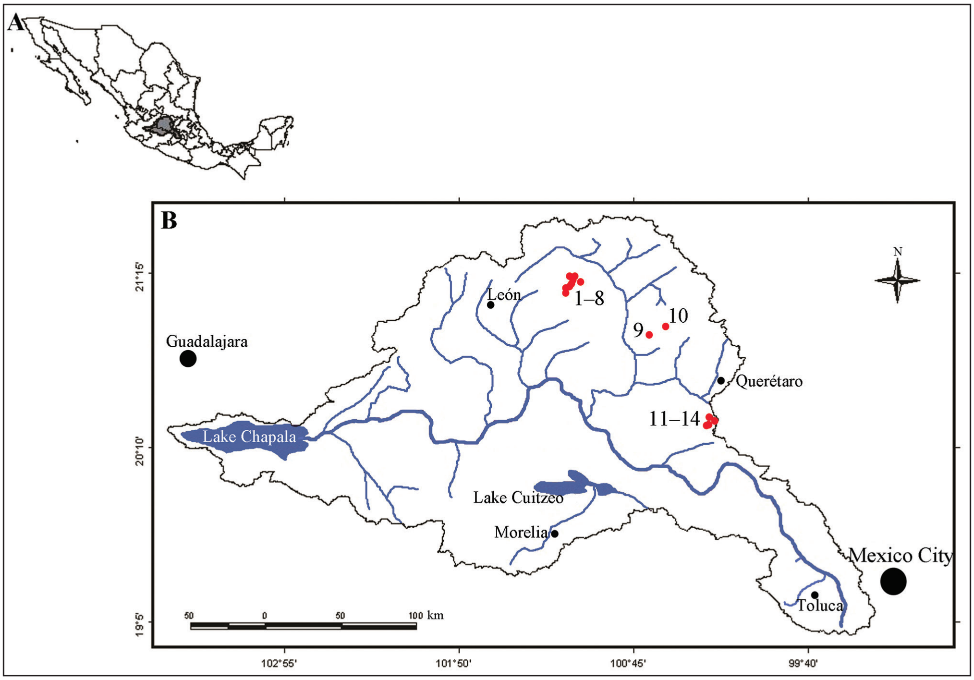


Figure 1. Location of the area of study. A Map of Mexico, showing the location of the Lerma-Chapala Basin in the center of the country. B Location of the 14 sampling sites in the Lerma-Chapala Basin, indicated by red dots. The numbers next to the red dots refer to the name of the sampling site in Table 1.

Table 1. Sampling sites in the Lerma-Chapala Basin, including site number and name, type of water body, geographical coordinates and elevation.

Site		Water body	Latitude (N)	Longitude (W)	Elevation (m a.s.l)
1	La Mesa	Stream	21°05'28.69"	101°08'18.98"	2215
2	Calvillo	Stream	21°06'50.40"	101°08'04.10"	2138
3	Ojo de Agua de Calvillo	Stream	21°07'41.80"	101°07'04.50"	2102
4	Peña Colorada	Stream	21°09'03.84"	101°05'58.96"	2110
5	San Martín	Stream	21°09'24.50"	101°03'11.30"	2017
6	Paredones	Stream	21°11'20.60"	101°06'53.40"	2089
7	La Laborcilla 1	Stream	21°11'04.70"	101°06'14.60"	2076
8	La Laborcilla 2	Stream	21°11'20.10"	101°05'37.90"	2065
9	El Membrillo	Stream	20°50'21.22"	100°38'43.46"	2114
10	Guanajuatito	Spring fed-creek	20°53'23.98"	100°32'30.72"	2120
11	Los Ailes 1	Stream	20°19'58.72"	100°15'17.09"	2358
12	Laguna de Servín 1	Stream	20°18'18.10"	100°17'38.10"	2409
13	Laguna de Servín 2	Stream	20°18'45.20"	100°17'25.60"	2409
14	Los Ailes 2	Stream	20°20'50.20"	100°16'45.50"	2317

factors for elevation and water temperature. Specific conductivity values were corrected to 25°C. Water velocity was recorded with a Global Water FP111 velocity meter (Texas, USA). At each sampling site, a 500 ml sample of water was filtered through 0.22 µm and 0.45 µm filter membranes (Millipore, Massachusetts, USA) and collected in sterile polypropylene bottles for chemical analysis. Samples were kept cold and in the dark before laboratory analysis. The subsequent chemical laboratory analyses were adapted from Standard Methods for the Examination of Water and Wastewater and analyzed using a DR 3900 laboratory Spectrophotometer (Hach Company, Loveland, Colorado) (HACH 2003, APHA 2005): nitrite nitrogen (NO_2^-–N), nitrate nitrogen (NO_3^-–N), ammonium nitrogen (NH_4^+–N), soluble reactive phosphorus (SRP, in theory, mostly in the form of orthophosphate, PO_4^{3-}–P) and total alkalinity (as $CaCO_3$). Dissolved inorganic nitrogen (DIN) was calculated as the sum of the three inorganic nitrogen forms in water (nitrites, nitrates and ammonium).

The Riparian Forest Quality index (QBR from its Catalan abbreviation) was calculated in order to evaluate the riparian habitat quality (Munné et al. 2003). This index evaluates quantitatively four components of the riparian habitat: 1) Total riparian vegetation cover, evaluates the vegetation cover of all plants except for annuals and also taking into account the connectivity between the riparian area and surrounding terrestrial vegetation. 2) Vegetation cover structure, it assesses the structural complexity of the riparian habitat, which is determined by the percent coverage and patch distribution of trees, shrubs and aquatic plants. 3) Cover quality, takes into account the number of native tree and shrub species (dependent of the river type) and also evaluates if the river has alterations such as man-made structures, presence of alien species and garbage. To determine the river type, the following geomorphological criteria are evaluated: slope and form of the riparian zone, presence of islands in the river and percentage of hard substrata. 4) River channel alterations, evaluates how pristine or altered is the river, considering if the river has been permanently channelized, if there are rigid structures or fluvial terraces constraining the flow. Each component of the index scores between 0 and 25, therefore the index score go from 0 to 100. The index has five classes: natural condition, good quality, fair quality, poor quality and bad quality. The native vegetation, needed to calculate this index, was identified following Zamudio et al. (1992), Carranza-González (1995), Carranza-González and Madrigal-Sánchez (1995), Calderón de Rzedowski and Rzedowski (2001), Rzedowski and Calderón de Rzedowski (2004).

Diatom analysis. Fractions of the diatom samples were cleaned by adding aliquots of 35% hydrogen peroxide and heating at 80°C until no bubbling was observed. After the digestion was completed, peroxide remnants were removed by rinsing at least three times with distilled water. Samples were finally diluted with distilled water in order to avoid high concentrations of valves and sediment. Three permanent slides per sample were made using the high refraction index mounting medium Naphrax®. The slides were scanned and the diatoms photographed under the light microscope (LM) in order to account for diatom diversity, using a Zeiss Axioscope microscope with Differential Interference Contrast equipped with an AXIOAM MRc camera. In order to estimate the relative abundance of the taxa, a minimum of 500 valves per sample were counted and identified with the 100x immersion oil objective. Aliquots of cleaned sample material for scanning electron microscopy observations were mounted on stubs, sputter-coated with gold-palladium and observed under a Hitachi FE 8010 scanning electron microscope (SEM) operated at 1.0 kV. Samples and slides are stored at the Diatom Collection of the Botanical Garden and Botanical Museum Berlin–Dahlem, Freie Universität Berlin. Diatoms were identified to the lowest taxonomical level possible using monographs as well as papers for particular taxa (Suppl. material 1). Taxa identified with 'cf.' (*confer*) before the epithet indicate that it could be that taxon but the taxonomic identity is still uncertain, 'aff.' (*affinis*) that it has some similarity to the taxon but it is not conspecific and 'sp.' (species) was used when the taxon showed no similarity with any known species after the literature review.

Data analysis. Only taxa with relative abundance ≥1% were included in the statistical analyses, resulting in 105 diatom taxa. Diatom abundances were transformed using Hellinger's transformation, which is suited to large abundance datasets with lots of low counts and zeros (Legendre and Gallagher 2001).

From the initial dataset composed of 42 samples, only 39 were used for the analysis of running waters, i.e. those streams with water velocity records in at least one of the sampling campaigns; the three samples of site 10 were omitted since no water velocity was recorded in this spring-fed creek at any of the three sampling campaigns, with 10 cm/s being the detection limit of the water velocity meter. All the environmental variables, except for temperature, pH and water velocity were transformed using $\log_{10}$ (x+1) because they had skew distributions. Distribution tests were run in STATISTICA 8.0.

Multivariate analyses were performed to explore gradients in diatom composition and its relation to environmental factors. Detrended Correspondence Analysis (DCA) was used to estimate gradient lengths. The first four axes showed lengths of 5.7, 3, 2.3 and 2.2, suggesting a strong unimodal response, meaning that a method based on unimodal models like Canonical Correspondence Analysis (CCA) would be appropriate for subsequent ordination. CCA was run to identify variation in species composition that can be determined by environmental variables. Since not all the environmental variables influence diatom distributions independently, CCA with forward selection and unrestricted Montecarlo permutation tests was used (999 permutations, $p<0.05$). All ordinations were done using CANOCO 4.5 for Windows (ter Braak and Šmilauer 2002), with downweighting of rare species in all cases.

The indicator value method (IndVal) (Dufrêne and Legendre 1997) was used to identify the most characteristic species of the groups visualized after the CCA. This method combines the specificity (relative abundance) and fidelity (relative frequency) of a species to a given group. The indicator value of a species is given in percentage, reaching its maximum when all the individuals of a species are present at all the sites of a single group. Species with high indicator values >50% are considered to be good indicators; species with values between 25–50% might be regarded as detector species of change, therefore detector species can be present in more than one group (Tornés et al. 2007, Carmona-Jiménez et al. 2016). IndVal calculations were run in PC–ORD

4 (McCune and Mefford 1999) with untransformed abundance data. The statistical significance of the IndVal was tested with a randomization Montecarlo test (10,000 permutations, $p<0.05$). The Shannon-Wiener diversity index and Pielou evenness index were calculated as in Peet (1974) for the groups visualized after the CCA.

Results

Species composition and taxonomy. A total of 196 taxa (species and varieties) were found while performing the counts to determine relative abundances. Seventy-eight additional taxa were observed by scanning the whole slides looking for rare taxa, bringing the total diversity to 274 taxa belonging to 48 genera (Suppl. material 1). Sixty-three taxa are new records for the Lerma-Chapala Basin. The most common taxa (relative abundances ≥1% in at least one sample), illustrated here (Figs 2–117), were included in subsequent statistical analyses.

A high specific taxa richness was found among the genera *Nitzschia* (35 taxa), *Gomphonema* (26 taxa), *Pinnularia* (21 taxa), *Navicula* (19 taxa), *Sellaphora* (18 taxa) and *Eunotia* (16 taxa). About a third of the diversity found, 94 taxa, did not fit completely into already described species. Most of the taxa were found in relatively low abundances while further scanning the slides under the LM after the enumeration of 500 valves; when scanning samples under the SEM, some of those rare unidentified taxa were found but in several cases not. When the taxa were found under the SEM, not enough valves were observed for reliable identification. This is why only two new species from those 94 unidentified taxa are here described as new, one belonging to the genus *Brachysira* and the other to *Sellaphora*. Furthermore, one *Eolimna* species is transferred to *Sellaphora*, this species sharing the same morphology of areolae as the *Sellaphora* species here described as new.

Brachysira altepetlensis **D.Mora, R.Jahn & N.Abarca, sp. nov.**

Figs 118–132

Holotype. B 40 0042006; Figure 121 represents the holotype.

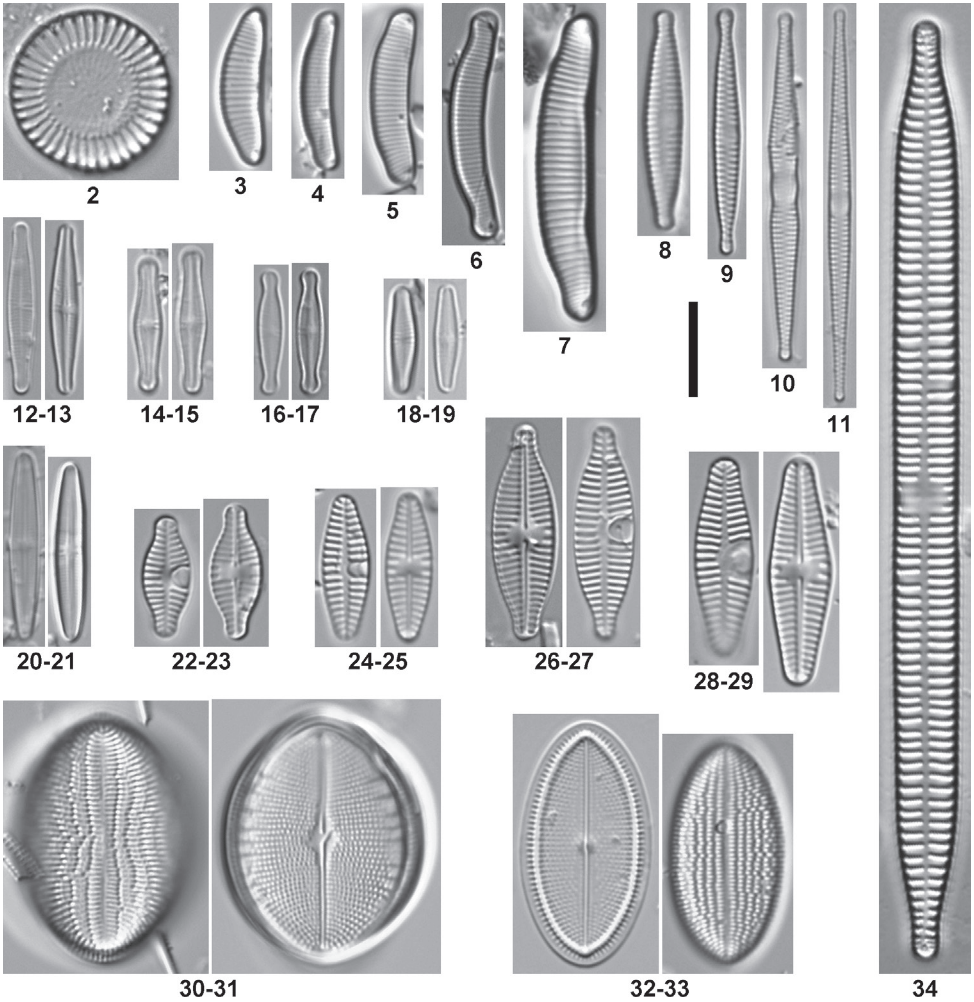
Isotypes. B 40 0042007 (SEM stub), QMEX DIAT0001 (Slide).

Cleaned unmounted material is available under the numbers B 40 0042008 and QMEX DIAT0002.

Type locality. Paredones stream, on the outskirts of Paredones village, Dolores Hidalgo, Guanajuato, Mexico (21°11'20.60"N; 101°06'53.40"W; 2089 m a.s.l). Collected by Demetrio Mora on 07.09.2014.

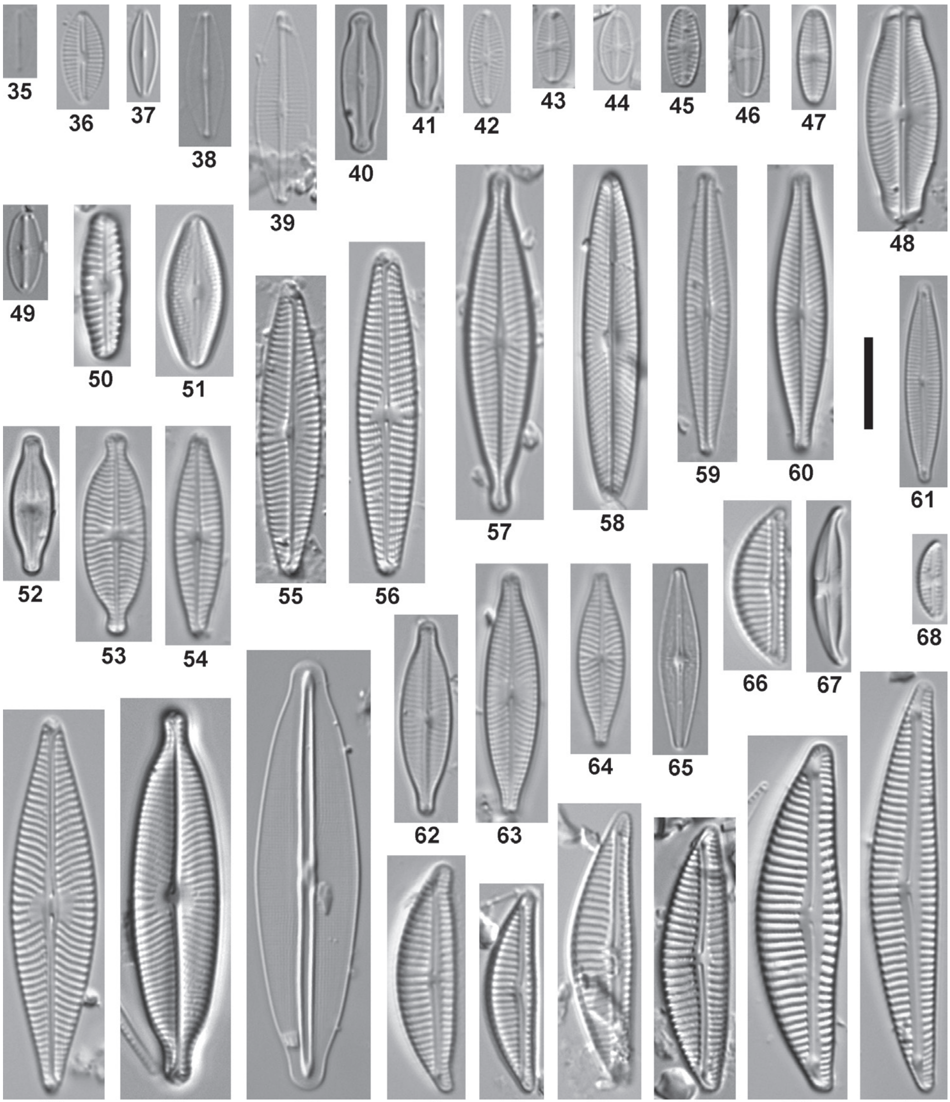
Registration. http://phycobank.org/100101

Description. the valves are lanceolate to linear–lanceolate with rostrate apices. The axial area is narrow–linear throughout the valve and the central area round to elliptical (Figs 118–128). Length: 12.6–23.1 µm, width: 3.2–4.5 µm, length/width ratio: 3.2–5.4; striae

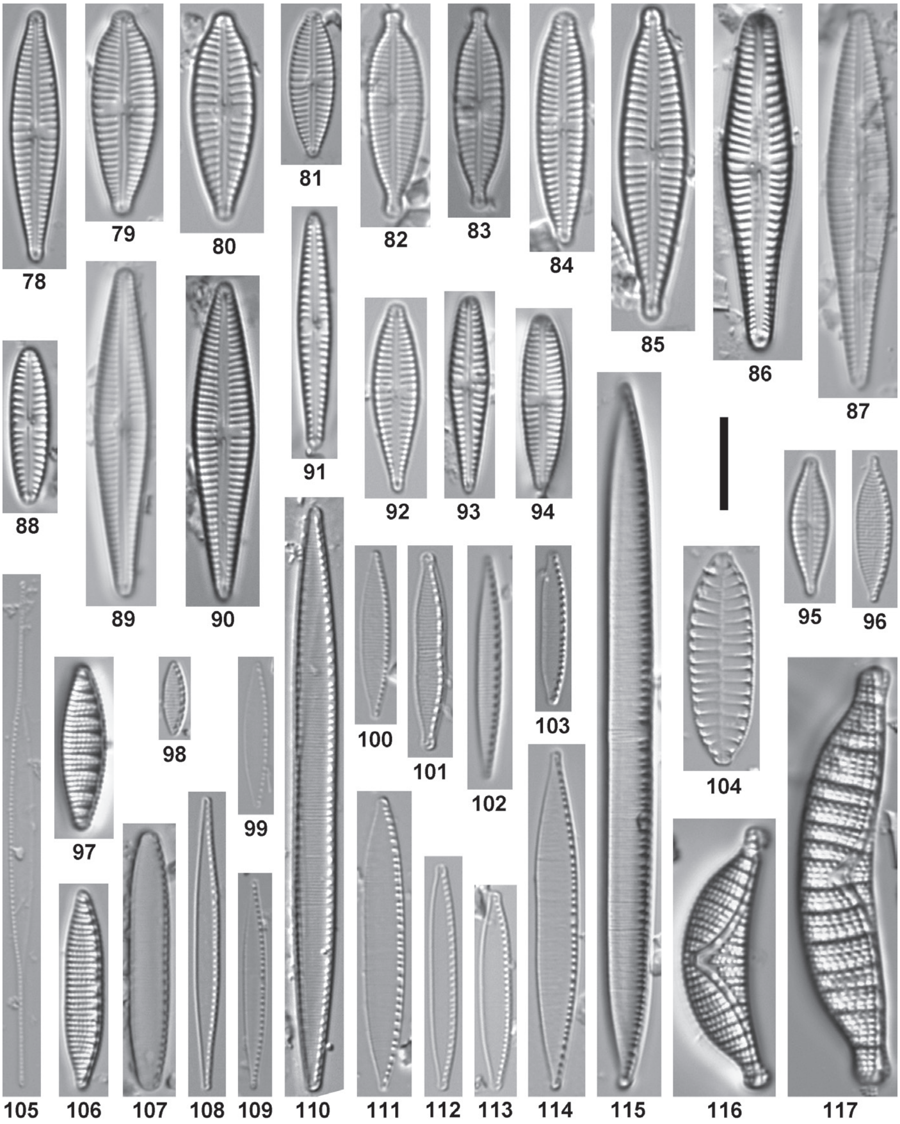


Figures 2–34. Overview of the most abundant taxa (≥ 1% relative abundance in at least one sample). **2** *Cyclotella meneghiniana* **3** *Eunotia* cf. *meridiana* **4** *Eunotia* sp. 1 **5** *Eunotia* sp. 3 **6** *Eunotia* sp. 2 **7** *Eunotia minor* **8** *Fragilaria pectinalis* **9** *Fragilaria austriaca* **10** *Fragilaria bidens* **11** *Fragilaria tenera* **12–13** *Achnanthidium* sp. 5 **14–15** *Achnanthidium* aff. *catenatum* **16–17** *Achnanthidium* sp. 1 **18–19** *Achnanthidium minutissimum* **20–21** *Achnanthidium* sp. 4 **22–23** *Planothidium rostratum* **24–25** *Planothidium victori* **26–27** *Planothidium incuriatum* **28–29** *Planothidium cryptolanceolatum* **30–31** *Cocconeis pediculus* **32–33** *Cocconeis* sp. 2 **34** *Ulnaria ulna*. Scale bar 10 µm.

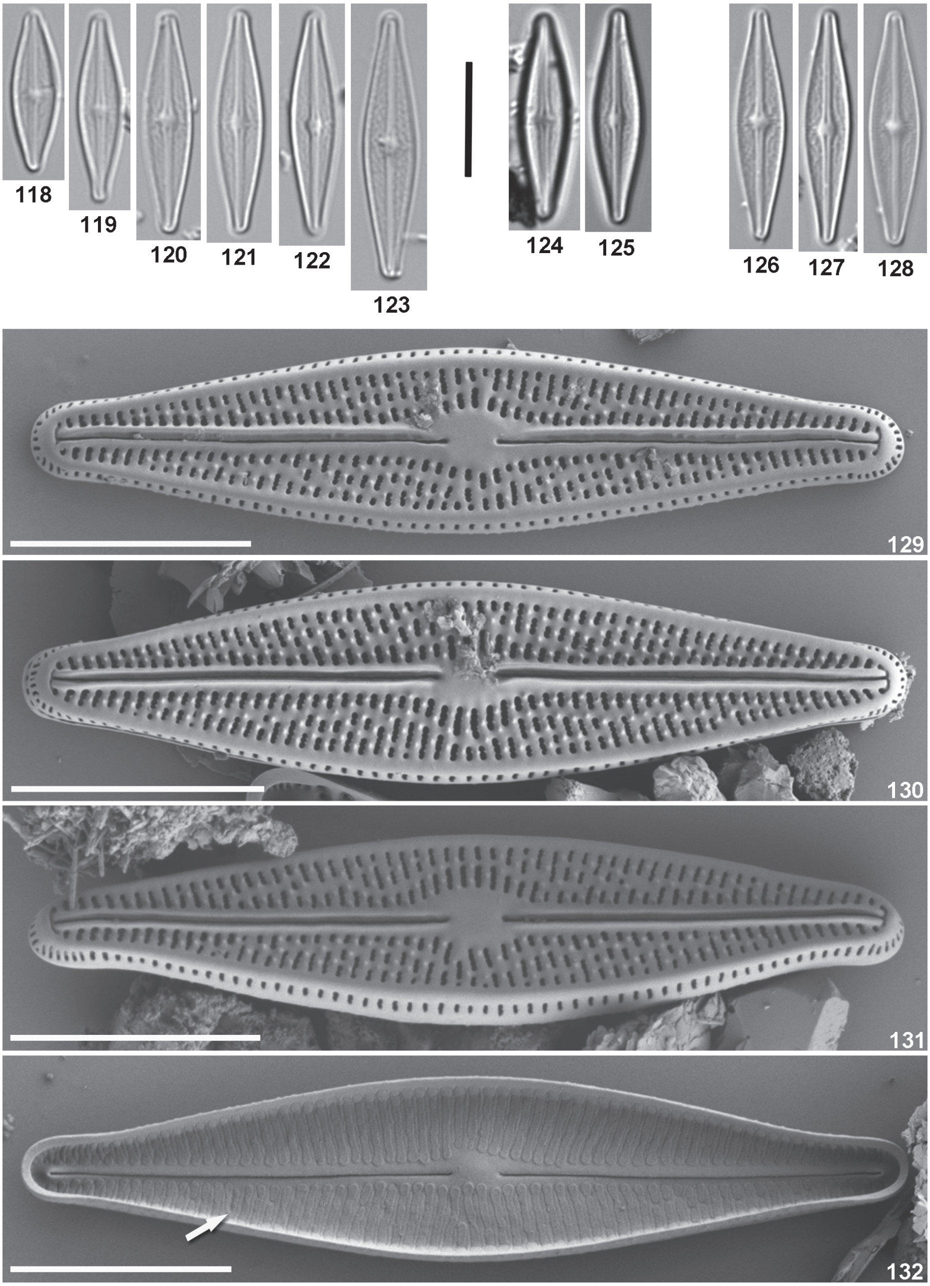
in 10 µm: 34–37. The raphe is filiform, slightly sinuous, bordered by a thickened longitudinal siliceous rib on both sides (Figs 129–131). The proximal raphe ends are straight, while the distal raphe endings are T-shaped (Figs 129–131). Internally, the proximal raphe endings are slightly bent to the same side of the valve and distally end in helictoglossa (Fig. 132). The striae are uniseriate and radiate throughout; composed of 2–3 transapically elongated areolae except close to the apices where only one elongated areola is present (Figs



Figures 35–77. Overview of the most abundant taxa (≥ 1% relative abundance in at least one sample). **35** *Fistulifera saprophila* **36** *Craticula subminuscula* **37** *Craticula* sp. 2 **38** *Craticula molestiformis* **39** *Craticula* cf. *pumilio* **40** *Sellaphora cosmopolitana* **41** *Sellaphora* sp. 3 **42** *Eolimna* sp. 1 **43** *Sellaphora nigri* **44** *Sellaphora madida* **45** *Sellaphora queretana* **46** *Sellaphora atomoides* **47** *Sellaphora saugerresii* **48** *Sellaphora pupula* **49** *Mayamaea permitis* **50** *Reimeria sinuata* **51** *Diadesmis confervacea* **52** *Nupela wellneri* **53** *Geissleria decussis* **54** *Navicula veneta* **55** *Navicula erifuga* **56** *Navicula libonensis* **57** *Navicula capitatoradiata* **58** *Navicula symmetrica* **59** *Navicula notha* **60** *Navicula* cf. *cryptocephala* **61** *Encyonopsis* cf. *thienemannii* **62** *Navicula gregaria* **63** *Navicula cryptocephala* **64** *Navicula reichardtiana* **65** *Brachysira altepetlensis* **66** *Encyonema minutum* **67** *Halamphora montana* **68** *Amphora pediculus* **69** *Navicula trivialis* **70** *Navicula rostellata* **71** *Frustulia crassinervia* **72** *Encyonema brevicapitatum* **73** *Encyonema minutiforme* **74** *Encyonema* cf. *minutiforme* **75** *Encyonema* cf. *hebridiforme* **76** *Encyonema jemtlandicum* **77** *Encyonema pergracile*. Scale bar 10 µm.



Figures 78–117. Overview of the most abundant taxa (≥ 1% relative abundance in at least one sample). **78** *Gomphonema exilissimum* **79** *Gomphonema parvuliforme* **80** *Gomphonema* cf. *parvuliforme* **81** *Gomphonema parvulum* **82** *Gomphonema lagenula* **83** *Gomphonema* cf. *lagenula* **84** *Gomphonema* aff. *sarcophagus* **85** *Gomphonema* aff. *mariovense* **86** *Gomphonema subclavatum* **87** *Gomphonema stonei* **88** *Gomphonema pumilum* **89** *Gomphonema graciledictum* **90** *Gomphonema naviculoides* **91** *Gomphonema minusculum* **92** *Gomphonema* sp. 4 **93** *Gomphonema* sp. 2 **94** *Gomphonema innocens* **95** *Gomphonema* aff. *parvulius* **96** *Nitzschia desertorum* **97** *Nitzschia semirobusta* **98** *Nitzschia inconspicua* **99** *Nitzschia* sp. 1 **100** *Nitzschia supralitorea* **101** *Nitzschia* cf. *hantzschiana* **102** *Nitzschia fonticola* **103** *Nitzschia perminuta* **104** *Surirella angusta* **105** *Nitzschia acicularis* **106** *Nitzschia amphibia* **107** *Nitzschia communis* **108** *Nitzschia gracilis* **109** *Nitzschia paleacea* **110** *Nitzschia intermedia* **111** *Nitzschia palea* **112** *Nitzschia palea* var. *tenuirostris* **113** *Nitzschia palea* var. *debilis* **114** *Nitzschia balcanica* **115** *Nitzschia linearis* **116** *Epithemia sorex* **117** *Epithemia adnata*. Scale bar 10 μm.



Figures 118–132. *Brachysira altepetlensis* D. Mora, R. Jahn & N. Abarca, sp. nov. LM (**118–128**) and SEM (**129–132**). **118–123** type material, from Paredones stream, Guanajuato, Mexico, collected on 07.09.2014 **121** designated as holotype **124–125** collected from type location but on 06.10.2013 **126–128** collected from type location but on 09.02.2014 **129–132** from type material: **129–130** external view of entire valves **131** external view of an entire valve showing elongated areolae in the valve mantle **132** internal view of entire valve, showing occlusion of the areolae by hymens. The arrow points at Voigt discontinuity. Scale bars 10 µm (**118–128**); 5 µm (**129–132**).

129–131). Striae in the valve mantle are composed of single elongated areola (Fig. 131). In some valves the Voigt discontinuity can be seen (Fig. 132). Internally the areolae are occluded by hymens (Fig. 132). The virgae have irregularly spaced papillae (Figs 129–131).

Differential diagnosis. *Brachysira procera* Lange-Bertalot & Gerd Moser is the species which most closely resembles *B. altepetlensis* in valve outline but is larger (25–60 µm), wider at valve center (4.5–6 µm) and has less striae in 10 µm (27–30) (Lange-Bertalot and Moser 1994). The valve outline of *Brachysira neglectissima* Lange-Bertalot also resembles that of *B. altepetlensis* but the valves of *B. neglectissima* are wider (4.3–4.5 µm), have more striae (36–40), the areolae are arranged in a way that they give the appearance of waves and each single areola is comparatively not as elongated as in *B. altepetlensis* (Lange-Bertalot and Moser 1994). *Brachysira guarrerai* Vouilloud, Sala & Núñez-Avellaneda is also similar in valve outline but the valves are wider (5.5–7 µm), have less striae (26–32) and lack papillae in the interstriae (Vouilloud et al. 2014).

The valve dimensions as well as the striae density of the new species fall within the range of the *Brachysira neoexilis* Lange-Bertalot species complex, but the type population of *B. neoexilis* has clear capitate apices and the larger specimens have a very slightly triundulate valve margins (Lange-Bertalot and Moser 1994). All the other populations from *B. neoexilis* species complex depicted in the original description (Lange-Bertalot and Moser 1994) have subcapitate to capitate apices, not matching at all the outline of *B. altepetlensis*. The specimens depicted in Rumrich et al. (2000), identified as *B. neoexilis* (Pl. 89: figs 18–20), closely resemble *B. altepetlensis* in valve outline but they clearly differ from specimens depicted in the type description of *B. neoexilis* (Lange-Bertalot and Moser 1994). The specimens of *Brachysira* found by Abarca-Mejía (2010) in a spring also in the Lerma-Chapala Basin, closely resemble *B. altepetlensis* in LM, but her identification was based on Rumrich et al. (2000), which led her to identify those valves as *B. neoexilis*.

Etymology. this new *Brachysira* species takes the name from the word "āltepētl" which means "water mountain" in Náhuatl language, that is how the surrounding mountains were used to be named by native people 500 years ago, at the time Spaniards first came to the region.

Distribution. apart from the type locality, this species was also found in four streams sampled for this study, namely Peña Colorada (site 4), San Martín (site 5), La Laborcilla 1 (site 7) and La Laborcilla 2 (site 8), all of these sites were characterized by low specific conductivity (≤ 100 µS/cm) and pH values going from acidic to slightly alcaline (5.1–7.9). But *B. altepetlensis* only reached high relative abundances (>10%) in acidic waters (pH= 5.1–5.8) with low specific conductivity (42–53 µS/cm).

Sellaphora queretana **D.Mora, N.Abarca & J.Carmona, sp. nov.**

Figs 133–144

Holotype. B 40 0042009; Figure 137 represents the holotype.

Isotypes. B 40 0042010 (SEM stub), QMEX DIAT0003 (Slide).

Cleaned unmounted material is available under the numbers B 40 0042011 and QMEX DIAT0004.

Type locality. stream Los Ailes 1, close to the town San Pedro, Huimilpan, Querétaro, Mexico (20°19'58.72"N; 100°15'17.09"W; 2358 m a.s.l). Collected by Demetrio Mora on 18.09.2013.

Registration. http://phycobank.org/100102

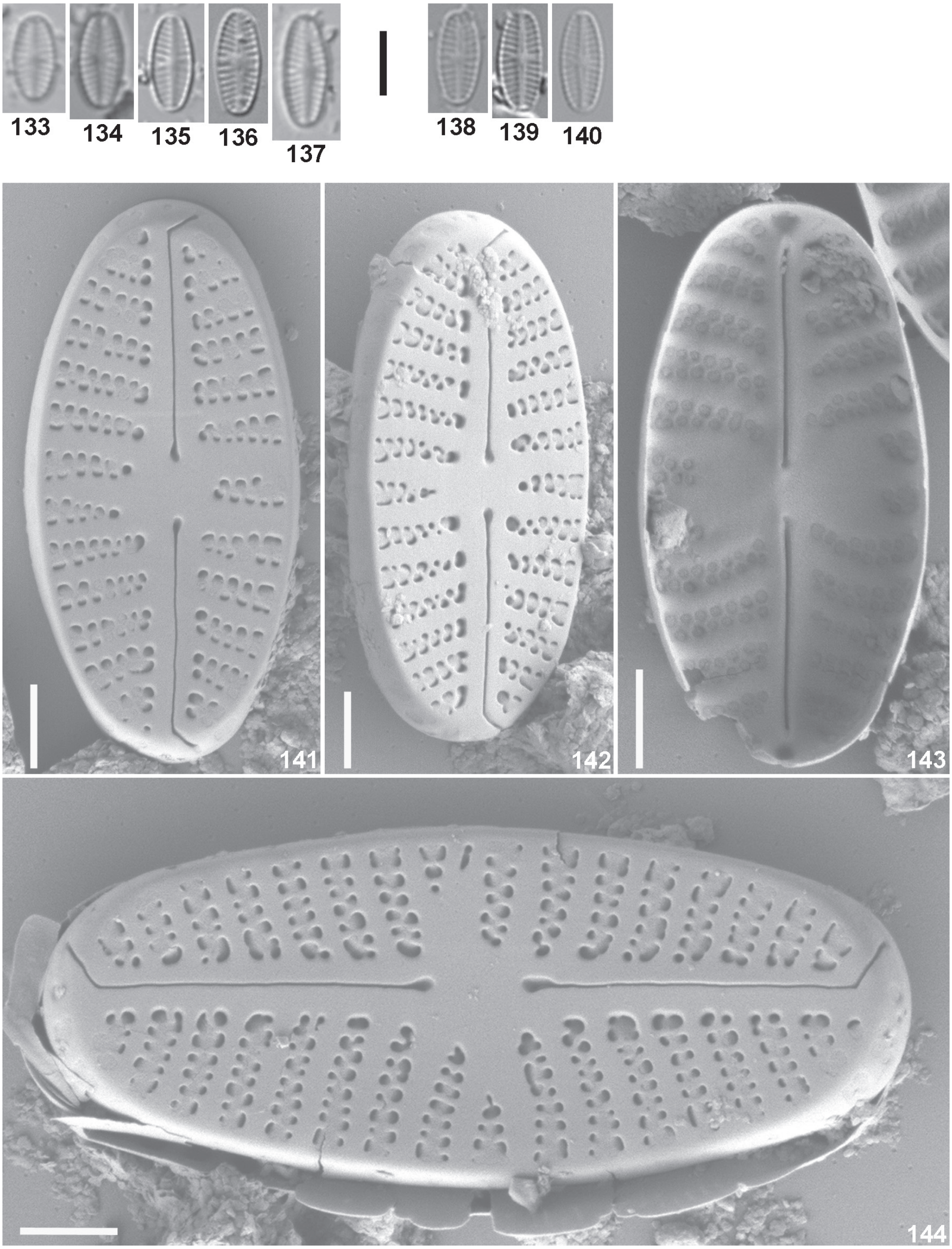
Description. the valves are linear–elliptical with broadly rounded apices (Figs 133–140). The axial area is narrow–linear throughout most of the valve, slightly widening close to the central area. The central area is asymmetrical due to irregular shortenings of the striae bordering it (Figs 141, 142 and 144). Length: 5.6–8.4 µm, width: 2.8–3.9 µm, length/width ratio: 1.9–2.4; striae in 10 µm: 19–22. The raphe is filiform with enlarged proximal raphe endings and slightly deflected to the same side of the valve; the distal raphe endings are strongly bent to the same side of the valve and extended onto the mantle (Figs 141, 142 and 144); the deflection of both proximal and distal raphe endings in external valve face is in the same direction (Figs 141, 142 and 144). Internally, the proximal raphe endings are straight and distally the raphe ends in helictoglossa (Fig. 143). The striae are biseriate and radiate throughout, however becoming uniseriate near the central area (Figs 141, 142 and 144). The areolae are lunate in form and are internally occluded by a hymen (Fig. 143). The hymenes are close to the foramina (seen on external view) (Figs 141, 142 and 144).

Differential diagnosis. there are no known taxa with the same combination of valve outline and areola type. The outline of *S. queretana* resembles that of *Sellaphora chistiakovae* (Kulikovskiy & Lange–Bertalot) C.E. Wetzel, Ector, Van de Vijver, Compère & D.G. Mann; the linear–elliptical forms of *Sellaphora crassulexigua* (E. Reichardt) C.E. Wetzel & Ector; and that of *Sellaphora nigri* (De Notaris) C.E. Wetzel & Ector. But *S. chistiakovae* has uniseriate to irregularly biseriate striae (Kulikovskiy et al. 2010); *S. crassulexigua* and *S. nigri* have uniseriate striae (Wetzel et al. 2015). Taxa with similar striae, with hymenes close to the foramina, include *Sellaphora labernardierei* Beauger, C.E.Wetzel & Ector, *Sellaphora rhombelliptica* (Gerd Moser, Lange–Bert. & Metzeltin) C.E. Wetzel & Ector, *Sellaphora rhombica* (Gerd Moser, Lange–Bert. & Metzeltin) D. Mora, N. Abarca & R. Jahn, comb. nov. (see new combination below) and *Sellaphora thioense* (Gerd Moser, Lange–Bert. & Metzeltin) C.E. Wetzel, Ector, Van de Vijver, Compère & D.G. Mann. But the valves of *S. labernardieri* are linear to linear–elliptical, slightly inflated at the center and have consistently more striae 10 µm (20–28, mainly 24–25) (Beauger et al. 2016). *Sellaphora rhombelliptica* has more striae (25), which are uniseriate and the valves are rhomboelliptic (Moser et al. 1998). *Sellaphora rhombica* has similar number of striae (17–21) but the valve outline is rhombic to rhombic–lanceolate (Moser et al. 1998). *Sellaphora thioense* has slender elliptical valves (2.5–2.8) with higher striae density (27–28) (Moser et al. 1998).

Etymology. this new *Sellaphora* species takes its name from the demonym of the Mexican state Querétaro, from where it was collected.

Distribution. so far only known from the type locality (sampling site 11 in this study) and from stream Laguna de Servín 2 (site 13) located 4 km away from the type location, in acidic waters (pH 5.9–6.2) with low conductivity (77–88 µS/cm).

Based on morphological similarities with other small *Sellaphora* species, *Eolimna rhombica* Gerd Moser, Lange–Bertalot & Metzeltin is transferred to *Sellaphora*:



Figures 133–144. *Sellaphora queretana* D. Mora, N. Abarca & J. Carmona, sp. nov. LM (**133–140**) and SEM (**141–144**). **133–137** type material, from stream Los Ailes 1, Querétaro, Mexico, collected on 18.09.2013 **137** designated as holotype **138–140** population from stream Laguna de Servín 2, collected on 29.09.2013 **141–144** from type material: **141, 142, 144** external views of entire valves **143** internal view of an entire valve. Scale bars 5 μm (**133–140**); 1 μm (**141–144**).

Sellaphora rhombica (Gerd Moser, Lange-Bertalot & Metzeltin) D.Mora, N.Abarca & R.Jahn, comb. nov.

Basionym. *Eolimna rhombica* Gerd Moser, Lange-Bertalot & Metzeltin, 1998, Bibliotheca Diatomologica, vol. 38, p. 156, pl. 23, figs 11–20.

Registration. http://phycobank.org/100103

Community analysis

The physical and chemical composition of the water from the sampling sites, as well as QBR values are enlisted in Table 2. From the original dataset of 14 environmental variables used in the DCA, total dissolved solids and total alkalinity were highly correlated with specific conductivity and therefore removed from the analysis. Dissolved oxygen and dissolved oxygen saturation percentage were also highly correlated, the latter being removed from further analysis. Dissolved inorganic nitrogen was also removed because it correlated strongly with nitrates. CCA with forward selection and unrestricted Monte Carlo permutations tests (999 permutations, $p<0.05$) identified temperature (F=1.60, p=0.028), pH (F= 2.53, p=0.0010), specific conductivity (F= 5.07, p=0.0010), soluble reactive phosphorous (F=1.68, p=0.0060) and the Riparian Forest Quality Index (F=2.47, p=0.0010) as the variables that significantly explained variation in the diatom data. The first two CCA axes accounted for 66.5 % of the cumulative variance of the species – environmental relation, both axes being significant (p=0.0010). The first CCA axis was strongly correlated with specific conductivity (inter-set correlation r= 0.93) and pH (r= 0.80). The second CCA axis was negatively correlated with QBR (r= -0.61) and positively correlated with temperature (r= 0.44).

On the CCA biplot three groups of samples were visualized (Fig. 145). The first group, situated at the bottom left part of the plot is composed of sites with the most acidic waters and lowest specific conductivity on average. The average number of species for this group was 16 (Table 3). This group was characterized by *Achnanthidium* sp. 1, the only taxon with a high indicator value (IndVal >50%). Other indicator taxa (IndVal 20–50%) for this group were *Achnanthidium* aff. *catenatum* (J.Bílý & Marvan) Lange-Bertalot, *Brachysira altepetlensis*, *Eunotia* sp. 3, *Fragilaria austriaca* (Grunow) Lange-Bertalot, *Frustulia crassinervia* (Brébisson) Lange-Bertalot & Krammer and *Gomphonema exilissimum* (Grunow) Lange-Bertalot & E. Reichardt (Table 4).

The second group, found on the upper middle side of the plot contains samples with circumneutral waters, low in specific conductivity and the highest mean temperature and soluble reactive phosphorous concentrations. The mean number of species was 17 (Table 3). These sites were characterized by *Craticula molestiformis* (Hustedt) Mayama, *Encyonema minutum* (Hilse) D.G. Mann, *Mayamaea permitis* (Hustedt) Bruder & Medlin and *Nitzschia palea* var. *tenuirostris* Grunow, all these taxa with high and significant IndVals (>50%) (Table 4).

Table 2. Physical and chemical composition of the water from the sampling sites in the Lerma−Chapala Basin. Samples were taken in September/October 2013 for sampling campaign I, in February 2014 for the campaign II and in September 2014 for campaign III. T= temperature in °C; Cond= specific conductivity corrected at 25°C (µS/cm); TDS= total dissolved solids as particles per million (ppm); TA= total alkalinity mg/L of $CaCO_3$; *v*= water velocity (cm/s); DO= dissolved oxygen (mg/L); DOS= dissolved oxygen saturation percentage; SRP = soluble reactive phosphorous (mg/L); NO_2^-−N = nitrite nitrogen (mg/L); NO_3^-−N = nitrate nitrogen (mg/L); NH_4^+−N= ammonium nitrogen (mg/L); DIN= dissolved inorganic nitrogen (mg/L); QBR= Riparian Forest Quality Index.

Sampling campaign	Site	T	pH	Cond	TDS	TA	*v*	DO	DOS	SRP	NO_2^-−N	NO_3^-−N	NH_4^+−N	DIN	QBR
I Rainy season	1	14.5	6.7	114	45	30	29	6.5	84	1.09	0.005	0.010	0.005	0.02	85
	2	16.1	7.5	417	173	91	33	8.2	107	0.92	0.005	0.010	0.050	0.06	75
	3	17.8	7.7	422	182	93	39	7.2	98	0.59	0.004	0.015	0.025	0.04	75
	4	26.3	7.4	59	30	12	11	6.5	103	0.59	0.004	0.010	0.020	0.03	55
	5	25.8	7.1	100	51	13	24	6.8	105	0.57	0.003	0.010	0.005	0.02	70
	6	20.0	5.8	48	21	9	15	6.7	94	0.49	0.002	0.010	0.000	0.01	75
	7	23.5	6.1	84	41	23	32	7.2	108	0.68	0.003	0.020	0.000	0.02	50
	8	25.4	6.3	70	35	18	38	5.9	91	0.50	0.004	0.020	0.010	0.03	75
	9	23.2	7.2	134	65	38	22	9.7	146	0.67	0.009	1.200	0.055	1.26	30
	10	20.7	7.6	777	357	369	0	16.2	233	0.55	0.176	8.800	0.140	9.12	35
	11	15.9	6.2	88	36	20	24	7.1	96	0.30	0.010	1.250	0.065	1.33	75
	12	16.3	5.8	58	24	10	9	7.2	98	0.36	0.005	0.750	0.000	0.76	60
	13	18.5	5.9	77	34	9	37	7.0	99	0.84	0.015	0.050	0.060	0.12	70
	14	16.4	6.5	96	40	26	38	7.3	99	0.83	0.018	0.140	0.105	0.26	65
II Dry season	1	13.8	7.5	432	170	152	18	8.3	105	0.24	0.015	0.025	0.010	0.05	85
	2	17.4	7.5	878	375	168	24	8.5	115	0.30	0.015	0.030	0.000	0.04	75
	3	18.5	7.7	857	376	168	13	8.7	119	0.23	0.016	0.025	0.000	0.04	75
	4	18.5	7.2	61	27	14	25	8.3	114	0.25	0.015	0.020	0.000	0.04	65
	5	20.5	6.8	79	36	16	19	9.3	131	0.28	0.016	0.020	0.015	0.05	70
	6	17.4	5.8	42	18	7	16	7.9	106	0.29	0.014	0.020	0.010	0.04	65
	7	25.6	7.4	71	36	21	14	9.2	144	0.26	0.016	0.030	0.035	0.08	50
	8	22.7	5.5	53	25	14	17	8.3	123	0.28	0.017	0.030	0.000	0.05	65
	9	14.7	6.1	283	113	83	0	4.2	54	0.32	0.016	0.030	0.000	0.05	30

Sampling campaign	Site	T	pH	Cond	TDS	TA	*v*	DO	DOS	SRP	NO_2^-–N	NO_3^-–N	NH_4^+–N	DIN	QBR
II Dry season	10	18.8	7.4	969	427	461	0	9.7	134	0.83	0.018	0.030	0.015	0.06	35
	11	9.9	6.4	279	99	91	0	6.1	71	0.28	0.015	0.025	0.000	0.04	75
	12	13.8	5.8	94	37	17	0	6.2	81	0.26	0.016	0.030	0.025	0.07	60
	13	12.0	6.3	129	48	22	0	6.4	80	0.26	0.017	0.030	0.015	0.06	60
	14	19.5	6.9	172	77	65	23	6.9	99	0.24	0.014	0.020	0.010	0.04	75
III Rainy season	1	16.5	7.7	125	53	41	32	5.3	71	0.38	0.007	0.015	0.040	0.06	75
	2	16.0	7.2	306	127	66	43	6.1	80	0.29	0.025	0.040	0.145	0.21	65
	3	18.0	7.7	313	136	72	68	6.1	82	0.29	0.017	0.025	0.115	0.16	75
	4	23.9	6.8	40	20	10	31	5.2	79	0.29	0.006	0.010	0.010	0.03	65
	5	26.1	7.9	65	33	19	27	5.5	86	0.31	0.005	0.010	0.005	0.02	70
	6	17.1	5.1	42	18	4	80	5.9	79	0.36	0.006	0.010	0.010	0.03	75
	7	19.9	5.3	55	25	16	62	5.2	73	0.27	0.011	0.020	0.055	0.09	50
	8	22.1	5.5	48	22	12	51	5.1	75	0.13	0.008	0.020	0.030	0.06	65
	9	24.2	6.8	138	68	56	36	5.1	77	0.50	0.005	0.010	0.015	0.03	30
	10	20.8	7.1	850	391	430	0	4.7	67	0.47	0.051	0.165	0.040	0.26	35
	11	15.2	6.8	91	37	34	18	5.0	66	0.71	0.010	0.030	0.140	0.18	65
	12	15.7	5.4	54	22	8	32	5.6	75	0.43	0.005	0.005	0.020	0.03	60
	13	15.8	5.9	78	32	15	45	5.9	80	0.55	0.010	0.030	0.015	0.05	70
	14	17.6	6.5	99	42	32	50	5.3	73	0.46	0.008	0.010	0.020	0.04	65

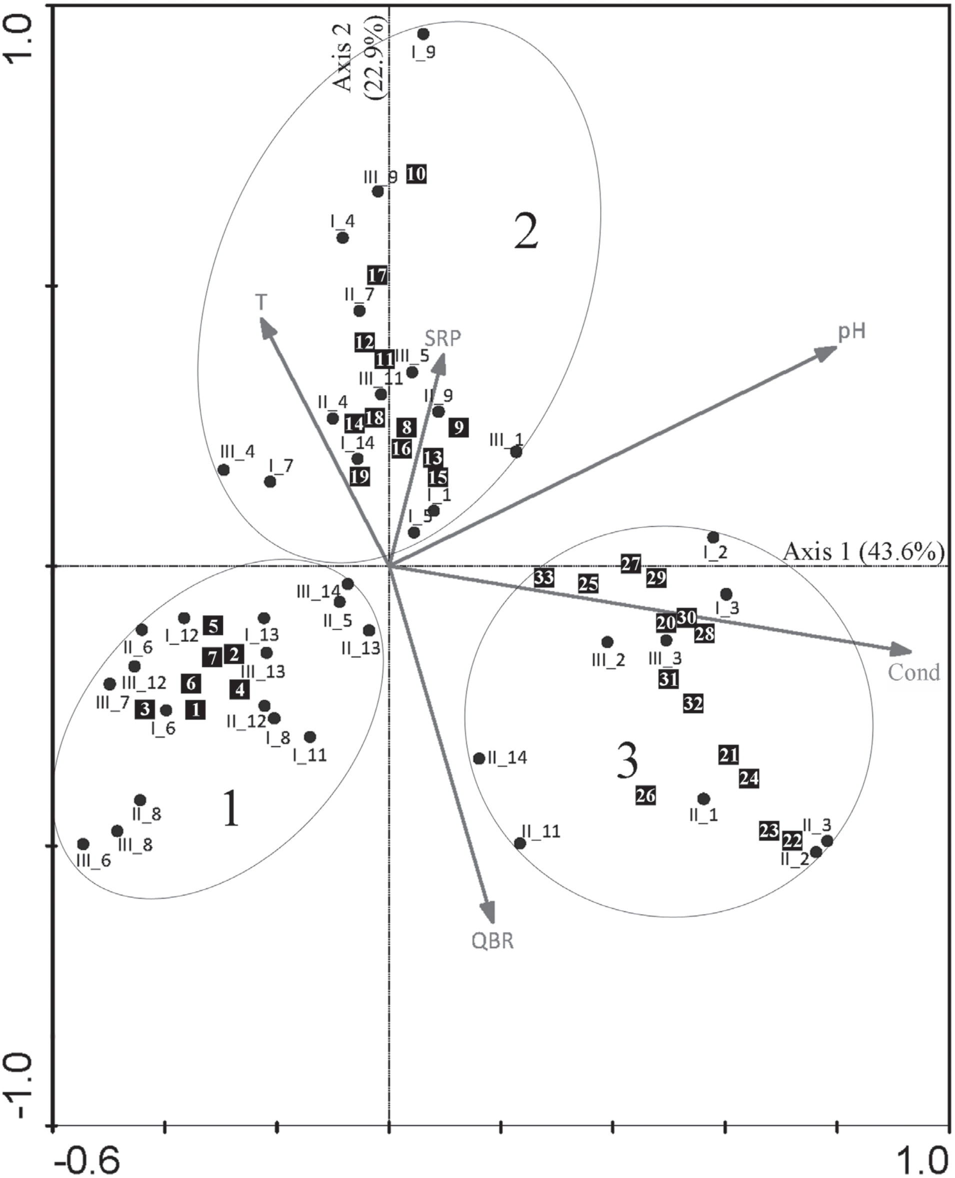


Figure 145. Canonical Correspondence Analysis (CCA) ordination plot. Distribution of sampling sites based on diatom abundance data in relation to statistically significant environmental variables. Three groups of samples are depicted within ovals. For visualization purposes, only species with significant IndVals ($p<$ 0.05) are included in the plot. Black squares correspond to species; numbers within the black squares refer to taxa names in Table 4. Sampling sites are codified as follows: a Roman numeral indicating the sampling campaign (I, II and III), followed by an underscore symbol and an Arabic numeral indicating the sampling site (sites 1 to 14). For abbreviations and units of the physical and chemical parameters refer to Table 2.

Table 3. Diversity indices and physical and chemical composition of the three groups visualized after the CCA. The mean value and standard deviation is provided for each variable. *S*= species richness; *H'*= Shannon-Wiener diversity index; *J'* = Pielou evenness index. For abbreviations and units of the physical and chemical variables refer to Table 2.

	Group 1	Group 2	Group 3
S	16±5	21±6	17±4
H'	2.43±0.33	2.75±0.40	2.53±0.30
J'	0.61±0.12	0.63±0.16	0.56±0.17
T	18.2 ± 3.5	21 ± 4.8	16 ± 2.9
pH	5.9 ± 0.5	7 ± 0.5	7.3 ± 0.5
Cond	70 ± 24	104 ± 59	453 ± 249
TDS	30 ± 9	47 ± 23	191 ± 110
TA	14 ± 7	30 ± 20	107 ± 43
v	31 ± 23	24 ± 11	29 ± 20
DO	6.6 ± 1.2	6.6 ± 1.7	7.3 ± 1.1
DOS	91 ± 18	95 ± 27	97 ± 16
SRP	0.38 ± 0.17	0.5 ± 0.25	0.37 ± 0.23
NO_2^-–N	0.010 ± 0.005	0.008 ± 0.005	0.014 ± 0.006
NO_3^-–N	0.14 ± 0.35	0.11 ± 0.32	0.02 ± 0.01
NH_4^+–N	0.022 ± 0.021	0.031 ± 0.043	0.039 ± 0.054
DIN	0.18 ± 0.35	0.15 ± 0.33	0.08 ± 0.06
QBR	66 ± 7	58 ± 18	75 ± 5

Samples from the third group correspond to well mineralized waters with the highest pH values on average, and also the lowest nitrogen concentrations. The sites in this group scored the higher values for the QBR on average. The mean species richness was 17 (Table 3). This group was characterized by *Cocconeis* sp. 2, *Navicula reichardtiana* Lange-Bertalot, *Nitzschia inconspicua* Grunow, *Planothidium victori* Novis, Braidwood & Kilroy, *Reimeria sinuata* (W. Gregory) Kociolek & Stoermer and *Sellaphora atomoides* (Grunow) C.E. Wetzel & Van de Vijver.

The three sampling campaigns of eight sites are within the same groups of the CCA plot (Fig. 145), pointing out to stability of the diatom communities: samples from sites 6, 8, 12 and 13 are within group 1; sites 4 and 9 within group 2; and sites 2 and 3 in group 3.

In contrast, in 5 sites there were changes of the samples among the three groups. For site 7, one sample from the rainy season is together with the sample from the dry season in group 2, whereas the other rainy season sample is in group 1. The three samples of sites 11 and 14 are one in each of the three different groups observed in the CCA plot (Fig. 145). Only in sites 1 and 5, both rainy season samples are together within the same group, whereas the samples of the dry season are located in a different group.

Table 4. Indicator taxa from the three groups visualized after the CCA. The indicator value of the taxa is accompanied by their relative abundance (RA) and relative frequency (RF) values. Significant IndVals (p< 0.05) are indicated in bold.

	Taxa	Group 1			Group 2			Group 3		
		RA	RF	IndVal	RA	RF	IndVal	RA	RF	IndVal
1	*Achnanthidium* sp. 1	99	69	**68**	0	7	2	1	11	0
2	*Achnanthidium* aff. *catenatum*	77	63	**48**	22	29	6	1	11	0
3	*Brachysira altepetlensis*	96	44	**42**	4	36	1	0	0	0
4	*Eunotia* sp. 3	99	31	**31**	1	7	0	0	0	0
5	*Fragilaria austriaca*	71	56	**40**	29	7	2	0	0	0
6	*Frustulia crassinervia*	100	31	**31**	0	0	0	0	0	0
7	*Gomphonema exilissimum*	64	75	**47**	31	43	13	5	22	1
8	*Craticula molestiformis*	16	31	5	74	79	**58**	10	33	3
9	*Craticula subminuscula*	3	6	0	84	57	**48**	13	56	7
10	*Cyclotella meneghiniana*	0	0	0	100	21	**21**	0	0	0
11	*Encyonema minutum*	11	13	1	85	64	**54**	4	11	0
12	*Eolimna* sp. 1	12	13	2	88	36	**31**	0	0	0
13	*Fistulifera saprophila*	4	6	0	79	57	**45**	17	22	4
14	*Gomphonema* aff. *sarcophagus*	3	13	0	96	43	**41**	1	11	0
15	*Mayamaea permitis*	9	31	3	69	86	**59**	22	67	15
16	*Navicula rostellata*	2	6	0	87	57	**50**	11	11	1
17	*Nitzschia gracilis*	0	0	0	100	29	**29**	0	0	0
18	*Nitzschia palea* var. *debilis*	8	25	2	91	50	**45**	1	11	0
19	*Nitzschia palea* var. *tenuirostris*	9	38	4	91	64	**58**	0	0	0
20	*Amphora pediculus*	0	0	0	3	7	0	97	44	**43**
21	*Cocconeis* sp. 2	0	0	0	2	14	0	98	67	**66**
22	*Cocconeis pediculus*	0	0	0	0	0	0	100	22	**22**
23	*Epithemia adnata*	0	0	0	0	0	0	100	33	**33**
24	*Epithemia sorex*	0	0	0	4	7	0	96	44	**43**
25	*Gomphonema pumilum*	0	6	0	28	21	6	72	67	**48**
26	*Gomphonema minusculum*	0	0	0	0	0	0	100	33	**33**
27	*Halamphora montana*	0	0	0	16	14	2	84	56	**46**
28	*Navicula reichardtiana*	0	0	0	0	0	0	100	56	**56**
29	*Navicula gregaria*	0	0	0	13	14	2	87	56	**48**
30	*Nitzschia inconspicua*	1	13	0	0	0	0	99	56	**55**
31	*Planothidium victori*	0	6	0	12	29	3	88	78	**69**
32	*Reimeria sinuata*	0	0	0	0	0	0	100	67	**67**
33	*Sellaphora atomoides*	10	31	3	20	29	6	70	78	**54**

Discussion

Species composition and taxonomy. The species richness found, 274 taxa, was relatively high compared to previous studies on the basin: 209 taxa were found by Abarca-Mejía (2010) from 59 samples analyzed from three substrates; 178 taxa by Segura-García (2012) from 66 epilithon samples analyzed; 173 taxa by Mora et al. (2015) from 12 epilithon samples; and 70 taxa by Segura-García (2016) from 16 epilithon samples.

This kind of comparison is difficult to make since it depends on the number of samples analyzed, the timing of the samplings, the physical and chemical composition of the waters, the number of substrates sampled and the taxonomic effort with which the diatom valves were analyzed (Morales et al. 2001, Veselá and Johansen 2009). Nevertheless, our results on taxa diversity are higher than the four previous studies conducted in the basin.

The resulting high diversity found in our study can be explained by the detail at which samples were analyzed under both LM and SEM, which resulted in the separation of several morphodemes instead of lumping them into species complexes. The fact that a third of the flora, 94 morphodemes, could not be assigned to described species is not surprising due to the nature of the samples, coming from within the tropics, for which no extensive identification floras have been produced yet, compared to northern temperate regions. Furthermore, it is encouraging to have such a big number of unidentified morphodemes, because they could be helpful in the quest of unravelling if the freshwater diatom floras of Mexico have certain biogeographical affinities, as it would be expected due to the fact that the country lies within the so called Mexican Transition Zone, a complex area in which Neotropical and Nearctic biotic elements converge (Huidobro et al. 2006). This task could be facilitated by coupling detailed morphological examinations with molecular tools (Trobajo et al. 2009, Abarca et al. 2014, Zimmermann et al. 2014).

In most of the freshwater diatom floras generated for Mexico, there seems to be a high intrinsic cosmopolitism, with a large proportion of taxa from north temperate waters. Nowadays it seems unlikely to find large amounts of shared species with north temperate regions due to mounting evidence that even microorganisms like diatoms have biogeography (Kociolek and Spaulding 2000, Vanormelingen et al. 2008, Abarca et al. 2014). This raises the question of identification literature and the detail with which samples are analyzed, such as force-fitting identifications to north temperate taxa and lumping into broad species complexes due to limited high resolution microscopy tools.

On the other hand, finding a large proportion of cosmopolitan taxa should not be that surprising since isolated areas such the Andes have shown to have as much as 42% cosmopolitan taxa, but also a considerable proportion of newly described taxa (9.5%) plus seemingly endemic regionals (Lange-Bertalot 2007). So far these 9.5% of newly described taxa have not been the case for the flora from the Lerma-Chapala Basin or even Central Mexico, for which no species from streams have been described as new in the last 25 years. Within the basin, the number of unidentified taxa, potentially containing undescribed species varies from 6% in Segura-García (2012), to 19% in Abarca-Mejía (2010) and 22% in Mora et al. (2015) but as those authors pointed out, further examinations on some of those taxa are needed to determine if they really should be described as new species.

Another hypothesis that could explain the high species richness found in our study is the heterogeneity of environmental conditions of the study areas: a) the sampling campaigns were done in both rainy and dry seasons; b) varied geomorphologies of the streams from headwaters to the midlands and also from the plains, resulting in different riparian communities, reflected in the QBR index values obtained; c) streams ranging from perennial to temporary; d) heterogeneity of physical and chemical composition of the water. Environmental heterogeneity of habitats has been proposed in other studies as a determinant of species richness and distribution (Petrov and Nevrova, 2014).

An additional indicator of the heterogeneity of the studied sites is the fact that no single taxon was found in all samples, which contrast with previous findings on the Lerma-Chapala Basin, where the following taxa were found in all sites and seasons *Craticula subminuscula*, *Gomphonema parvulum*, *Navicula veneta*, *Nitzschia amphibia*, *N. capitellata*, *N. palea* and *Sellaphora pupula* (Segura-García 2012, Mora et al. 2015).

When looking at the macroalgae of the studied streams, it is worth mentioning that sampling sites 11–14 host red algae like *Batrachospermum gelatinosum* (Linnaeus) De Candolle, *Paralemanea mexicana* (Kützing) Vis & Sheath and *Sirodotia suecica* Kylin, species typically found in headwater mountain streams of temperate regions (Bojorge-García et al. 2010). On the other hand, in sites 1–10 species rather associated to warmer waters were found, such as *Cladophora mexicana* P. Crouan & H. Crouan. This is another indicator of the heterogeneity of the sampling sites.

Diatom communities. The different diatom compositions found in the Lerma-Chapala Basin were mainly driven by specific conductivity and pH. Temperature, soluble reactive phosphorous and the Riparian Forest Quality Index were statistically significant but when analyzing the mean values and their standard deviations, the border between each group was not distinct.

For both specific conductivity and pH, the lowest values were recorded in the streams located in the headwaters, which is logical since water there has not gone deep into the geological matrix and therefore is not well mineralized. On the other hand, the higher values for both specific conductivity and pH were recorded on the midland and plains, where the streams received more contributions of well mineralized waters, for example from springs. There is no better example of this than what was recorded at sampling site 10, where pH values were high and specific conductivity values were the highest recorded for this study. This phenomenon is shown by Mahlknecht et al. (2004) in an aquifer recharge model for the same area where sampling sites 1–10 from our study are located. In the model, rain water normally has a pH of 5 but as water goes through the geological matrix it can reach pH values of up to 9 through several mineral dissolution processes and cation exchange, before it appears again at the surface i.e. springs.

No clear seasonal effect (rainy and dry seasons) was observed on the three groups of sampling sites observed after the CCA because in every group there are samples from both rainy seasons together with the dry season. Even though there were seasonal variations in physical and chemical factors such as specific conductivity, pH and water velocity, the community composition (species richness and abundance) apparently did not respond to those seasonal fluctuations (Rothfritz et al. 1997, Bojorge-García et al. 2014). This is well exemplified by the fact that the three samples of eight out of 13 sites included in the CCA remained within the same group during the three sampling periods, showing an overall stability of the diatom communities. This stability can be attributed to the fact that seasonal changes, e.g. in water velocity, discharge and chemical variables do not have long term effects so communities revert to their pre-disturbance state after the disappearance of the perturbation (Connell and Sousa 1983, Soininen and Eloranta 2004). On the other hand, perturbations such as mine tailings spills can have long lasting effects on diatom communities due to heavy metal pollution (Sabater 2000). The time it takes for communities to revert to a pre-disturbance state will largely depend on life span, reproduction and recolonization rates of the organisms as well as on the magnitude of the perturbation (Townsend et al. 1997, Soininen and Eloranta 2004). In order to relate seasonal changes in the community structure to fluctuations in environmental conditions, the timing and scale at which samplings should be made has to be proportional to the life span of the organism in question and cover a complete turnover of all individuals or longer (Soininen and Eloranta 2004). Since diatoms have short life cycles, high reproduction rates and recolonization rates that are within weeks (Round 1991, Licursi and Gómez 2009, Lowe 2011), it should be necessary to conduct intensive samplings to demonstrate dependency of changes in community structure due to fluctuations in environmental factors. This could be a reason why we observed an overall stability of the diatom communities. On the other hand, there were changes in the samples from 5 sampling sites, which can be attributed to the timing, since at the time of sampling the community composition was representing the changes due to seasonal fluctuations and not in an overall stable state after reverting from a perturbation (e.g. major flood, drought).

Regarding the characteristic species of the three groups visualized after the CCA, there are several similarities with previous reports on the ecological preferences of these taxa. Some species were found in all three groups but with varying relative abundances, so only those with the largest abundances were taken as the representative for a group.

For group 1, species from genera such as *Brachysira*, *Eunotia* and *Frustulia* are well regarded as characteristic from acidic and electrolyte poor waters (van Dam et al. 1994; Wolfe and Kling 2001; Hofmann et al. 2013; Vouilloud et al. 2014), which fits well to the chemical composition of the waters from the sites of this group. *Fragilaria austriaca*, *Frustulia crassinervia* and *Gomphonema exilissimum* are also regarded as indicators of low nutrients (van Dam et al. 1994). It is interesting to notice the presence of three taxa with uncertain identity, namely *Achnanthidium* aff. *catenatum*, *Achnanthidium* sp. 1 and *Eunotia* sp. 3, characteristic taxa of this group, which hints at the possibility to regard them as characteristic of acidic, and electrolyte and nutrient poor waters. But before their taxonomic position is confirmed, no comparisons about ecological preferences can be made.

The representative species from group 2 were taxa well regarded as indicators of circumneutral and eutrophic waters with varying degrees of perturbation such as *Craticula molestiformis*, *Mayamaea permitis* and *N. palea* var. *tenuirostris* (van Dam et al. 1994; Besse-Lototskaya et al. 2011; Hofmann et al. 2013). Other representatives of the beforehand conditions include *Craticula subminuscula* (Manguin) C.E. Wetzel & Ector, *Cyclotella meneghiniana* Kützing, *Fistulifera saprophila* (Lange-Bertalot & Bonik)

Lange-Bertalot and *Navicula rostellata* Kützing (van Dam et al. 1994; Besse-Lototskaya et al. 2011; Hofmann et al. 2013). The exception for group 2 is *Encyonema minutum*, normally reported from oligo-mesotrophic waters, but the precise ecological preference of this taxon is difficult to tell since it has been long confounded with *Encyonema silesiacum* (Bleisch) D.G. Mann (Hofmann et al. 2013). In the sampling sites belonging to this group, the highest average phosphorous concentrations were recorded. Regarding the degree of perturbation, the QBR values for these sites scored the lowest values on average, which were related to human perturbation on the riparian forest. Some of these sites are in fact close to diffuse pollution sources such as cattle grazing and agriculture.

Regarding group 3, its characteristic species also confirm the meso-eutrophic, mineralized and alkaliphilous nature of its waters, with taxa such a *Cocconeis* sp. 2 (*C. placentula* Ehrenberg *sensu lato* based only on LM observations), *Navicula reichardtiana*, *Nitzschia inconspicua*, *Planothidium victori* (formerly within *Planothidium frequentissimum* (Lange-Bertalot) Lange-Bertalot *sensu lato*), *Reimeria sinuata* and *Sellaphora atomoides* (former *Eolimna tantula* (Hustedt) Lange-Bertalot) (van Dam et al. 1994; Lange-Bertalot 2001). Other taxa characteristic of this conditions include *Amphora pediculus* (Kützing) Grunow, *Epithemia adnata* (Kützing) Brébisson, *Epithemia sorex* Kützing, *Gomphonema pumilum* (Grunow) E. Reichardt & Lange-Bertalot, *Halamphora montana* (Krasske) Levkov and *Navicula gregaria* Donkin (van Dam et al. 1994; Lange-Bertalot 2001). When looking at the average dissolved inorganic nitrogen from the group, the lowest of all three groups, it is hard to explain it based on the seasonal inputs from the surrounding environment. But when looking at the algae present on the water, it is worth mentioning that on all of the sites from this group *Nostoc* spp. was found, in some cases blooming. The presence of these nitrogen-fixing cyanobacteria is regarded as an indicator of poor nitrogen concentrations since these algae can thrive under this condition by actively fixating atmospheric nitrogen (Grimm and Petrone 1997).

Conclusion

This work contributed to increase the knowledge of the diatom flora from the Lerma-Chapala Basin, Central Mexico, providing a diversity baseline and evidence of its distinctiveness from the floras of other areas in Mexico, with a large proportion of unidentified taxa to be described as new. The studied diatom communities are subjected to moderate environmental disturbance, representing a transition between warm and cold waters, with ionic composition, temperature and the quality of the riparian forest being the main factors defining the community composition observed. The next approach to investigate the diatom diversity of the region would be by means of environmental DNA metabarcoding in combination with the development of a taxonomic reference database, in order to highlight the complementary aspect of classical taxonomy and eDNA metabarcoding, i.e. the importance of the reciprocal illumination (Visco et al. 2015; Zimmermann et al. 2015).

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Supplementary material 1

Diatom taxa list from the Lerma-Chapala Basin, Central Mexico and identification references

Authors: Demetrio Mora, Javier Carmona, Regine Jahn, Jonas Zimmermann, Nélida Abarca

Data type: species data

Explanation note: Diatom taxa list from the Lerma−Chapala Basin, Central Mexico

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The Mosses of Crocker Range Park, Malaysian Borneo

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Abstract

This paper reports the mosses from Crocker Range Park (CRP) in Sabah, Malaysian Borneo. In total, 293 species, three subspecies and eight varieties belonging to 118 genera and 36 families are reported. This represents about 40% and 47% of the species and infra-specific taxa reported from Borneo and Sabah, respectively. Out of these, six species are new records for Borneo, namely *Barbella horridula*, *Chaetomitrium lancifolium*, *Distichophyllum leiopogon*, *Rhaphidostichum luzonense*, *Rosulabryum capillare* and *Taxiphyllum taxirameum* and 12 species and one variety are new to Sabah. With these additions, the current number of mosses in Sabah and Borneo are 651 and 766, respectively. The largest family of mosses is Calymperaceae with 35 species and one subspecies, followed by Sematophyllaceae with 32 species and two varieties and Pylaisiadelphaceae with 21 species and one variety. In conclusion, CRP has a very high species richness of mosses which is the second highest in Borneo, after Mount Kinabalu.

Keywords

Bryophytes, CRP, Crocker Range, East Malaysia, Sabah

Introduction

Crocker Range Park (CRP) is located in the west coast of Sabah, East Malaysia in Borneo (latitude 5°07' to 5°56'N and longitude 115°50' to 116°28'E). This park is about 110 km long and 15 km wide, covering an area of 139,919 ha, making it the largest terrestrial park and protected area in Sabah. This park was first designated as a Forest Reserve under the Forest Ordinance in 1969 but was subsequently converted to a State Park in 1984 for the conservation of natural resources and ecosystems, under the jurisdiction of Sabah Parks Trustees (Usui et al. 2006). In June 2014, Crocker Range was designated as a UNESCO Biosphere Reserve consisting of the whole area of CRP and the three forest reserves within the range.

CRP, in the past, had received less attention from bryologists when compared to Kinabalu Park. These two parks are both on the Crocker Range which is the longest range in Sabah, extending from Kudat (northern tip of Borneo) to Sipitang (southern part of Sabah). CRP has become more accessible after the establishment of seven substations within the park between the years 2003 and 2005 and the opening of a new road system from Ulu Kimanis (western part) to Keningau Town (eastern part), cutting through the central part of the park. Another factor which may have contributed to the lesser attention received by CRP is the fact that its highest peak is only 2,076 m a.s.l., just half of that of Mount Kinabalu (4,059 m a.s.l.). Nevertheless, 27% of the total area of CRP is more than 1,000 m a.s.l., with 16 peaks above this height (Usui et al. 2006).

To date, only two studies on mosses from this park have been published. Suleiman and Akiyama (2004) reported 126 species of mosses belonging to 74 genera and 27 families, collected during the CRP Scientific Expedition in 2002 at Ulu Kimanis and adjacent areas within the elevations of 500–1,400 m a.s.l. Recently, Suleiman and Jotan (2015) reported 38 species and three varieties of mosses belonging to 17 genera and 11 families collected during a diversity study of epiphytic mosses along the Minduk Sirung Trail, a new 12 km trail connecting Mount Alab and Mahua substations (north-eastern part). In their study, mosses were collected from only three sampling areas of 20 m × 20 m.

There are two other unpublished studies on mosses in CRP. The first one was by Kong (2006), who conducted a study on the diversity of mosses in Keningau Research Permanent Plot which is only 50 m × 50 m. She collected 40 species belonging to 26 genera and 14 families. The second one was by Chin (2008), who has studied the diversity of epiphytic mosses within 0–2 m of tree trunks, in the Mount Alab Permanent Research Plot (50 m × 50 m). She collected 20 species in 10 genera and seven families in this mossy forest (1,700–1,800 m a.s.l.). The present report attempts to produce a comprehensive checklist of mosses found in CRP based on collections from the year 2002 to 2008 and herbarium specimens deposited in the BORNEENSIS Herbarium of the Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah (BORH) and Herbarium of the Museum of Nature and Human Activities, Hyogo (HYO).

Methods

All specimens of mosses from the following 12 localities within the park were examined and identified. Areas covered are Inobong Visitor and Research Station, Mount Alab, Mile 32-Longkogungan Village, Longkogungan-Kuyungon Village, Salt Trail, Mahua Substation, Mount Minduk Sirung, CRP Headquaters, Ulu Senagang Substation, Melalap Substation, Ulu Membakut Substation and Ulu Kimanis Substation (Figure 1). These locali-

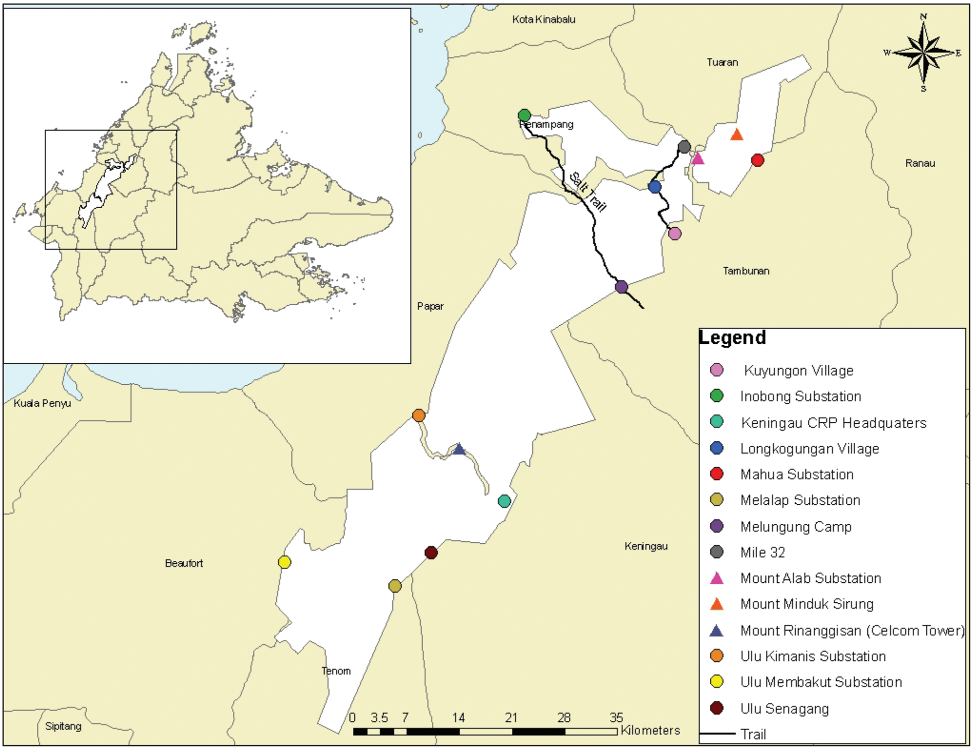

Figure 1. Map of Crocker Range Park showing the localities of collections from the year 2002 to 2008. Inset is map of Sabah, Malaysian Borneo.

ties range from lowland to upper montane forests, covering secondary to primary forests, from 50 m to 2,000 m a.s.l. Details of the collection localities are listed in Table 1. Identified specimens were deposited at BORH and a set of duplicates were sent to the Herbarium of Sabah Park (SNP). Some duplicates were also deposited at HYO, Herbarium of University of Malaya (KLU) and Herbarium of Royal Botanic Gardens Victoria (MEL).

Results and discussion

A total of 1,403 specimens of mosses from CRP were examined during this study. Amongst these, 293 species, three subspecies and eight varieties belonging to 118 genera and 36 families were identified (Table 2 and Appendix 1). The five dominant families of mosses in CRP are Calymperaceae with 35 species and one subspecies (11.8%), followed by Sematophyllaceae with 32 species and two varieties (11.2%), Pylaisiadelphaceae with 21 species and one variety (7.2%), Dicranaceae with 21 species (6.9%) and Daltoniaceae with 20 species (6.6 %). All of these families, except for Dicranaceae, are lowland families as ca. 70% of CRP land area is below 1,000m a.s.l.

Table 1. Locality and collection details of mosses from Crocker Range Park from the year 2002 to 2008. CMK - Chin Mui Ken; DPM - Dunstan Polus Masundang; HA-Cr - Hiroyuki Akiyama-Crocker; KWL - Kong Wai Ling; MS - Monica Suleiman.

Collection numbers	Locality
MS 877–1006	Ulu Kimanis, Mt. Rinangisan and surrounding areas, 5°28.15'N, 116°03.53'E, 27–30 Aug. 2002.
HA-Cr 1–467	Ulu Kimanis, CRP Headquaters and Mt. Alab pass, 27 Aug.–15 Sept. 2002.
MS 1182–1244	Mahua Waterfall, 5°49.60'N, 116°23.11'E, 8-23 July 2003.
MS 1245–1263	Salt Trail, Tikolod to Inobong, 5°39.62'N, 116°15.49'E to 5°51.51'N, 116°8.33'E, 23–28 Aug. 2003.
MS 1386–1391	Mahua Waterfall, Nature Trail and trail to Minduk Sirung, 5°49.60'N, 116°23.11'E, 12–13 Dec. 2003.
MS 1406–1407	Mt. Alab, above Gunung Emas Restaurant, 14 Dec. 2003.
MS 1430–1461	Tenom, Melalap, trail to Tarangtali Hill, along Mesisilad River and Kallang Waterfall, 27–29 Jan. 2004.
KWL 1–96	CRP Headquaters, Permanent Research Plot, 5°23.97'N, 116°06.16'E, 12 Oct. 2005.
MS 1488–1489	Mt. Alab, Permanent Research Plot, 5°49.31'N, 116°20.49'E, 5 July 2006.
CMK 1–163	Mt. Alab, Permanent Research Plot, 5°49.31'N, 116°20.49'E, 24–25 May 2007.
MS & DPM 2357–2434	Mt. Alab, around Mt. Alab Garden, 5°49.31'E, 116°20.49'E, 13 Dec. 2007.
DPM 2–112	Mt. Alab, vicinity of Mt. Alab Substation and Permanent Research Plot, 5°49.31'N, 116°20.49'E, 19–20 Jan. 2008.
MS & DPM 2533–2712	Mahua, Mt. Minduk Sirung, 5°49.60'N, 116°23.11'E, 1–3 Apr. 2008.
DPM 126–180	Ulu Senagang, trail to waterfall and along park boundary, 5°21.78'N, 116°1.72'E, 28–29 Aug. 2008.
DPM 181–258	Inobong Visitor and Research Station, trail to waterfall and Buayan Village, 5°51.51'N, 116°8.33'E, 1–2 Sept. 2008.
MS & DPM 3776–3877	Mt. Alab, vicinity of Mt. Alab Substation, 5°49.31'N, 116°20.49'E, 8–10 Sept. 2008
MS & DPM 3878–3936	CRP Headquaters, Permanent Research Plot & Crocker Trail, 5°23.97'N, 116°06.16'E, 11 Sept. 2008.
DPM 259–318	Ulu Membakut, along Membakut River and park boundary adjacent to Inantul Village, 5°20.97'N, 115°54.06'E, 18–20 Sept. 2008.
MS & DPM 3937–4057	Longkogungan and Kuyungon Village, 5°49.97'N, 116°19.33'E to 5°42.56'N, 116°19.33'E, 22–23 Sept. 2008.
MS & DPM 4058–4095	Bolotikon Village to Melungung Camp, 25 Sept. 2008.
MS 4123–4130	Ulu Kimanis, Mt. Rinangisan and Permanent Research Plot, 5°28.15'N, 116°03.53'E, 13–14 Nov. 2008.
MS 4131–4136	CRP Headquaters, Permanent Research Plot, 5°23.97'N, 116° 06.16'E, 19 Dec. 2008.

The species richness of mosses in the study area is very high; 40% of the total of 766 species and infra-specific taxa reported from Borneo and 47% of the total of 651 species and infra-specific taxa reported from Sabah (Andi and Suleiman 2005, Suleiman et al. 2006, 2009, 2011a, 2011b, 2017, Suleiman and Akiyama 2007, Higuchi et al. 2008, Akiyama 2010, Ho et al. 2010, Ellis et al. 2010, 2015, 2016a, 2016b, Andi et al. 2015, Chua and Suleiman 2015, Mohamed et al. 2010, Suleiman and Rimi 2016).

Table 2. Mosses reported from Crocker Range Park (See Appendix 1 for species checklist).

No.	Families	Genera	Species, subspecies and varieties
1.	Bartramiaceae	1	3 spp.
2.	Brachytheciaceae	3	4 spp.
3.	Bryaceae	4	7 spp.
4.	Calymperaceae	7	35 spp. and 1 subsp.
5.	Cryphaeaceae	1	1 sp.
6.	Daltoniaceae	6	20 spp.
7.	Dicranaceae	8	21 spp.
8.	Diphysciaceae	1	3 spp.
9.	Ditrichaceae	1	1 sp.
10.	Entodontaceae	3	3 spp.
11.	Fissidentaceae	1	13 spp. and 1 var.
12.	Garovagliaceae	1	4 spp. and 1 var.
13.	Hookeriaceae	1	1 sp.
14.	Hypnaceae	6	12 spp.
15.	Hypnodendraceae	3	6 spp.
16.	Hypopterygiaceae	3	4 spp.
17.	Leskeaceae	2	2 spp.
18.	Leucobryaceae	6	16 spp. and 2 var.
19.	Leucomiaceae	1	1 sp.
20.	Meteoriaceae	7	11 spp.
21.	Mniaceae	1	3 spp.
22.	Myuriaceae	1	1 sp.
23.	Neckeraceae	7	14 spp.
24.	Orthotrichaceae	2	7 spp.
25.	Pilotrichaceae	4	5 spp.
26.	Polytrichaceae	2	8 spp. and 2 subsp.
27.	Pottiaceae	3	4 spp.
28.	Pterobryaceae	7	9 spp.
29.	Pylaisiadelphaceae	6	21 spp. and 1 var.
30.	Racopilaceae	1	3 spp. and 1 var.
31.	Regmatodontaceae	1	1 sp.
32.	Rhizogoniaceae	2	4 spp.
33.	Sematophyllaceae	10	32 spp. and 2 var.
34.	Sphagnaceae	1	3 spp.
35.	Symphyodontaceae	2	4 spp.
36.	Thuidiaceae	2	6 spp.
	Total	118	293 spp., 3 subsp. and 8 var.

Out of the 293 species, three subspecies and eight varieties of mosses in CRP, six are new to Borneo and 13 are new to Sabah (Table 3). Amongst the six species new to Borneo, four were found in the lowland areas between 70 m and 680 m a.s.l. Lowland areas in Borneo have not been given enough bryological attention, probably due to the misconception that the lowland rainforest has poor species richness of bryophytes. For instance, *Chaetomitrium lancifolium,* which was collected at 70 m a.s.l. in CRP, represents a second known record after its type collection from the Maluku Islands (see Appendix 1 for details).

Table 3. New records of mosses to Borneo and Sabah.

No.	Moss species and variety	New records	
		Borneo	Sabah
1.	*Acroporium macroturgidum*		+
2.	*Acroporium ramicola*		+
3.	*Barbella horridula*	+	+
4.	*Chaetomitrium lancifolium*	+	+
5.	*Clastobryum scalare*		+
6.	*Distichophyllum leiopogon*	+	+
7.	*Leucobryum javense* var. *cyathifolium*		+
8.	*Leucobryum juniperoideum*		+
9.	*Papillidiopsis malayana*		+
10.	*Rhaphidostichum luzonense*	+	+
11.	*Rosulabryum capillare*	+	+
12.	*Schoenobryum concavifolium*		+
13.	*Taxiphyllum taxirameum*	+	+
	Total	6	13

Table 4. Moss species and infra-specific taxa reported from mountainous areas in Borneo.

Geographical area	Elevation Range (m a.s.l.)	Number of moss species and infra-specific taxa	% of moss species and infra-specific taxa
Kinabalu Park	600-4,095	386	51
Crocker Range Park	50-2,076	304	40
Mount Trus Madi	600-2,642	194	26
Mount Lumaku	700-1,966	130	17

Several of the mosses found in CRP are of temperate entities and rarely reported in Borneo, namely *Claopodium prionophyllum*, *Elmeriobryum philippinense*, *Entodon plicatus*, *Erythrodontium squarrosum*, *Leucomium strumosum*, *Mesonodon flavescens*, *Oxyrrhynchium vagans*, *Pseudoleskeopsis zippelii*, *Regmatodon declinatus* and *Schoenobryum concavifolium*. Five of these species, namely *Claopodium prionophyllum*, *Entodon plicatus*, *Erythrodontium squarrosum, Mesonodon flavescens* and *Oxyrrhynchium vagans*, have only been collected once in Borneo (Dixon 1916, Iwatsuki and Noguchi 1975, Akiyama et al. 2001). *Elmeriobryum philippinense* was collected during the study and reported as new to Borneo by Ellis et al. (2016a). In addition, three species endemic to Borneo were also found in this park: *Benitotania elimbata*, *Ectropothecium ptychofolium* and *Acroporium ramicola* (Appendix 1).

Crocker Range Park ranks the second highest (cf. Table 4) in terms of number of mosses reported from mountainous areas in Borneo (Frahm et al. 1990, Suleiman and Edwards 2002, Suleiman and Akiyama 2004, Higuchi et al. 2008, Akiyama et al. 2001, Andi et al. 2015, Suleiman et al. 2011b). CRP recorded about 40% of the mosses reported from Borneo although the highest point in CRP is only 2,076 m a.s.l. This indicates that CRP has high species richness of mosses, second to that of Mount Kinabalu. Meanwhile, the number of mosses on Mount Trus Madi and Mount Lumaku were much lower, with 26% and 17%, respectively. Although Mount Trus Madi is much higher in terms of elevation, the number of mosses reported from the mountain was far lower than from CRP. Mount Lumaku, on the other hand, has a similar height to the highest peak of CRP but its species richness is only about half that of CRP. Two of the contributing factors are that CRP receives a high annual rainfall and it has a relatively larger area of pristine primary lowland forests than Mount Trus Madi and Mount Lumaku. Nonetheless, a diversity study should be carried out to determine the true diversity of these areas.

Conclusion

CRP is a huge protected area and large parts of this park have not been surveyed during the present study. Thus, additional explorations in less accessible areas will definitely increase the number of mosses in this park and provide a better understanding of the distribution of species within the park. The large area of lowland forests in CRP is an asset to this protected area as it harbours important species of mosses and other plants. Large areas of lowland forest in other parts of Borneo have been cleared for agriculture and development, adding to the importance of conservation of this UNESCO Biosphere Reserve. This study identifies CRP as one of the hotspots of moss diversity in Borneo.

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Appendix I

Checklist of mosses from Crocker Range Park.

The families, genera and species were arranged in alphabetical order. Species reported for the first time for Sabah and Borneo are marked with '*' and '**', respectively. CMK - Chin Mui Ken; DPM - Dunstan Polus Masundang; HA-Cr - Hiroyuki Akiyama-Crocker; KWL - Kong Wai Ling; MS - Monica Suleiman.

Bartramiaceae
Philonotis bartramioides (Griff.) D.G. Griffin & W.R. Buck
On boulders by river banks and road sides, 500–1580 m, DPM 128; MS & DPM 3939.

Philonotis hastata (Duby) Wijk & Margad.
On boulders, 385 m, MS 1447, 1448, 1458.

Philonotis secunda (Dozy & Molk.) Bosch & Sande Lac.
On soil by road sides and along trails in partially shaded and open areas, 680–1800 m, HA-Cr 140; MS 927; MS & DPM 3814, 3873

Brachytheciaceae
Oxyrrhynchium vagans (A. Jaeger) Ignatov & Huttunen
On a rock by a river, 1020 m, MS 1199.

Rhynchostegiella vriesei (Dozy & Molk.) Broth.
On a tree trunk, 940–1120 m, HA-Cr 263.

Rhynchostegium celebicum (Sande Lac.) A. Jaeger
On rotten logs and rocks, 400–1030 m, DPM 184; MS 1210.

Rhynchostegium javanicum (Bél.) Besch.
On a wet rock beside waterfall, 980–1100 m, HA-Cr 292.

Bryaceae
Brachymenium nepalense Hook.
On fallen logs, and tree and shrub trunks, 1150–1400 m, HA-Cr 191, 359; MS 946; MS & DPM 4033.

Bryum apiculatum Schwägr.
On soil and boulders, 650–1800 m, MS & DPM 3875, 3991; HA-Cr 210.

Bryum clavatum (Schimp.) Müll. Hal.
On concrete in open area by road-side, 900 m, MS & DPM 3912.

Bryum coronatum Schwägr.
On crevice by a road-side in open area, 1370 m, MS 925.

Rhodobryum aubertii (Schwägr.) Thér.
On rock by a river, 1030 m, MS 1215, 1219.

Rosulabryum rubens (Mitt.) J.R. Spence
On soil in an open area, 50 m, DPM 295.

***Rosulabryum capillare* (Hedw.) J.R. Spence
On rotten log by a stream, 1600 m, MS & DPM 2695.

Plants yellowish-red, forming lax tufts, 1.5 cm tall, matted with rhizoids at base. Leaves large, flaccid, spatulate, 2.0–2.7 mm × 0.5–0.7 mm; apex broad, rounded with an abruptly long piliform apiculus, arista 0.4–0.6 mm long, coloured; costa reddish, very strong at base, attenuate towards apex; margins revolute, plane 1/3 above, denticulate in apical region, strongly bordered throughout by 1–4 rows of elongated cells, strongly thick-walled, reddish, Mid lamina cells rhomboidal, 49–54 µm × 17–25 µm, thin-walled, rectangular towards leaf base. Sporophyte not seen.

This species is almost cosmopolitan in distribution but is not common in Malesia where it has been recorded previously only from New Guinea, the Philippines and Malaya. It is easily identified by the spatulate leaves with broadly and rounded apex and an abruptly long piliform apiculus as illustrated by Eddy (1996).

Calymperaceae
Arthrocormus schimperi (Dozy & Molk.) Dozy & Molk.
On humus, rotten logs, tree trunks and tree bases, 80–1145 m, DPM 200, 278, 311; KWL 51; MS 1445; MS & DPM 4064.

Calymperes afzelii Sw.
On boulder by river, open area, 550 m, MS & DPM 3996.

Calymperes boulayi Besch.
On tree trunk in open area, 100 m, DPM 317.

Calymperes fasciculatum Dozy & Molk.
On a tree trunk, 1280 m, MS & DPM 3956.

Calymperes lonchophyllum subsp. *beccarii* (Hampe) M. Menzel
On rocks, roots and tree bases by streams, 70–100 m, DPM 259, 292, 308.

Calymperes porrectum Mitt.
On boulder and tree bases by streams, 100–680 m, DPM 135, 268; HA-Cr 154.

Calymperes robinsonii B.C. Tan & W.D. Reese
On boulders and stone-wall by rivers, 410 m, MS 1457.

Calymperes serratum A. Braun ex Müll. Hal.
On shrub trunks, 680–1600 m, HA-Cr 141; MS & DPM 2675.

Calymperes strictifolium (Mitt.) G. Roth
On tree trunks and tree bases, 680 m, HA-Cr 139.

Calymperes taitense (Sull.) Mitt.
On tree root, 500 m, DPM 139.

Exostratum blumii (Nees ex Hampe) L.T. Ellis
On boulders, roots, tree trunks and tree bases, 400–1400 m, DPM 194, 198, 202; HA-Cr 61, 257, 351, 395.; KWL 126a, 22b, 23, 25a, 26, 34, 43, 52a, 53a, 56, 60, 62, 84, 90, 93, 100b, 101, 114.

Exostratum sullivantii (Dozy & Molk.) L.T. Ellis
On a tree trunk, 1310 m, MS 981.

Leucophanes angustifolium Renauld & Cardot
On stone-walls, boulders, roots, tree trunks and bases, 100–1025 m, DPM 131, 155, 160, 162, 271; MS 1209; MS & DPM 3926, 3982.

Leucophanes candidum (Schwägr.) Lindb.
On rotten logs and tree trunks by river banks, 100 m, DPM 272, 313, 318.

Leucophanes octoblepharioides Brid.
On boulders, rotten logs, tree trunk, roots and tree stump, 80–1230 m, DPM 163, 165, 179, 180, 207, 267, 310; KWL 22a, 23, 25c, 93; 126b; HA-Cr 138, 389; MS 1435; MS & DPM 2533.

Mitthyridium fasciculatum (Hook. & Grev.) H. Rob. subsp. *fasciculatum*
On rotten logs, treelet trunks and river bank, 100–1220 m, DPM 274; HA-Cr 181; MS 997.

Mitthyridium fasciculatum subsp. *cordotii* (M. Fleisch.) B.C. Tan & L.T. Ellis
On rotten and fallen logs, and tree trunks, 550–1145 m, DPM 147; HA-Cr 427; MS & DPM 3883.

Mitthyridium repens (Harv.) H. Rob.
On decaying logs, tree trunks and tree bases, 400–800 m, DPM 205, 221; HA-Cr 121.

Mitthyridium subluteum (Müll. Hal.) H.K. Nowak
On climber, 1220 m, MS 996.

Mitthyridium undulatum (Dozy & Molk.) H. Rob.
On tree trunk beside streams, 950–1050 m, KWL 20a; MS 1212; MS & DPM 3932.

Octoblepharum albidum Hedw.
Growing on rotten logs, tree trunks and tree bases, 50–900 m, DPM 204, 222, 249, 281, 304; HA-Cr 317; MS 1431, 1434; MS & DPM 4013, 4014.

Syrrhopodon albo-vaginatus Schwägr.
On tree trunks and bases, and rotten logs, 50–1145 m, DPM 181, 156, 305; HA-Cr 422; KWL 95.

Syrrhopodon aristifolius Mitt.
On tree trunks and rotten logs, 650–1145 m, DPM 244, 257; KWL 91.

Syrrhopodon ciliatus (Hook.) Schwägr.
On rotten logs by river, 80–100 m, DPM 273, 309, 315, 316.

Syrrhopodon confertus Sande Lac.
On tree ferns, palm trees, tree trunks, tree bases and roots 610–1145 m, HA-Cr 423; KWL 2, 25b, 122; MS & DPM 3878.

Syrrhopodon croceus Mitt.
On rotten logs, 50–900 m, DPM 299; HA-Cr 202.

Syrrhopodon gardneri (Hook.) Schwägr.
On rotten logs, decaying logs, tree trunks and tree bases, 1100–1800 m, DPM 79; HA-Cr 326; MS 885; MS & DPM 3816, 3881.

Syrrhopodon involutus Schwägr.
On rotten logs, 705 m, MS 1432.

Syrrhopodon japonicus (Besch.) Broth.
On soil, climbers, tree trunks, bases and buttress, tree stumps and rotten logs, 1100–1800 m, HA-Cr 83, 91, 198, 321; MS 899, 924; MS & DPM 2547, 2615, 3830, 3950, 4030.

Syrrhopodon laevis (Dixon) Mohamed & W.D. Reese
Growing on rotten logs and tree trunks, 1700–1800 m, CMK 58, 52; DPM 25; MS & DPM 2616, 3791, 3817.

Syrrhopodon loreus (Sande Lac.) W.D. Reese
On roots, buttress, tree trunks and bases, 100–750 m, DPM 201, 266, 270; MS 4129; MS & DPM 4071.

Syrrhopodon muelleri (Dozy & Molk.) Sande Lac.
On tree trunks and bases, 1100–1300 m, HA-Cr 96; KWL 104; MS & DPM 2538, 3908.

Syrrhopodon prolifer Schwägr.
On soil, tree trunk and tree bases, 600–1800 m, DPM 229; CMK 84, 158; HA-Cr 363; MS & DPM 2706.

Syrrhopodon spiculosus Hook. & Grev.
On rotten logs, 600–1200 m, DPM 225; HA-Cr 87.

Syrrhopodon tjibodensis M. Fleisch.
On decaying logs, climbers and tree trunks, 1350–1800 m, MS 908, 919, 948; MS & DPM 3781, 4046.

Syrrhopodon tristichus Nees ex Schwägr.
On humus, tree stumps, rotten logs, shrub trunks and branches, tree branches and roots, 1370–1810 m, DPM 5, 67; HA-Cr 15, 199; MS 886, 923; MS & DPM 2541, 2624, 3855, 3942, 4043.

Cryphaeaceae
**Schoenobryum concavifolium* (Griff.) Gangulee
On concrete in an open area, 800 m, MS & DPM 4054.
This species has been reported as new to Borneo based on a collection from Kalimantan (Akiyama, 2012).

Daltoniaceae
Achrophyllum javense (Dixon ex J. Froehl.) Z. Iwats., B.C. Tan & Touw
On a wet boulder at streambed, 1600 m, MS & DPM 2693.

Benitotania elimbata H. Akiyama, T. Yamag. & Suleiman
On tree trunks, 1800 m, MS & DPM 3825.

Calyptrochaeta parviretis (M. Fleisch.) Z. Iwats., B.C. Tan & Touw
On tree trunks, rotten logs, boulders and shrub branches, 680–1425 m, HA-Cr 150, 399, 408, 410; MS 961; MS & DPM 3898.

Calyptrochaeta cf. *ramosa* (M. Fleisch.) B.C. Tan & H. Rob.
On the base of tree trunk, 1300 m, HA-Cr 63, det. B.C. Ho.
It has all the characteristics of the species but the leaf border has 3–4 rows of elongated cells instead of 2–3 rows.

Calyptrochaeta remotifolia (Müll. Hal.) Z. Iwats., B.C. Tan & Touw
On fallen logs and boulders, 770–1800 m, HA-Cr 280; MS & DPM 3864, 4084.

Daltonia armata E.B. Bartram
On rotten logs, bamboo stump and tree trunks, 750–1350 m, HA-Cr 111; MS & DPM 3897, 3907, 4031, 4095.

Daltonia contorta Müll. Hal.
On shrub trunks and branches, 1150–1400 m, HA-Cr 14, 192, 358.

Distichophyllum acuminatum Bosch & Sande Lac
On shrubs, 1240–1360 m, HA-Cr 30a, 277, 346.

Distichophyllum catinifolium J. Froehl.
On tree trunk and bases beside a stream, 1160 m, HA-Cr 396.

Distichophyllum cirratum Renauld & Cardot
On rocks, rotten logs and soil, 1100–1700 m, HA-Cr 29, 31, 32, 354, 355, 356, 375; MS & DPM 3854, 3892.

Distichophyllum cuspidatum (Dozy & Molk.) Dozy & Molk.
On tree trunk and branches, shrub trunks and decaying logs, 1150–1800 m, CMK 163; DPM 58, 96a, 98, 108; HA-Cr 30b, 33, 74, 196, 336; MS 976; MS & DPM 2597, 2625, 3826.

***Distichophyllum leiopogon* Dixon
Growing on soil in partially shaded area, 1700 m, MS & DPM 3853, det. B.C. Ho.
Leaves crisped when dry, spathulate, 3.0 mm × 1.2–1.3 mm, apex rounded to obtuse, with a small mucro, costa reaching 3/4 of leaf length, margin entire, border with 1–3 of cell. Lamina cells rectangular to hexagonal, 40–50 µm × 15–32 µm, thin walled. Calyptra smooth, fringed at base. Seta 7 mm, papillose throughout.

This species was previously recorded in the Philippines and New Guinea (Ho et al. 2010). Its cells near the leaf margin are only slightly smaller than the paracostal regions, distinguishing it from other species with spathulate or obovate leaf shapes.

Distichophyllum malayense Damanhuri & Mohamed
On fallen decaying tree trunks and rotten logs, 750–1800 m, HA-Cr 381, 357; MS & DPM 3858, 4040, 4073, 4075, 4077, 4080.

Distichophyllum mittenii Bosch & Sande Lac.
On rotten logs and tree roots, 750–1880 m, HA-Cr 7, 285, 353; MS 986; MS & DPM 2652, 2681, 2696, 3844, 4037, 4072, 4076, 4087.

Distichophyllum nigricaule Mitt. ex Bosch & Sande Lac.
On moist to wet rocks by streams 560 m, HA-Cr 304, 313.

Distichophyllum osterwaldii M. Fleisch.
On moist to wet rocks and boulders, and rotten logs, 750–1800 m, HA-Cr 100, 286, 377, 385; MS & DPM 3862, 4079.

Distichophyllum subcuspidatum Nog. & Z. Iwats.
On trunk of a shrub, 1512 m, MS 921.

Distichophyllum spathulatum (Dozy & Molk.) Dozy & Molk.
On a rotten log, 1127 m, MS 1392.

Distichophyllum cf. *tortile* Dozy & Molk. ex Bosch & Sande Lac.
On a rotten log, 750 m, MS & DPM 4081.
This specimen has all the characteristics of the species except for its leaf border which consists only of 1–2 rows of cells. Commonly, the species has 2–3 rows of cells.

Ephemeropsis tjibodensis K.I. Goebel
On palm, tree and shrub leaves by rivers, 750–1700 m, HA-Cr 20; MS & DPM 2666, 3843, 3887, 3976, 4074.

Dicranaceae
Braunfelsia dicranoides (Dozy & Molk.) Broth
On tree trunk, tree base and humus, 1100–1200 m alt, HA-Cr 84, 182, 222.

Braunfelsia edentula (Mitt.) Wijk & Margad.
On humus and shrub trunks, 1730–1800 m, MS & DPM 2606, 3803.

Braunfelsia plicata (Sande Lac.) Broth.
On fallen log, 1200–1730 m, MS & DPM 3836, 4025.

Campylopus ericoides (Griff.) A. Jaeger
On boulders and soil, 500–1000 m, DPM 212, 213, 216; MS & DPM 3993, 4053.

Campylopus exasperatus (Nees & Blume) Brid. var. *exasperatus*
On soil, 1800 m, DPM 110.

Campylopus fragilis subsp. *zollingerianus* (Müll. Hal.) J.-P. Frahm
On soil in an open area, 1150 m, HA-Cr 178.

Campylopus laxitextus Sande Lac.
On rotten branches and logs, and humus on tree bases, 1080–1800 m, MS & DPM 3815, 3900, 4049; HA-Cr 51, 187, 360.

Campylopus serratus Sande Lac.
On soil and rotten logs, 500–700 m, DPM 217; MS & DPM 4062.

Campylopus umbellatus (Schwägr. & Gaudich. ex Arn.) Paris
On soil, crevice, gravel, concrete and humus, 900–1800 m, HA-Cr 22, 56, 208; MS 926, 952; MS & DPM 3801, 3813, 3938.

Cryptodicranum armittii (Müll. Hal.) E.B. Bartram
On tree trunk, 1700–1800 m, MS & DPM 2603, 3828.

Dicranella setifera (Mitt.) A. Jaeger
On wet soil in open areas, 680–1800 m, HA-Cr 113, 426; MS & DPM 3874.

Dicranoloma assimile (Hampe) Paris
On tree buttress, trunks and roots, rotten logs and soil, 1160–1760 m, MS 889, 1257; MS & DPM 2554, 2566; 2635, 2636, 2638, 3948, 3951, 4028.

Dicranoloma billardierei (Brid.) Paris
On humus and rotten logs, 1720–1800 m, MS & DPM 2610, 2640, 3821, 3792.

Dicranoloma blumii (Nees) Paris
On trunks of shrubs and trees, 1100–1800 m, CMK 42, 151; HA-Cr 92; MS & DPM 2565, 2569, 3787.

Dicranoloma braunii (Müll. Hal.) Paris
On shrub and tree trunks, tree bases, roots and rotten stumps, 1080–1800 m, CMK 33, 123; KWL 59; MS & DPM 2536, 2560, 2605, 2621, 2622, 2671, 3905, 3937.

Dicranoloma brevisetum (Dozy & Molk.) Paris
On tree and shrub trunks, rotten logs and climbers, 1150–1870 m, CMK 33; CMK 131; DPM 3, 6, 81; HA-Cr 215, 320, 369; MS & DPM 2564, 2580, 2585, 2593, 2598, 2649, 2687, 3789, 3798, 3856, 4039.

Dicranoloma reflexum (Müll. Hal.) Renauld
On fallen log, 1100 m, MS 1387.

Holomitrium cylindraceum (P. Beauv.) Wijk & Margad.
On fallen log, 1090 m, MS 1388.

Leucoloma molle (Müll. Hal.) Mitt.
On boulders, tree and shrub trunks, 680–1600 m, HA-Cr 48, 155, 240; KWL 110; MS 1239, 1240, 2673, 3888, 4023.

Leptotrichella brasiliensis (Duby) Ochyra.
On rock by road side, 1340 m, MS 956.

Leptotrichella miqueliana (Mont.) Lindb. ex Broth.
On soil of trail banks, 680–950 m, HA-Cr 425; MS & DPM 3929.

Diphysciaceae
Diphyscium foliosum (Hedw.) D. Mohr
On wet rock, 1400 m, HA-Cr 349.

Diphyscium longifolium Griff.
On rocks, 1200–1340 m, MS 974, 985, 1393.

Diphyscium mucronifolium Mitt.
On rocks and wet boulders, 560–1700 m, HA-Cr 42, 160, 161, 171, 308, 347; MS 938, 939; MS & DPM 3848, 3891.

Ditrichaceae
Garckea phascoides Müll. Hal.
On road banks in sunny and open areas, 680–800 m, HA-Cr 116.

Entodontaceae
Entodon plicatus Müll. Hal.
On soils, boulders, rocks, tree branches and rotten logs, 600–1130 m, MS 1194, 1221, 1243; MS & DPM 3994, 4006.

Erythrodontium squarrosum (Hampe) Paris
On a shrub trunk by a road side, 900 m, MS & DPM 3911.

Mesonodon flavescens (Hook.) W.R. Buck
On concrete, boulders and tree trunks in open areas, 600–800 m, MS & DPM 4003, 4005, 4055, 4057.

Fissidentaceae
Fissidens ceylonensis Dozy & Molk.
On rocks, wet boulders and soil, 900–1700 m, HA-Cr 411; MS 975a; MS & DPM 3847, 3849, 3916.

Fissidens crassinervis Sande Lac.
On rocks, 1370 m, MS 884.

Fissidens crenulatus var. *elmeri* (Broth.) Z. Iwats. & Tad. Suzuki
On termite mount and rocks, 1080–1145 m, KWL 111, 124; MS & DPM 3902.

Fissidens crispulus Brid. var. *crispulus*
Growing on rocks, roots, boulders, stone-walls, soils and rotten logs, 100–1120 m, DPM 117, 149, 182, 264, 282, 269; MS 1441; HA-Cr 125, 256, HA-Cr 429; MS 1450, 1460, 3978, 4059, 4069.

Fissidens crispulus var. *robinsonii* (Broth.) Z. Iwats. & Z.H. Li
On rock, soil and stone-wall by streams and road side, 100–680 m, DPM 133, 286, 287; HA-Cr 126.

Fissidens geppii M. Fleisch.
On wet boulders and rocks by waterfall, and on soil in disturbed area, 900–1120 m, HA-Cr 247, 250; MS & DPM 3921, 3925.

Fissidens hollianus Dozy & Molk.
On tree branches, rotten logs, boulders and tree bases, 400–1600 m, DPM 132, 203; MS & DPM 2698, 2700, 3917.

Fissidens hyalinus Wilson & Hook.
Growing on wet rocky cliff and rocks by waterfall, 900–1100 m, HA-Cr 293; MS & DPM 3924.

Fissidens javanicus Dozy & Molk.
On soil, roots, rocks and boulders at streambed and by rivers, 560–1020 m, HA-Cr 143, 316; MS 1197; MS & DPM 3998, 3999, 4068.

Fissidens kinabaluensis Z. Iwats.
On soil and termite mount 1100 m, MS & DPM 3886.

Fissidens nobilis Griff.
On soil and rocks along trail and river banks, 410–1250 m, DPM 134; HA-Cr 156; MS 1397; MS & DPM 3927, 3966, 4060.

Fissidens pallidus Hook. f. & Wilson
On soil and rock, 700–1300 m, DPM 253; HA-Cr 86; MS 989, 1002, 1252; MS & DPM 3952, 4020.

Fissidens polypodioides Hedw.
Growing on soil, 1550–1600 m, MS & DPM 2703, 2707.

Fissidens taxifolius Hedw.
On stream bank, 680 m, HA-Cr 153.

Garovagliaceae
Garovaglia angustifolia Mitt. var. *angustifolia*
On tree trunks and branches and rotten branches, 770–1770 m, KWL 98; MS 1489; MS & DPM 3975, 4083.

Garovaglia angustifolia var. *bogorensis* (M. Fleisch.) During
On tree branches, and fallen and rotten logs, 650–1145 m, DPM 255; KWL 11, 67; MS 1205; MS & DPM 3977, 4008.

Garovaglia brachythecioides Nog. & Z. Iwats.
On fallen logs and tree branches, 650–1100 m, MS 3896; MS & DPM 4009.

Garovaglia elegans (Dozy & Molk.) Hampe ex Bosch & Sande Lac.
On shrub branches, tree trunks and fallen branches, 1320–1700 m, HA-Cr 391; MS 942, 958; MS & DPM 2591, 3850.

Garovaglia plicata (Brid.) Bosch & Sande Lac. subsp. *plicata*
On climber, shrub and tree trunks, and fallen branches, 1090–1750 m, MS 1389; MS & DPM 2631, 3824, 3852.

Hookeriaceae
Hookeria acutifolia Hook. & Grev.
On moist to wet boulders beside streams, 1160–1230 m, HA-Cr 383, HA-Cr 398.

Hypnaceae
Ectropothecium eleganti-pinnatum (Müll. Hal.) A. Jaeger
On a rock, 400 m, DPM 197.

Ectropothecium ichnotocladum (Müll. Hal.) A. Jaeger
On shrub leaves, 1440–1600 m, HA-Cr 25; MS & DPM 2676, 2688.

Ectropothecium moritzii A. Jaeger
On a decaying log, 1800 m, DPM 60.

Ectropothecium ptychofolium N. Nishim.
On tree trunk and base, and shrub branches, 1220–1800 m, DPM 74; HA-Cr 272, 468; MS 983; MS & DPM 2704.

Ectropothecium striatulum Dixon ex E.B. Bartram
On a rotten log and stone-wall, 500–1240 m, DPM 176; MS 1396.

Ectropothecium cf. *falciforme* (Dozy & Molk.) A. Jaeger
On tree trunks, 1800 m, CMK 40, 69; MS & DPM 3802.
It has all the gametophytic characters of the species but sporophytes are not present to confirm its identity.

Elmeriobryum philippinense Broth.
On concrete and rocks by road sides in open areas, 1800 m, MS & DPM 3805, 3808, 3809.

Pseudotaxiphyllum pohliaecarpum (Sull. & Lesq.) Z. Iwats.
On soil and stone-wall, 600–1400 m, HA-Cr 23, 80; DPM 167, 227.

***Taxiphyllum taxirameum* (Mitt.) M. Fleisch.
On rocks beside stream, 400 m, DPM 188, det. B.C. Tan & B.C. Ho.
Plant small, stems long-creeping, flattened, yellowish-green. Leaves ovate-lanceolate, 1.1–1.2 mm × 0.4 mm, apex gradually finely acuminate, costa short, double and indistinct, inflexed on basal part, margin denticulate. Lamina cells long-rhomboidal, 40–52 µm × 5–7 µm, thin-walled. Sporophyte not seen.

This species has a wide distribution and has been recorded in Java, Malaya, Singapore, Sumatra and the Philippines. It is characterised by its complanate and spreading leaves, with elongated stems as illustrated by Noguchi et al. (1994).

Trachythecium verrucosum (A. Jaeger) M. Fleisch.
On soil, 940–1120 m, HA-Cr 246; MS 1226.

Vesicularia dubyana (Müll. Hal.) Broth.
On rocks beside stream, 130 m, DPM 284.

Vesicularia reticulata (Dozy & Molk.) Broth.
On rocks and stone-wall, 400–450 m, DPM 211, 183, 190.

Hypnodendraceae
Dendro-hypnum beccarii Hampe
On tree branches, tree trunks and shrub stems, 1370–1800 m, DPM 35, 80, 94; MS 929; MS & DPM 2658, 2583, 3822.

Dendro-hypnum fuscomucronatum (Müll. Hal.) N.E. Bell, A.E. Newton & D. Quandt
On boulders and rocks by streams and rivers, 1000–1030 m, G.Gunsalam s.n.; MS 1183, 1184, 1186, 1236.

Dendro-hypnum milnei (Mitt.) N.E. Bell, A.E. Newton & D. Quandt
On rocks and boulders by rivers, 680–1230 m, HA-Cr 132, 384; MS 1234, 1227, 1250; MS & DPM 3963, 4092.

Dendro-hypnum subspininervium subsp. *arborescens* (Mitt.) N.E. Bell, A.E. Newton & D. Quandt
On roots, stumps, tree trunks and boulders, 100–1360 m, DPM 289; HA-Cr 26, 168; MS & DPM 4070.

Mniodendron dendroides (Brid.) Wijk & Margad.
On shrub and tree branches, roots and rotten logs, 1240–1800 m, DPM 59, 62, 63, 73, 84; HA-Cr 18, 76, 281; MS & DPM 2685, 3947.

Touwiodendron diversifolium (Broth. & Geh.) N.E. Bell, A.E. Newton & D. Quandt
On rotten logs and soils, 1160–1750 m, HA-Cr 380, 402; MS 934, 936, 1404; MS & DPM 2563, 3834, 3945, 4041.

Hypopterygiaceae
Cyathophorum spinosum (Müll. Hal.) M. Fleisch.
On rotten logs, boulders and shrub trunks, 830–1100 m, MS 1230, 1391; MS & DPM 3988.

Hypopterygium tamarisci (Sw.) Brid. ex Müll. Hal.
On rocks, boulders and rotten logs, 500–1600 m, DPM 161; HA-Cr 130, 268; MS 1202; MS & DPM 2686, 3919, 3961.

Hypopterygium vriesei Bosch & Sande Lac.
On boulders, 650–830 m, DPM 170; MS & DPM 3986.

Lopidium struthiopteris (Brid.) M. Fleisch.
On shrub and tree trunks, roots and rotten logs, 560–1600 m, HA-Cr 244, 299; KWL 86; MS & DPM 2539, 1229, 1394, 2692, 3933.

Leucobryaceae
Bryohumbertia subcomosa (Dixon) J.-P. Frahm
On rotten logs, stumps, humus and soil, 1350–1850 m, DPM 4; HA-Cr 361; MS & DPM 2647b, 3796, 4048.

Campylopus comosus (Schwägr.) Bosch & Sande Lac.
On soil, 600–1150 m, DPM 230; HA-Cr 188.

Cladopodanthus speciosus (Dozy & Molk.) M.Fleisch.
On fallen log, 1200 m, MS & DPM 4024.

Dicranodontium uncinatum (Harv.) A. Jaeger
On humus and tree trunks, 1800–1900 m, MS & DPM 2642, 2647a, 2653, 3869.

Leucobryum aduncum Dozy & Molk. var. *aduncum*
On soil, roots, rotten logs, tree trunks and bases, 50–1400 m, DPM 164, 218, 294, 296; KWL 15a; MS & DPM 2545, 2710, 3946, 4050.

Leucobryum aduncum var. *scalare* (Müll. Hal. ex M. Fleisch.) A. Eddy
On soil, root, rotten logs and tree trunks, 550–1450 m, DPM 175, 154, 220, 231, 232, 243; HA-Cr 135, 372; KWL 81; MS 998, 1430; MS & DPM 2555, 4012.

Leucobryum arfakianum Müll. Hal. ex Geh.
On soil, tree trunks and tree bases, 750–1700 m, MS 902, 903, 913, 918, 920, 1245; MS & DPM 2618.

Leucobryum bowringii Mitt.
On humus and rotten logs, 1280–1600 m, MS & DPM 2669, 3954, 4045.

Leucobryum chlorophyllosum Müll. Hal.
On soil, rotten logs, tree trunks and stump, 400–1150 m, DPM 208, 219, 226, 233, 234, 251; KWL 100a, 53b; MS 1439, 3880; MS & DPM 4015, 4052.

Leucobryum javense (Brid.) Mitt. var. *javense*
On soil, humus, rotten logs, tree trunks, roots and climbers, 600–1800 m, CMK 46, 70; DPM 27, 31, 224, 228, 236, 246, 250, 258; HA-Cr 400; MS 880, 892, 911; MS & DPM 1253, 2617, 2627, 3867,4091, 4011.

**Leucobryum javense* var. *cyathifolium* (Dixon) T. Yamag.
On humus, 1800 m, MS & DPM 3786.
This is the second report of this variety in Borneo; the first one was from Mount Mulu, Sarawak (Yamaguchi, 1993).

**Leucobryum juniperoideum* (Brid.) Müll. Hal.
On humus and tree bases, 1150–1800 m, MS & DPM 2534, 3870.
In Borneo, this species has been previously reported from Kalimantan and Sarawak. It is widespread in Europe, Macronesia, Madagasca, Turkey, Caucasus, Asia and Malesia (Yamaguchi, 1993).

Leucobryum sanctum (Nees ex Schwägr.) Hampe
On humus, soil, root and rotten logs, 50–1400 m, DPM 152, 254, 261, 298; HA-Cr 6; MS 969, 1249, 1263, 1433, 1437, 1440, 1444; MS & DPM 4044, 4047, 4067.

Leucobryum scabrum Sande Lac.
On tree trunks, 1400–1800 m, CMK 60, 115; HA-Cr 371.

Leucobryum sumatranum Broth. ex M. Fleisch.
On humus, roots and rotten logs, 1100–1620 m, HA-Cr 93; MS 992, 1254; MS & DPM 2586, 3955, 4029.

Schistomitrium apiculatum (Dozy & Molk.) Dozy & Molk.
On tree branch, 1150–1770 m, DPM 102; HA-Cr 233.

Schistomitrium mucronifolium (A. Braun in Müll. Hal.) M. Fleisch.
On climbers, branches, tree trunks and rotten logs, 1100–1800 m, DPM 21, 32, 34; HA-Cr 79, 183; MS 995; MS & DPM 2578, 2705, 3795, 3835.

Schistomitrium robustum Dozy & Molk.
On treelet trunk, 1700 m, MS & DPM 2600, 2604.

Leskeaceae
Claopodium prionophyllum (Müll. Hal.) Broth.
On boulders and soils, 940–1260 m, HA-Cr 245, 269; MS 1191, 1399; MS & DPM 3960.

Pseudoleskeopsis zippelii (Dozy & Molk.) Broth.
On wet boulders in river beds, 1010–1030 m, MS 1193, 1213.

Leucomiaceae
Leucomium strumosum (Hornsch.) Mitt.
On moist boulder, 1120 m, HA-Cr 258.

Meteoriaceae
Aerobryopsis crispifolia (Broth. & Geh.) M. Menzel
On tree trunks, and fallen leaves and branches, 850–1425 m, MS 945, 957, 1248.

Aerobryopsis longissima (Dozy & Molk.) M. Fleisch.
On twigs, shrub branches, rotten logs and tree trunks, 100–1400 m, DPM 275, 277; HA-Cr 50, 77; MS 949; MS & DPM 3893, 3957.

Barbella flagellifera (Cardot) Nog.
On shrub branches, 1600 m, MS & DPM 2667.

***Barbella horridula* Broth.
On a tree trunk, 550 m, DPM 146.
Plants yellowish-green, laxly branched, branches strongly complanate, 1–3 cm long and 5 mm wide, sparsely leaved, often with long flagellae at tips. Branch leaves spread-

ing, narrowly linear-lanceolate, 3.2–3.3 mm × 0.4–0.5 mm, slightly plicate, apex gradually acuminate; margin serulate throughout, recurved on one side at the base; costa single, faint and reaching half of midleaf. Mid lamina cells linear, 108–113 µm × 10–12, rather thin-walled, sometimes with minute 1 (–2) papillae adaxially, long-rhomboidal and thick-walled across insertion. Sporophyte not seen.

This species was previously reported from the Philippines and Sumatra. It can be recognised by its strongly complanate foliation, laxly branched, and linear-lanceolate leaves which are gradually attenuate. The minute papillae are difficult to observe and absent in some leaves. *Barbella horridula* can be distinguished from *B. stevensii* (Renauld et Cardot) M. Fleisch. in Broth. from the former hyaline lamina cells (Noguchi, 1976).

Cryptopapillaria fuscescens (Hook.) M. Menzel
On shrub and tree branches and treelet trunks, 1070–1700 m, HA-Cr 415; MS 971, 1006, 1233; MS & DPM 3840, 3941.

Floribundaria floribunda (Dozy & Molk.) M. Fleisch.
On termite mount and shrub branches, 850–1080 m, HA-Cr 207; MS 928; MS & DPM 3903, 3968.

Floribundaria intermedia Thér.
On shrub trunks and leaves, tree branches and buttress, 580–1200 m, MS & DPM 2535, 3987, 4000, 4086.

Floribundaria pseudofloribunda M. Fleisch.
On tree trunks, treelet stumps, rocks, boulders, stone-wall, climbers and soil, 550–1090 m, DPM 129, 158, 159, 169; MS 1189, 1231, 1232, 1237; MS & DPM 3915, 3990, 3997.

Meteoriopsis reclinata (Müll. Hal.) M. Fleisch.
On a shrub trunk by road side, 900 m, MS & DPM 3913.

Meteorium polytrichum Dozy & Molk.
On tree and shrub branches, and fallen logs, 750–1600 m, MS 1192, 1211, 1390; MS & DPM 2665, 2679, 3972, 3984a, 3985, 4094.

Pseudobarbella ancistrodes (Renauld & Cardot) Manuel
On a shrub branch by rivers, 850 m, MS & DPM 3984b, 3973.

Mniaceae
Plagiomnium integrum (Bosch & Sande Lac.) T.J. Kop.
On rocks and tree roots, 640–1240 m, HA-Cr 163, 283.

Plagiomnium rhynchophorum (Harv.) T.J. Kop.
On rocks, 850–1800 m, MS 1182; MS & DPM 3861, 3962.

Plagiomnium succulentum (Mitt.) T.J. Kop.
On wet boulders beside waterfall, 900–1030 m, HA-Cr 254; MS 1207, 1216; MS & DPM 3922.

Myuriaceae
Oedicladium rufescens (Reinw. & Hornsch.) Mitt.
On a decaying log, 1500 m, MS 1403.

Neckeraceae
Circulifolium exiguum (Bosch & Sande Lac.) S. Olsson, Enroth & D. Quandt
On tree trunks, shrub trunks and bases, roots and rotten logs, 500–1021 m, DPM 157; HA-Cr 122; MS 1200, 1201; MS & DPM 4078.

Circulifolium microdendron (Mont.) S. Olsson, Enroth & D. Quandt
On stone-walls, boulders, rocks, tree trunks and stumps, 550–1160 m, DPM 143; HA-Cr 129; MS 1244; MS & DPM 3931, 3958.

Himantocladium cyclophyllum (Müll. Hal.) M. Fleisch.
On soil, stone-walls, tree trunks, shrub trunks and boulders, 100–1600 m, DPM 171, 178, 263, 312; MS 1442; MS & DPM 2659, 3959.

Himantocladium plumula (Nees) M. Fleisch.
On boulders, rocks, and tree trunks, branches, twigs, bases and roots, 100–1145 m, DPM 136, 166, 168, 193, 283, 290; HA-Cr 146, 159, 267; KWL 16, 41, 63; MS 1190; MS & DPM 3910, 3928, 3970, 4085.

Himantocladium warburgii (Broth.) M. Fleisch.
On tree trunks, 1300–1650 m, HA-Cr 58, 461.

Homaliodendron flabellatum (Sm.) M. Fleisch.
On tree and shrub trunks, and rotten logs, 1100–1700 m, HA-Cr 403; MS 967,1241; MS & DPM 2664, 3846, 4038.

Neckeropsis gracilenta (Bosch & Sande Lac.) M. Fleisch.
On climbers, tree trunks, twigs, and decaying logs, 100–1100 m, DPM 280; HA-Cr 169; MS 1228; MS & DPM 3934, 4090.

Neckeropsis lepineana (Mont.) M. Fleisch.
On fallen logs and tree trunks, 800–1030 m, MS 1188; MS & DPM 3983, 4089.

Pinnatella kuehliana (Bosch & Sande Lac.) M. Fleisch.
On tree roots and stone-walls, 550–1120 m, DPM 150; HA-Cr 249; MS & DPM 3979.

Pinnatella mucronata (Bosch & Sande Lac.) M. Fleisch.
On tree trunks and bases, 100–1145 m, DPM 144, 291; HA-Cr 137; KWL 45.

Thamnobryum incurvum (Nog.) Nog. & Z. Iwats.
On moist to wet boulders by streams and waterfall, 940–1120 m, HA-Cr 251, 264.

Thamnobryum subserratum (Hook. ex Harv.) Nog. & Z. Iwats.
On boulders and wet rocks by waterfall and rivers, 1040–1100 m, MS 1225, 1235, 1238.

Touwia elliptica (Bosch & Sande Lac.) S. Olsson, Enroth & D. Quandt
On rocks and boulders, 400–1230 m, DPM 185; HA-Cr 158, 265, 291, 379; MS & DPM 4088.

Touwia negrosensis (E.B. Bartram) S. Olsson, Enroth & D. Quandt
On wet boulders, 900 m, MS & DPM 3920.

Orthotrichaceae
Macromitrium cuspidatum Hampe
On tree trunk, 1150 m, HA-Cr 176.

Macromitrium longicaule Müll. Hal.
On boulders, fallen branches, shrub branches and tree trunks, 600–1710 m, MS 944b; MS & DPM 2623, 2711, 3980, 4002, 4007.

Macromitrium longipilum A. Braun ex Müll. Hal.
On tree trunks, rotten logs and fallen logs, 1150–1800 m, DPM 106; HA-Cr 227, 228; MS & DPM 3793, 3837, 3800.

Macromitrium ochraceum (Dozy & Molk.) Müll. Hal.
On fallen tree branches and tree trunks, 1340–1800 m, MS 944a; MS & DPM 2587, 2691, 3784.

Macromitrium orthostichum Nees ex Schwägr.
On boulders and fallen branches, 650–1150 m, HA-Cr 193; MS & DPM 3992, 4093.

Macromitrium salakanum Müll. Hal.
On fallen branches, leaves and logs, 400–1380 m, HA-Cr 147; KWL 68, 102; MS 970, 1259, 1260.

Schlotheimia wallisii Müll. Hal.
On climber and treelet trunk, 1720–1770 m, MS 1488; MS & DPM 3839.

Pilotrichaceae

Actinodontium rhaphidostegum (Müll. Hal.) Bosch & Sande Lac.
Growing on rotten logs, shrub branches and fallen branches, 1080–1400 m, HA-Cr 21, 184; MS & DPM 3906.

Callicostella papillata (Mont.) Mitt. var. *papillata*
On rotten logs, 400–1250 m, DPM 192, 209; HA-Cr 148; MS & DPM 3989, 4051, 4058.

Callicostella papillata var. *prabaktiana* (Müll. Hal.) Streimann
On rotten logs, boulders and on rocky cliffs, 100–1360 m, DPM 285; HA-Cr 41, 259, 282, 314.

Cyclodictyon blumeanum (Müll. Hal.) Kuntze
On moist to wet rocks, 940–1120 m, HA-Cr 243, 294.

Hookeriopsis utacamundiana (Mont.) Broth.
On a wet rock by a streamlet, 1240 m, HA-Cr 284.

Polytrichaceae

Dawsonia beccarii Broth. & Geh.
On rocky cliff in open area, 1780 m, MS & DPM 3877.

Dawsonia longifolia (Bruch & Schimp.) Zanten
On soil, 1600–1800 m, DPM 65, 69; MS & DPM 2590, 3940.

Pogonatum cirratum (Sw.) Brid. subsp. *cirratum*
On soil, 1350–1490 m, MS 1402; HA-Cr 53, 55.

Pogonatum cirratum subsp. *fuscatum* (Mitt.), Hyvönen
On soil and humus, 750–1340 m, MS 1255, 1256; MS & DPM 4066; MS & DPM 3909; HA-Cr 201; MS 955.

Pogonatum cirratum subsp. *macrophyllum* (Dozy & Molk.) Hyvönen
On soil, 1220–1800 m, DPM 95; MS & DPM 2561, 3811, 3876, 3944, 4042; MS 991, 954.

Pogonatum iwatsukii Touw
On boulders and rocks, 1320–1400 m, MS 930, 940; HA-Cr 350.

Pogonatum neesii (Müll. Hal.) Dozy
On soil and boulders in open areas, 680–1800 m, MS & DPM 3871, 3995; MS 951; HA-Cr 54, 120, 424.

Pogonatum piliferum (Dozy & Molk.) Touw
On rocks and soil, 400–1360 m, DPM 199; MS & DPM 4018, 4065; HA-Cr 27, 134, 306, 311, 428; MS 990.

Pogonatum rutteri (Thér. & Dixon) Dixon
On soil, 1070–1360 m, HA-Cr 28, 394; MS 1003, 1004.

Pogonatum subtortile (Müll. Hal.) A. Jaeger
On soil in an open area, 900–1160 m, HA-Cr 204, 406.

Pottiaceae
Chionoloma bombayense (Müll. Hal.) P. Sollman (1996)
On concrete and stone-wall, 1040–1820 m, DPM 112; MS 1224.

Barbula javanica Dozy & Molk.
On thin soil covering wet rocks along stream, 410–1800 m, MS 1461; MS & DPM 3872.

Barbula consanguinea (Thwaites & Mitt.) A. Jaeger
On moist stone-wall along river, 1040 m, MS 1223.

Hyophila involuta (Hook.) A. Jaeger
Growing on boulders, concrete and stone-walls by waterfall and rivers in open and partially shaded areas, 100–1820 m, DPM 111; DPM 127, 148; DPM 279; HA-Cr 253; MS 1446; MS 1217, 1218; MS & DPM 3923, 4001, 4056.

Pterobryaceae
Calyptothecium recurvulum (Broth.) Broth.
Hanging on tree trunks by rivers or waterfall, 850–1030 m, MS 1187; MS & DPM 3969, 3974.

Cryptogonium phyllogonioides (Sull.) Isov.
On a tree trunk, 940–1120 m, HA-Cr 248.

Neolindbergia rigida (Bosch & Sande Lac.) M. Fleisch.
On fallen trees, 1040–1100 m, MS 1195; MS & DPM 3884.

Neolindbergia rugosa (Lindb.) M. Fleisch.
On tree trunks and fallen logs, 530–1120 m, HA-Cr 260; MS 1443.

Pterobryopsis crassicaulis (Müll. Hal.) M. Fleisch.
On rotten logs and fallen branches, 680–1460 m, HA-Cr 145; MS 1401; MS & DPM 4027.

Symphysodon neckeroides Dozy & Molk.
On a tree trunk, 750 m, DPM 256.

Symphysodontella attenuatula M. Fleisch.
On tree trunks, 550–1650 m, DPM 145; HA-Cr 438.

Symphysodontella cylindracea (Mont.) M. Fleisch.
On shrub trunks, rotten logs, tree trunks and branches, and climbers, 560–1650 m, HA-Cr 300, 439; MS 962, 968, 1405; MS & DPM 2589, 2674, 3894.

Trachyloma indicum Mitt.
On rotten logs and tree trunks, 1425–1650 m, HA-Cr 459; MS 960.

Pylaisiadelphaceae
Brotherella falcata (Dozy & Molk.) M. Fleisch.
On a shrub branch, 1400 m, HA-Cr 339, det. B.C. Tan.

Clastobryum cf. *asperrimum* (Dixon) B.C. Tan
On a decaying log, 1765 m, DPM 90.
The specimen is similar to the species except for its leaves that are much larger, reaching 1.6 mm long.

Clastobryum cuculligerum (Sande Lac.) Tixier
On a fallen branch, 1150 m, HA-Cr 180.

Clastobryum epiphyllum (Renauld & Cardot) B.C. Tan & Touw
On rotten twigs and tree trunks, 500–1080 m, DPM 126; MS & DPM 3899a.

**Clastobryum scalare* (Müll. Hal.) Tixier
On tree trunks and branches, leaves and shrub branches, 1800 m, MS & DPM 3790.
In Borneo, this species has been reported from Sarawak and Kalimantan (Dixon 1935; Tixier 1977).

Isocladiella surcularis (Dixon) B.C. Tan & Mohamed
On shrub and tree trunks, and roots, 1100–1800 m, CMK 12; HA-Cr 81; KWL 17, 54, 71, 112, 121; MS 993; MS & DPM 2558, 3882, 4019.

Isopterygium albescens (Hook.) A. Jaeger
On rotten logs and decaying stump, 1100–1145 m, KWL 8, 12, 70, 85, 105a, 106, 109; MS & DPM 3885.

Isopterygium bancanum (Sande Lac.) A. Jaeger
On lianas and fallen trees, 1145 m, KWL 7, 72.

Isopterygium minutirameum (Müll. Hal.) A. Jaeger
On a tree base, 500 m, DPM 214.

Mastopoma armitii (Broth. & Geh.) Broth.
On shrub and tree trunks and leaves, and rotten logs, 900–1800 m, CMK 44, 47; DPM 39; HA-Cr 11, 203.

Mastopoma brauniana (Bosch & Sande Lac.) H. Akiyama
On a tree trunk, 1400 m, HA-Cr 3.

Mastopoma papillosum Broth.
Growing on shrub branches, 1730 m, MS & DPM 3838.

Mastopoma uncinifolium (Broth.) Broth.
On shrub branches, rotten logs, roots, tree trunks and humus, 1150–1770 m, DPM 82, 101a, 103; HA-Cr 13, 221; MS & DPM 2709, 3833.

Taxithelium lindbergii (A. Jaeger) Renauld & Cardot
On tree trunk, branches of shrubs and leaves, 1160–1800 m, HA-Cr 273, 401; MS & DPM 2662, 3866.

Taxithelium instratum (Brid.) Broth.
On rotten logs and rocks, 50–800 m, DPM 187, 300, 306; HA-Cr 119, 420.

Taxithelium isocladum (Bosch & Sande Lac.) Renauld & Cardot
On a small shrub branch, 1600–1650 m, HA-Cr 455.

Taxithelium vernieri (Duby) Besch.
Growing on shrub branches, twigs and fallen tree, 1100–1400 m, KWL 87, 125; HA-Cr 78, 236, 337.

Trismegistia brachyphylla M. Fleisch.
On shrub branches and trunks, tree trunks and bases, and rotten logs, 1100–1190 m, HA-Cr 101, 102, 105, 110, 223; MS 999.

Trismegistia calderensis (Sull.) Broth. var. *calderensis*
On tree branches, shrub trunks and tree stump, 1220–1800 m, MS 937; MS & DPM 1258, 2582, 3797, 3819.

Trismegistia calderensis var. *subintegrifolia* (Broth.) H. Akiyama
On tree trunks and bases, rotten logs, rotten wood, fallen log, tree branches, soil and rocks, 560–1810 m, HA-Cr 1, 5, 26, 47, 66, 67, 70, 103, 106, 107, 109, 194, 213, 214, 229, 230, 322, 324, 390, 392, 393.

Trismegistia lancifolia var. *valetonii* (M. Fleisch. ex Dixon) H. Akiyama
On tree trunks and roots, shrub branches, fallen branches, decaying tree, rotten logs and boulders, 610–1150 m, HA-Cr 107, 127, 128, 166, 167, 194, 212, 419, 421; KWL 10, 21, 24, 30, 32, 49, 50, 52b, 57, 61, 65, 74, 82, 88, 92, 96, 99, 103; 113; MS 1438.

Trismegistia panduriformis var. *prionodontella* (Broth.) H. Akiyama
On shrub branches, tree trunks and bases, rotten logs, decaying wood and boulders, 1100–1770 m, DPM 83, 86, 92, 2672, 4022; HA-Cr 45, 104; MS 935.

Racopilaceae
Racopilum cuspidigerum (Schwägr.) Ångström
On moist rock beside a stream, 680 m, HA-Cr 131.

Racopilum laxirete Broth.
On tree root, 950 m, MS & DPM 3930.

Racopilum spectabile Reinw. & Hornsch. var. *spectabile*
On shrub leaves and trunks, rotten logs, soils and boulders by rivers, 550–1600 m, DPM 151; HA-Cr 72, HA-Cr 151, 386; MS & DPM 2701; MS 931, 1206, 1398; MS & DPM 3967, 3981.

Racopilum spectabile var. *subisophyllum* Herzog
On rotten branches and roots, 1600–1800 m, DPM 85; MS & DPM 2678, 3857.

Regmatodontaceae
Regmatodon declinatsus (Hook.) Brid.
On a boulder beside a stream, 1350 m, MS & DPM 4034.

Rhizogoniaceae
Pyrrhobryum latifolium (Bosch & Sande Lac.) Mitt.
On tree trunks and bases, and rotten logs, 940–1280 m, HA-Cr 90, 220, 241; MS & DPM 3949.

Pyrrhobryum spiniforme (Hedw.) Mitt.
On tree trunks, rotten logs, humus, roots and stone-walls, 400–1780 m, DPM 49, 89, 97, 142, 206, 237, 252; HA-Cr 275, 378; KWL 13, 28, 58, 66, 77, 94, 97, 107; MS 882, 1185; MS & DPM 3832, 3879, 4016, 4017.

Rhizogonium graeffeanum (Müll. Hal.) A. Jaeger
On tree trunks and bases, and rotten stumps, 1400–1800 m, HA-Cr 12, 319; MS 901; MS & DPM 3831.

Rhizogonium lamii Reimers
On tree buttress and trunks, 1600–1800 m, MS & DPM 2599, 2626, 2668, 3827.

Sematophyllaceae
Acanthorrhynchium papillatum (Harv.) M. Fleisch.
On tree trunks and tree bases, 560–1145 m, HA-Cr 309; KWL 117; MS & DPM 1436.

Acroporium adspersum (Hampe) Broth.
On a tree trunk, 1800 m, CMK 125.

Acroporium convolutum (Sande Lac.) M. Fleisch. var. *convolutum*
On a tree trunk, 1425 m, MS 963, det. B.C. Tan.

Acroporium convolutum var. *elatum* (Dixon) B.C. Tan
On rotten logs, 550–1400 m, DPM 153, 239; HA-Cr 296, 310, 368.

Acroporium diminutum (Brid.) M. Fleisch.
On tree trunks and branches, decaying logs, climber trunks and shrub branches, 1150–1810 m, CMK 28; DPM 71; HA-Cr 190, 231, 327, 335, 342, 370; MS 877, 893, 959; MS & DPM 2581, 2619, 2629, 2663.

Acroporium downii (Dixon) Broth.
On rotten logs and bamboo stumps, 50–1770 m, DPM 101b, 301, 314; KWL 15b; MS & DPM 4063.

Acroporium johannis-winkleri Broth.
On tree trunks and branches, roots, rotten logs, fallen logs and shrub branches, 1100–1880 m, CMK 103, 148; DPM 7, 10, 12, 13, 18, 26, 28, 29, 42, 50, 52, 55, 57, 66, 72, 77, 78, 99, 105, 107; HA-Cr 82; MS 987; MS & DPM 2601, 2650, 4021.

Acroporium lamprophyllum Mitt.
On leaves, tree trunks, treelet trunks, fallen logs, rotten logs, 1145–1850 m, DPM 9, 24, 38, 44; KWL 18; MS 915; MS & DPM 2648.

**Acroporium macroturgidum* Dixon
On humus, 1800 m, MS & DPM 3818, confirmed by B.C. Tan.
In Borneo, this species has been previously reported from Kalimantan and Sarawak (Suleiman et al. 2006).

Acroporium praelongum var. *aciphylloides* B.C. Tan
On tree trunks, rotten logs and fallen tree, 1340–1800 m, MS 977; MS & DPM 2607, 3799.

**Acroporium ramicola* (Hampe) Broth.
On tree shrub branches, 1400–1800 m, CMK 6, 90; HA-Cr 367, det. B.C. Tan.
In Borneo, this species has been known only from the type collection from Sarawak (Suleiman et al. 2006).

Acroporium rigens (Broth. ex Dixon) Dixon.
On rocks and on rotten logs 600–1370 m, DPM 238; MS 883.

Acroporium rufum (Reinw. & Hornsch.) M. Fleisch.
On tree tree trunks and branches, and decaying logs, 1400–1800 m, CMK 76, 133; DPM 8, 33, 51; HA-Cr 73; MS & DPM 2595, 3794.

Acroporium secundum (Reinw. & Hornsch.) M. Fleisch.
On shrubs and branches, decaying logs and rotten climbers, 1300–1780 m, DPM 47; HA-Cr 276; MS & DPM 2549, 2609.

Acroporium stramineum (Reinw. & Hornsch.) M. Fleisch. var. *stramineum*
On tree trunks, decaying fallen log, climbers, shrub branches and fallen branches, 1150–1850 m, DPM 14, 37, 61; CMK 22, 5; HA-Cr 185, 189, 362; MS 912, 953; MS & DPM 2646, 3785.

Acroporium stramineum var. *hamulatum* (M. Fleisch.) B.C. Tan
On tree trunks, bases and branches, and decaying fallen branches, 1150–1520 m, HA-Cr 177, 186; MS 890, 900, 914; MS & DPM 2553.

Acroporium strepsiphyllum (Mont.) B.C. Tan var. *strepsiphyllum*
On a fallen log in an open area, 1790 m, DPM 43.

Chionostomum hainanense B.C. Tan & Y. Jia
On a tree trunk beside a small pond, 1800 m, MS & DPM 3812, det. K.T. Yong & B.C. Tan.

Meiothecium hamatum (Müll. Hal.) Broth.
On tree trunks on shrub branches in open areas, 1150–1800 m, HA-Cr 172, 418; MS & DPM 3778, 3782.

Meiothecium microcarpum (Harv.) Mitt.
On boulders in an open area, 600 m, MS & DPM 4004.

**Papillidiopsis malayana* (Dixon) BC. Tan
On a tree branch, 1800 m, MS & DPM 3863, det. B.C. Tan.
In Borneo, this species has been previously reported only from Kalimantan (Dixon, 1935).

Papillidiopsis ramulina (Thwaites & Mitt.) W.R. Buck & B.C. Tan
On moist soil in steep galley, 900 m, HA-Cr 205, det. B.C. Tan.

Papillidiopsis stissophylla (Hampe & Müll. Hal.) B.C. Tan & Y. Jia
On *Melastoma* branch, shrub branches and trunks, 1600–1800 m, MS & DPM 2690, 3841, 3842, 3865, det. B.C. Tan & K.T. Yong.

Radulina barbonica var. *barbonica* (Bél.) W.R. Buck
On palm leaves, 385–1400 m, MS 1452; HA-Cr 343.

Rhaphidostichum piliferum (Broth.) Broth.
On rotten shrub branch and trunk, 1720 m, MS & DPM 2608, 2612.

***Rhaphidostichum luzonense* (Broth.) Broth.
On boulder s in streambed, 680 m, HA-Cr 149, det. B.C. Tan.
Plants large, yellowish-green, glossy, stems elongate, prostrate, densely branched. Leaves broadly ovate to oblong-ovate, 2.7–3.0 mm × 0.6–0.7 mm, semitubulose, concave, abruptly contracted to a long acuminate apex, ecostate, margin entire below and denticulate at extreme apex. Lamina cells vermicular, 66–98 µm × 5–7 µm, thin-walled, smooth; alar cells large, oval, coloured, inflated. Sporophyte not seen.

This species is characterised by the broadly ovate to oblong-ovate leaves and abruptly contracted into long acuminate apex with denticulate acumen. It was previously only reported from the Philippines (Bartram, 1939; Tan & Iwatsuki, 1991).

Sematophyllum subpinnatum (Brid.) E. Britton
On tree and shrub trunks, 900–950 m, MS & DPM 3914, 3935, det. B.C. Tan.

Trichosteleum boschii (Dozy & Molk.) A. Jaeger
On shrub trunks and leaves, twigs, tree trunks and branches, rotten logs and rock, 600–1800 m, DPM 87, 100, 242; HA-Cr 35, 39, 142, 407; MS & DPM 2614, 2655, 3829.

Trichosteleum pseudomammosum M. Fleisch.
On a tree trunk, 1800 m, CMK 99.

Trichosteleum cf. *saproxylophilum* (Müll. Hal.) B.C. Tan, W.B. Schofield & H.P. Ramsay
On a tree trunk, 370 m, MS 1261, det. B.C. Tan.
This specimen has all the characteristics of *T. saproxylophilum* except for the larger size of the perichaetial leaves (1.7 mm × 0.4 mm) and branch leaves (2.5 mm–2.9 mm × 0.4 mm–0.5 mm).

Trichosteleum stigmosum Mitt.
On tree trunks and base, rotten logs and soil, 50–730 m, DPM 215, 240, 248; DPM 297; HA-Cr 318, 307.

Warburgiella cf. *breviseta* (Broth.) Broth.
On shrub and pandanus leaf, 1400 m, HA-Cr 10, 352, det. B.C. Tan.
The specimens have all the characteristics of the species but the leaf cells are smooth throughout.

Warburgiella cupressinoides Müll. Hal. ex Broth.
On a rotten log, 1800 m, MS & DPM 3820.

Warburgiella circinata Dixon
On humus, 1400 m, HA-Cr 364, det. B.C. Tan.

Sphagnaceae
Sphagnum cuspidatulum Müll. Hal.
On humus, 1800 m, MS & DPM 3776, 3788.

Sphagnum junghuhnianum Dozy & Molk.
On humus and tree trunk, 1800 m, MS & DPM 3807, 3780, 3804; DPM 19, 54; CMK 78.

Sphagnum perichaetiale Hampe
On humus, 1800 m, MS & DPM 3806.

Symphyodontaceae
Chaetomitrium orthorrhynchum (Dozy & Molk.) Bosch & Sande Lac.
On shrub leaves and branches, tree branches and climber, 310–1600 m, HA-Cr 239; MS 1203, 1262; MS & DPM 2689, 4036.

***Chaetomitrium lancifolium* Mitt.
On a tree branch by a river, partially shaded in secondary lowland forest, 70 m, DPM 307.

Plants medium size for the genus, stems to 3 cm long, irregularly and rather laxly branched. Branches 6–10 mm long, sometimes cuspidate at tips, with clusters of filamentous propagules at tips, sometimes extending to the mid of branches, propagules 1/3 of leaf length. Branch leaves erect to erect-spreading when dry, slightly homomallous, leaves often twisted half above; little altered when wet, except not twisted above; oblong-lanceolate to ovate-lanceolate, concave, 1.3–1.4 mm × 0.4–0.5 mm, apex gradually long-acuminate ending in a narrow point, strongly constricted below apices, costa distinct but short, margin sometimes slightly undulate in upper 1/3, strongly regularly serrate to denticulate to the base, teeth strongly bifid, trifid or multifid. Lamina cells linear, 60 µm × 5 µm in mid-lamina, thick-walled, strongly prorate to spiculose-prorate to the base in adaxial and abaxial sides; alar cells small forming 5–6 short-rectangular cells. Sporophyte not seen.

This species has only been recorded from the Maluku Islands, its type locality. The distinguishing features of this species have been reported recently by Suleiman and

Akiyama (2014). It is closely related to *C. papillifolium* Bosch & Sande Lac., differing only in seta length and leaf apex. Based on the type material, this species has a very short seta measuring only 4.4–4.5 cm.

Chaetomitrium leptopoma (Schwägr.) Bosch & Sande Lac.
On shrub leaves and branches, 850–1600 m, HA-Cr 234, 325, 334; MS & DPM 2702, 3964.

Dimorphocladon borneense Dixon
On ginger leaves by rivers, 748–770 m, MS 1246; MS & DPM 4082, det. B.C. Ho

Thuidiaceae
Pelekium bifarium (Bosch & Sande Lac.) M. Fleisch.
On a moist stone-wall by a river, 410 m, MS 1456.

Pelekium velatum Mitt.
Growing on rocks, tree trunks, rotten logs and stone-walls, 400–900 m, HA-Cr 164; DPM 130; 172, 173, 191; MS & DPM 3918.

Pelekium versicolor (Hornsch. ex Müll. Hal.) Touw
On a decaying log, 1050 m, MS 1386.

Thuidium cymbifolium (Dozy & Molk.) Dozy & Molk.
On boulders, rocks, stone-wall, rotten logs, stumps, climber and soils, 500–1800 m, DPM 93, 138; HA-Cr 404; MS 1208, 1214, 1220; MS & DPM 2677, 3851, 3860, 3971.

Thuidium plumulosum (Dozy & Molk.) Dozy & Molk.
On tree bases, rotten logs, stone-wall, rocks and boulders, 100–680 m, DPM 141, 186, 189, 260; HA-Cr 144, 162; MS 1449, 1451.

Thuidium pristocalyx (Müll.Hal.) A. Jaeger var. *pristocalyx*
On boulders, tree trunks and buttress, climbers, roots and lianas, 850–1600 m, KWL 29, 37, 38, 39, 40; HA-Cr 88, 344; MS 984; MS & DPM 2670, 3904, 3965.

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RESEARCH ARTICLE

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Coelogyne magnifica (Orchidaceae), a new species from northern Myanmar

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Abstract

Coelogyne magnifica (Orchidaceae), a new species from Putao, Kachin State, Myanmar, is described and illustrated. It belongs to *Coelogyne* section *Ocellatae* Pfitzer & Kraenzl. and it is morphologically similar to *Coelogyne corymbosa* and *C. taronensis*, but can be distinguished from these species by its larger flowers, lanceolate sepals and petals, a narrowly ovate lip, which has two bright yellow patches surrounded by shiny brownish red and two fimbriate or erose-lacerate lateral keels on the lip. The major differences between these species are outlined and discussed.

Keywords

Kachin state, section Ocellatae, key, plant taxonomy, IUCN, Hponkan Razi

Introduction

The genus *Coelogyne* Lindl. (Lindley 1821), which consists of approximately 200 species, is distributed from South India, through tropical Asia and the Malay Archipelago into the Pacific as far east as Fiji, with the main centres being in Borneo, Sumatra and the Himalayas (Gravendeel 2000, Clayton 2002, Gravendeel et al. 2001, 2005, Chen and Clayton 2009, George and George 2011). It belongs to the subfamily Epidendroideae, tribe Coelogyneae, subtribe Coelogyninae (Gravendeel et al. 2005). As currently circumscribed based on molecular phylogenetic evidence, *Coelogyne* is polyphyletic and composed of species belonging to two unrelated groups. It would thus be questionable whether to adopt a *Coelogyne s.s.* generic delimitation or a *Coelogyne s.l.* generic circumscription (Gravendeel 2000, Gravendeel et al. 2001). Although revisions of several sections of *Coelogyne* have been published in the last decade (Gravendeel and de Vogel 1999, Pelser et al. 2000), a comprehensive infrageneric delimitation combined with descriptions of morphological and molecular characters based on more extensive sampling within *Coelogyne* is needed (Gravendeel et al. 2000, Sierra et al. 2000).

Historically, the study of *Coelogyne* in Myanmar dates back to Hooker (1890), who reported three *Coelogyne* species and added one new species *Coelogyne longibractata* Hook. f.. Currently, 43 species of *Coelogyne* have been recorded in Myanmar (Kress et al. 2003), although in a recently published field guide to the orchids of Myanmar, only 33 *Coelogyne* species are described (Kurzweil and Lwin 2014). The most recently identified new species of *Coelogyne* was *Coelogyne putaoensis* X.H. Jin, L.A. Ye & Schuit. is from north Myanmar (Aung et al. 2017). Since the publication of Kress's checklist (Kress et al. 2003), more than 10 new species and 40 new records of Orchidaceae species have been added to the flora of Myanmar from 2001 to the present (Yang and Tan, unpublished data).

During recent China–Myanmar joint field expeditions to survey plant diversity in north Myanmar in May 2016 and 2017, specimens of *Coelogyne* were found in Putao, Kachin State. On the basis of a detailed examination of the morphological and anatomical characters of this material and of presumed closely similar species (Clayton 2002, Kress et al. 2003, Chen and Clayton 2009, George and George 2011, Subedi 2011, Yonzone 2012a, 2012b, Li and Dao 2014, Gogoi et al. 2015, Aung et al. 2017), the conclusion was made that the specimens collected in Myanmar belong to a species new to science, which is herein described and illustrated.

Material and methods

Measurements and morphological character assessments of the putative new *Coelogyne* species were performed and described using specimens and fresh material observed in the field. These data were compared with those for the morphologically similar species *C. corymbosa* Lindl. and *C. taronensis* Hand.-Mazz. based on the descriptions of dried herbarium specimens deposited at Xishuangbanna Tropical Botanical Garden herbarium (HITBC), field notes (for *C. corymbosa* which has also been collected from north Myanmar) and literature descriptions (Chen and Clayton 2009, Subedi 2011, Li and Dao 2014). Protologues and images of type specimens were obtained from Tropicos (http://www.tropicos.org), JSTOR Global Plants (http://plants.jstor.org) and the International Plant Names Index (http://www.ipni.org).

Taxonomic treatment

***Coelogyne magnifica* Y.H. Tan, S.S. Zhou & B. Yang, sp. nov.**
urn:lsid:ipni.org:names:60475278-2
Figures 1, 2

Diagnosis. *Coelogyne magnifica* is similar to *C. corymbosa* and *C. taronensis*, but can be distinguished from these two species by its larger flowers (tepals 4.0–4.9 cm long), broadly lanceolate sepals and petals, narrowly ovate lip, which has two bright yellow patches surrounded by shiny brownish red and two fimbriate or erose-lacerate keels on the lip.

Type. MYANMAR. Kachin State: Putao, Hponkan Razi Wildlife Sanctuary, 96°58'56.45"E, 27°36'32.42"N, alt. 2450 m, 11 May 2017, *Myanmar Exped. 2046* (holotype, HITBC).

Description. Epiphytic or lithophytic herb, 11–15 cm tall. Rhizome stout, 3–4 mm in diameter, covered by brown, scaly sheaths. Pseudobulbs clustered, developing serially, less than 1 cm apart from each other, ovoid or oblong-ovoid, strongly wrinkled when dried, 3–3.5 × 1.1–1.7 cm, covered with brown sheaths at the base, sheaths narrow triangular ovate, 1.5–4.5 × 0.7–1.5 cm long; bifoliate at apex. Leaf blade obovate-oblong or narrowly ovate, coriaceous, 8–11.2 × 1.8–2.6 cm, with 6–7 veins, acute; petiole grooved, 0.4–0.8 cm long. Inflorescence proteranthous to synanthous, peduncle arching, 5–6 cm long, embraced by sheaths below middle, rachis 1.5–2 cm long; raceme 2- to 3-flowered (simultaneously opening); floral bracts oblong-lanceolate, 1.9–2.1 × 0.4–0.5 cm, acute, caducous. Flowers fleshy, white, lip adaxially on mid-lobe with two bright yellow patches surrounded by shiny brownish red and connected to front part of each of the side lobes, keels consisting of two parallel crests with white fimbriate prominence. Pedicel and ovary ca. 1.8–2.5 cm long, glabrous. Dorsal sepal lanceolate, 4.0–6.0 × 1.0–1.3 cm, with 7–9 veins, acute or shortly acuminate; lateral sepals similar to dorsal sepal, somewhat narrower than dorsal sepal, 5.0–5.5 × 0.9–1.5 cm, with 5-7 veins, acute or shortly acuminate; petals lanceolate, 4.0–5.3 × 0.6–1.0 cm, acute or shortly acuminate; lip narrowly ovate when flattened, 3.8–4.9 × 1.7–2.2 cm, 3-lobed; lateral lobes erect, sub-orbicular, 2.0–2.5 × 0.7–1.0 cm, fimbriate or erose-lacerate on margin, adaxially with reddish brown longitudinal stripe; median lobe ovate-triangular or triangular-lanceolate, 1.8–2.5 × 1.0–1.2 cm, acute to apiculate, margin fimbriate or erose-lacerate; two low lateral keels, extending from lip base to base of median lobe, margin fimbriate or erose-lacerate; column arcuate, 2.0–2.5 × 0.4–0.6 cm long, yellow at front below apex, both sides winged, wings gradually broadening from the middle to the apex, apex margin white, irregularly toothed; anther cap elliptic triangular, adaxially light pale yellow-green, abaxially white, margin membranous at base, apex obtuse; pollinia two; rostellum ligulate-triangular.

Phenology. Flowering from April to May and fruiting from June to July.

Etymology. The species epithet refers to its large attractive flowers.

Distribution and habitat. *Coelogyne magnifica* is currently known only from the type locality of Putao, Kachin State, northern Myanmar. It is a predominantly epi-

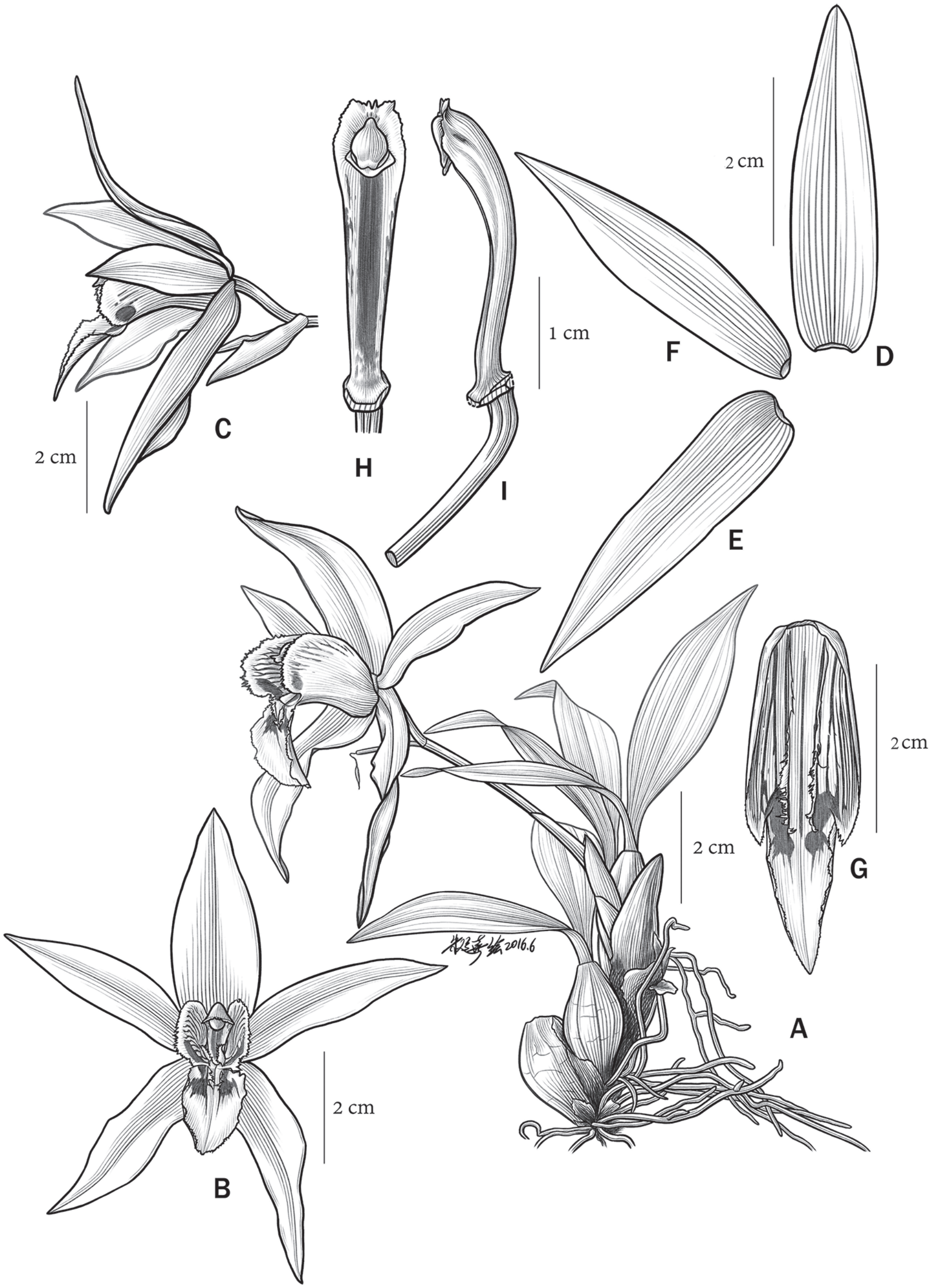

Figure 1. *Coelogyne magnifica* Y.H. Tan, S.S. Zhou & B. Yang sp. nov. **A** Habit **B** Flower (front view) **C** Flower (side view) **D** Dorsal sepal **E** Lateral sepal **F** Petal **G** Lip **H** Column (frontal view) **I** Column (lateral view). Illustration by Yunxi Zhu.

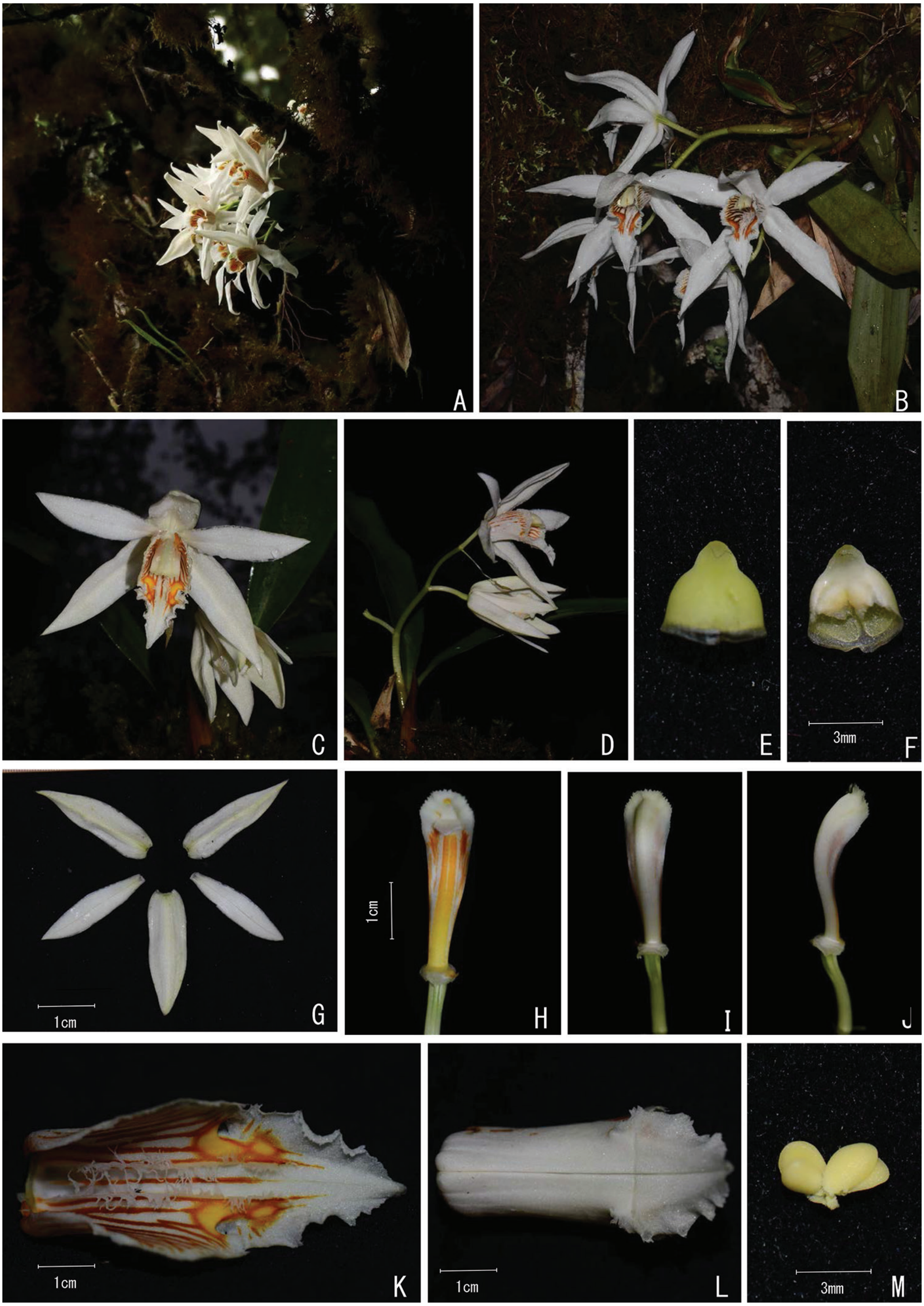

Figure 2. *Coelogyne magnifica* Y.H. Tan, S.S. Zhou & B. Yang sp. nov. **A–D** Habit **E** Anther cap (abaxial view) **F** Anther cap (adaxial view) **G** Tepals **H** Column (adaxial view) **I** Column (abaxial view) **J** Column (lateral view) **K** Lip (adaxial view, showing the two lateral keels and two patches) **L** Lip (abaxial view) **M** Pollinia. Photographed by Y.H. Tan, Q. Liu & X.L. Zeng.

phytic species that grows on moss-covered branches and tree trunks and sometimes also on rocks, in humid montane forests, at an elevation 2400–2500 m a.s.l.

Conservation status. The type locality of this new species is within the Hponkanrazi Wildlife Sanctuary, which is an officially protected area under the management of the Myanmar Forest Department. During field investigations in 2016 and 2017, three populations were found in the reserve area, each of which consisted of ca. 100 individuals. As found, inhabitants are well protected and almost undamaged and flowering individuals are not vulnerable to human interference or picking. Based on current information and according to IUCN Red List category (IUCN 2012), *Coelogyne magnifica* is assigned a preliminary status of Least Concern (LC).

Additional specimens examined (paratypes). Myanmar. Kachin State: Putao, Hponkanrazi Wildlife Sanctuary, 97°53'10.48"E, 27°41'17.60"N, alt. 2400 m, 4 May 2016, *Myanmar Exped. 0100* (HITBC). Ibid., alt. 2450 m, 7 May 2016, *Myanmar Exped. 0188* (HITBC).

Key to the species of *Coelogyne* sect. *Ocellatae*, adapted from Li and Dao (2014)

1 Inflorescence hysteranthous **2**
– Inflorescence proteranthous or synanthous **3**
2 Lowermost bract of rachis with flower .... ***C. hysterantha***
– Lowermost bract of rachis sterile .... ***C. punctulata***
3 Pseudobulb obovoid, born distantly, 1.3–5.0 cm apart .... ***C. occultata***
– Pseudobulb ellipsoid, born clustered, less than 1.3 cm apart **4**
4 Keels on lip plate-like shaped .... ***C. platylamellata***
– Keels on lip clavate or rod-shaped **5**
5 Keels starting 0.3 cm away from the base of the hypochile. ***C. gongshanensis***
– Keels starting right from the base of the hypochile **6**
6 Lateral lobes of lip length 3–3.2 cm when flattened .... ***C. wardii***
– Lateral lobes of lip length 1–2.5 cm when flattened **7**
7 Margin of lateral lobes of lip crenulate or crispate **8**
– Margin of lateral lobes of lip erose or denticulate **9**
8 Flowers almost solid yellowish brown, lip with a large, bright yellow patch... .... ***C. putaoensis***
– Flowers creamy-yellow, lip with four dark red patches .... ***C. taronensis***
9 Lateral keels of lip clavate and with erose lacerate or crenulate margins **10**
– Lateral keels of lip rod-shaped and with entire margins **11**
10 Sepals and petals more than 4.0 cm long .... ***C. magnifica***
– Sepals and petals less than 3.5 cm long **12**
11 Flowers 4–8, mid-lobe acute at apex .... ***C. nitida***
– Flowers 2–3, mid-lobe cuspidate at apex .... ***C. ttyuii***
12 Yellow eyelike blotches surrounded by reddish orange on lip .... ***C. corymbosa***
– Dark brown eyelike blotches surrounded by brownish-yellow on lip .... ***C. pianmaensis***

Discussion

According to monographic works (Clayton 2002, Chen and Clayton 2009, George and George 2011, Subedi 2011), *Coelogyne magnifica* obviously belongs to sect. *Ocellatae* Pfitzer & Kraenzl. (Pfitzer and Kraenzlin 1907), which is characterised by the white or pale coloured flowers with colourful eyelike blotches on the lateral lobes and lip. This section shows its centre of diversity in the Himalayas (Subedi 2011). *Coelogyne magnifica* is similar to both *C. corymbosa* and *C. taronensis* in terms of vegetative morphology and shape of the flowers, but differs mainly with respect to the characters of patches and keels on the lip. Morphologically, the new species is most similar to *C. corymbosa*, with both having white flowers, ovoid pseudobulbs sometimes and obovate-oblong leaf blades. These two species are also distributed in the same locality in north Myanmar. Nevertheless, the new species differs from *C. corymbosa* in having slightly smaller pseudobulbs, shorter leaf blades, a greater number of larger flowers, two bright yellow patches surrounded by shiny brownish red (vs. four yellow eye-like blotches) and two fimbriate or erose-lacerate lateral keels on the lip (vs. two–three keels, with margins wavy or crenulate) (Table 1). The tepals (perianth lobes, including sepals, petals and lip) of *C. magnifica* are lanceolate, 4.0–4.9 cm long (vs. mostly elliptic to ovate,

Table 1. Morphological comparison of *Coelogyne magnifica* and its closely related species.

Characters	*Coelogyne magnifica*	*Coelogyne corymbosa*	*Coelogeny taronensis*
Pseudobulbs	ovoid or oblong-ovoid, 2–2.5 × 1–1.3 cm	oblong-ellipsoid to ovoid, 2–6 × 1.1–2.5 cm	ovoid, 2–2.5 × 1.3–1.8 cm
Leaf blade	obovate-oblong or narrowly ovate, 4–6 × 0.8–1.4 cm, 5–7 veined	oblong-oblanceolate to obovate-oblong, 4.5–15 × 1–3 cm	elliptic or obovate, 9.8–13.5 × 2.2–2.3 cm
Pedicel and ovary	1.3–1.6 cm	2.5–3.1 cm	2.9–3.2 cm
Flowers	white	white	creamy-yellow
Dorsal sepal	lanceolate, 4.0–6.0 × 1.0–1.3 cm	elliptic to narrowly ovate, 2.6–3.5 × 0.8–1.3 cm	elliptic to narrowly ovate, 3–3.5 × 1.3–1.7 cm
Lateral sepals	lanceolate, 5.0–5.5 × 0.9–1.5 cm	oblong-elliptic or narrowly ovate, 2.6–3.7 × 0.7–2.1 cm	oblong-elliptic or narrowly ovate, 3.2–3.5 × 0.8–1.2 cm
Petals	lanceolate, 4.0–5.3 × 0.6–1.0 cm	narrowly elliptic or narrowly obovate, 2.4–3.2 × 0.6–1.2 cm	elliptic-oblong, 2.8–3.5 × 0.6–0.8 cm
Lip	narrowly ovate, 3.8–4.9 × 1.7–2.2 cm	ovate or elliptic, 2.1–3.3 × 1.4–2.1 cm	ovate, 2.8–3.9 × 2.1–2.6 cm
Patches or blotches	two bright yellow patches surrounded by shiny brownish red	four yellow blotches surrounded by reddish orange	four dark red patches
Keels	2 fimbriate or erose lacerate	2–3 wavy, entire or crenulate	3 crenulate to wavy and slightly papillose

2.4–3.7 cm long in *C. corymbosa*). Although the other morphologically similar species, *C. taronensis*, is similar to the new species with respect to ovoid pseudobulbs and in flower size, the new species differs from *C. taronensis* with regards to its white flowers (vs. creamy yellow in *C. taronensis*) (Figure 2), smaller leaf blades (Table 1), patches (two bright yellow patches vs. four dark red patches) and keels (two keels vs. three keels) on the lip. The major differences between the species are outlined in Table 1.

Acknowledgements

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DATA PAPER

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Data Release: DNA barcodes of plant species collected for the Global Genome Initiative for Gardens Program, National Museum of Natural History, Smithsonian Institution

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Abstract

The Global Genome Initiative has sequenced and released 1961 DNA barcodes for genetic samples obtained as part of the Global Genome Initiative for Gardens Program. The dataset includes barcodes for 29 plant families and 309 genera that did not have sequences flagged as barcodes in GenBank and sequences from officially recognized barcoding genetic markers meet the data standard of the Consortium for the Barcode of Life. The genetic samples were deposited in the Smithsonian Institution's National Museum of Natural History Biorepository and their records were made public through the Global Genome Biodiversity Network's portal. The DNA barcodes are now available on GenBank.

Keywords

DNA barcoding, GenBank, land plants

Introduction

The Global Genome Initiative (GGI) is a Smithsonian Institution program to collect, organize, share, and study genomic samples of non-human species. The mission of GGI is to preserve and understand Earth's genomic biodiversity. In pursuit of this mission, GGI aims to collect and preserve genome-quality tissue samples from all major lineages of life on Earth; foster biodiversity genomics research by generating DNA barcodes for dark taxa (i.e., those with no genetic data in online repositories); and promote the use of new technologies to study genomics across the tree of life. GGI supports the Global Genome Biodiversity Network (GGBN), an international network of institutions interested in the preservation of non-human genomic samples (Seberg et al. 2016). Members of GGBN can make their DNA and tissue collections discoverable on GGBN's data portal (http://www.ggbn.org/ggbn_portal/), ensuring transparent access and visibility to the genetic resources to the research community.

The Global Genome Initiative for Gardens Program (GGI-Gardens) is a GGI-funded effort to collect and preserve genetic material from the plant Tree of Life that is not yet represented in any of GGBN's partner institutions, and that are currently found in living collections around the globe. In its first phase, the program targeted living plant collections in the Washington, DC area and collected more than 1,800 genome-quality tissues from 209 families, 1007 genera and 1631 species. Moving forward, GGI-Gardens is focused on expanding its partnerships internationally to continue sample and preserve genomic biodiversity from all families and genera, and, potentially, species of plants on Earth.

The genetic samples collected to date have been deposited in the Smithsonian Institution's National Museum of Natural History Biorepository (http://naturalhistory.si.edu/rc/biorepository) and are available upon request to researchers across the globe (regulations on sampling leaf material can be found here). All corresponding specimen vouchers have been accessioned in the United States National Herbarium (US) or other recognized, partner herbaria. The GGI-Gardens protocol (Gostel et al. 2016) and US National Herbarium best practices (Funk et al. 2017) have been published to facilitate the establishment of voucher programs at partner institutions.

GGI's barcoding strategy data-mines GenBank to detect taxonomic groups that do not have sequences flagged as barcodes, thus allowing GGI to focus sequencing efforts on lineages that are not represented in this repository. Using this method, GGI selected more than 500 plant genera from GGI-Gardens collections and generated sequences for four genetic markers according to the DNA barcode data standard (Consortium for the Barcode of Life 2005). As a result, all sequences from officially accepted barcoding regions (two of the four markers targeted, see below) have been labeled with the keyword "BARCODE" in GenBank. All samples were determined at least to genus by the time of publication of this release paper by staff at the living collection where they were collected. Our intentions are to make these data publicly available, to contribute to the DNA Barcode library to assist further research, and to make the presence of these genomic-quality tissues known and available for the academic community for genomic research and education purposes via a documented application process. All DNA barcode sequences were submitted to GenBank as part of the GGI-Gardens BioProject (ID: PRJNA389125), which is included in Global Genome Initiative's DNA Barcoding umbrella BioProject (ID: PRJNA384793).

Data resources and contents of the dataset

Data are deposited in GenBank under accession numbers MF348326-MF350286 (see supplementary file 1 for the full list of accession numbers). A total of 1961 sequences have been submitted to GenBank representing 160 families and 521 plant genera, including 29 families and 309 genera that previously did not have sequences flagged as barcodes in this data repository. Two of the four genetic markers sequenced, *rbcL* and *matK*, have been officially recognized as barcoding regions for land plants (CBOL Plant Working Group 2009). The other two loci targeted in this study, the nuclear ribosomal internal transcribed spacer (nrITS) and the plastid *psbA-trnH* intergenic spacer, are commonly used for barcoding in angiosperms (Kress et al. 2005, Kress and Erickson 2009, Hollingsworth et al. 2016).

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Supplementary material 1

List of samples collected for the Global Genome Initiative for Gardens project selected for DNA barcoding, with GenBank accession numbers and genetic sample identification numbers. All the sequences are included in the GGI-Gardens BioProject.

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Data type: Microsoft Word Document (.docx)

Explanation note: List of samples collected for the Global Genome Initiative for Gardens project selected for DNA barcoding, with GenBank accession numbers and genetic sample identification numbers.

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REVIEW ARTICLE

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Ontogenetic variability in old and new collections of *Dicranophyllum gallicum* Grand'Eury from the late Palaeozoic of Europe

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Abstract

Dicranophyllum gallicum Grand'Eury is described by means of a morphometric analysis of eighty two samples from various old and new localities in western and central Europe. Stem, leaf cushions, leaf scars, leaves, axillary structures and potential seeds are described in detail, and discussed in comparison to earlier studies. The encountered variability in size and structure is shown to be higher than what was described earlier. The organisation of the leaf cushion and scar density vary gradually with the stem width, while stratigraphic position and ecology do not relate to it. It is concluded that the described variability represents an ontogenetic feature rather than a phylogenetic or ecologic one. The juvenile plants are characterised by small stems, a high leaf scar density and elongated leaf cushions with a dominant apical field, while mature specimens are characterized by a wide stem, a relatively low leaf scar density and relatively wide leaf cushions with a pronounced basal field. Axillary shoots and potential seeds of *D. gallicum* are described and illustrated in detail for the first time. A reconstruction based on the studied material is presented.

Keywords

Dicranophyllales, Early conifers, Carboniferous, Permian

Introduction

Dicranophyllum gallicum Grand'Eury (1877) is a characteristic species of the late Mississippian to early Permian of Euramerica (Wagner 2005). The genus is typified by bifurcating leaves, inserted on the stem in helical arrangement, forming rhomboidal leaf cushions (Grand'Eury 1877). It has characters reminiscent of several higher taxonomic groups. The needle-like leaves may be associated to conifers, their bifurcations are reminiscent of ginkgophytes and the leaf cushions are found in lycophytes. *Dicranophyllum gallicum* Grand'Eury, the type species of the genus, is characterized by short, tough leaves bifurcating twice, with a central vein and two lateral stomatiferous furrows (Barthel 1977, Meyen and Smoller 1986). *Dicranophyllum gallicum* variatio *parchemineyi* was described by Renault and Zeiller (1888) to have a double row of small conical seeds attached to the unbifurcated base of the leaf (Renault and Zeiller 1888).

Given the divergent set of properties and the paucity of fertile specimens, taxonomic placement is difficult. Indeed, the genus is presented as a ginkgophyte in Taylor et al. (2009), while Anderson et al. (2007), following Cleal (1993), presented it as a member of the Dicranophyllales within the conifers. In the past, Grand'Eury (1877) compared *Dicranophyllum* to *Salisburya* (*Ginkgo*), but considered it as representing a new Paleozoic group of conifers. In the absence of insight in the internal organisation of the seeds, positioning within the cordaites, the cycads or the conifers was considered impossible to establish, but the conifers were preferred because of the position of the seeds (Renault and Zeiller 1888). Neuburg (1948) placed the species within the Ginkgoales. Němejc (1959) put *Dicranophyllum* and *Trichopitys* together in the new class Dicranophyllopsida, considering them to be intermediate between ginkgophytes and conifers, while having descended from the pteridosperms. Meyen and Smoller (1986) partly adopted this suggestion by assigning *Dicranophyllum* and *Trichopitys* to the order of the Dicranophyllales, which was placed within the Coniferopsida. Meyen (1987) stressed that the microdenticulate leaf margin observed in *D. gallicum* was absent in Ginkgoopsida, which pointed towards an affiliation with the Coniferopsida and the Cordaithantales. Archangelsky and Cúneo (1990) described *Polyspermophyllum sergii*, which shows similarities to both *Trichopitys* and *Dicranophyllum*. They created two separate families Trichopityaceae and Dicranophyllaceae within the Dicranophyllales. Considering it difficult to relate the Dicranophyllales to either the Cycadopsida or the Coniferopsida, they interpreted them as an order of primitive gymnosperms. A phylogenetic analysis has indicated that *Dicranophyllum hallei* is represented by a branch basal to all earliest conifers, the Voltziales (Rothwell et al. 2005)

The present contribution provides a detailed description of *Dicranophyllum gallicum* specimens from French, German and new Czech collections. Potential fertile organs are documented in detail for the first time and strong variability within the species is shown to relate to the plants ontogeny rather than its phylogeny or ecology.

Materials and methods

A total of 82 samples holding *Dicranophyllum gallicum* are described in this study (Suppl. material 1). These samples were assembled from the collections of the Museum d'Histoire Naturelle Jacques de la Comble in Autun, the Museum d'Histoire Naturelle in Paris, the collection at the Naturhistorisches Museum Schloss Bertholdsburg, Schleusingen, the collections at the Naturkundemuseum in Berlin, the Paläon-

Table 1. Stratigraphy, age and lithology of the different localities.

Locality	Country	Stratigraphic unit	Lithology	Age
Kladno	Czech Republic	Radnice Member	tuff	Westphalian C (Roscher and Schneider 2006)
Lubná, Filip II quarry	Czech Republic	Radnice Member	tuff	Westphalian C (Roscher and Schneider 2006)
Zwickau	Germany	Zwickau Formation	volcanics	Westphalian D-Cantabrian (Schneider and Romer 2010)
Ronchamp	France	?	coaly mudstone, black coal	Stephanian (Aubouin 1965)
Mont-Pelé	France	? Mont-Pelé Formation	tuff	Stephanian (Doubinger 1970)
Saint-Étienne	France	? Assise des couches de St Etienne	shale	Stephanian (Becq Giraudon et al. 1995)
Knoviz	Czech Republic	? Hredle Member	shale	Stephanian (Oplustil et al. 2016)
Commentry	France	?	shale	Late Stephanian (Krings and Kerp 1999)
Sperbersbach	Germany	Goldlauter Formation	tuff	Asselian (Schneider and Romer 2010)
Kammerberg	Germany	Manebach Formation	grey facies of fluvial deposits	Asselian (Schneider and Romer 2010)
Oelsnitz	Germany	Hartensdorf Formation	?	Asselian (Schneider and Romer 2010)
Oberhof	Germany	Oberhof Formation	red and grey facies with up to 90% of volcanics	Asselian/Sakmarian (Schneider and Romer 2010)
Winnweiler	Germany	Donnersberg Formation	tuff	Sakmarian/Artinskian (Schneider and Romer 2010)
Rotterode	Germany	Rotterode Formation	?	Sakmarian/Artinskian (Schneider and Romer 2010)

tologisches Museum in Munich, the collections at the National Museum of Natural History in Prague (where the Lubná samples came from a new collection), the Czech Geological Survey in Prague and the Faculty of Geosciences of the Utrecht University in the Netherlands. The samples came from Ronchamp, Mont Pelé, Saint Etienne, Commentry and Lodève in France, Kladno, Knoviz and the new locality Lubná in Czeck Republic, and Zwickau, Sperbersbach, Kammerberg, Oelsnitz, Oberhof, Winnweiler and Rotterode in Germany (Table 1).

Thirty-eight specimens from the Muséum d'Histoire Naturelle Jacques de la Comble in Autun, France, were borrowed by Naturalis Biodiversity Center in Leiden, the Netherlands, and detailed measurements of these fossils were carried out by use of a Zeiss SteREO Discovery.V20 microscope with a Zeiss AxioCam MRc 5 for photography, and the associated program AxioVision. The other collections were visited by the authors. Measuring was performed using the means available at each collection. Where digital measuring equipment was not available measurements were carried out by hand (i.e., with a binocular microscope and protractors). Photographs were made using a Lumix Panasonic DMC FZ 18 camera. Pictures of the fossils in the Prague collection were taken using the equipment available at the Paleontology department; measurements on these pictures were carried out in Leiden using AxioVision.

Measured characters for the stem (Suppl. material 2) were stem width, total, basal and apical leaf cushion length, leaf scar width and length (Fig. 1), and scar density. Measured characters of the leaf (Suppl. material 3) were the length of the middle leaf segment only (as basal and top parts were often missing), the width of each segment and its angle of bifurcation. Length and width of axillary shoots were measured (Suppl. material 4), as well as the length and width of seeds found in close proximity to the leaves, the size of their nucellus and the thickness of their integumentary coat (Suppl. material 5). The compilation of this primary data set was carried out using the paleontological statistics software package PAST 3.01 (Hammer et al. 2001).

Results

Properties from the axis were recorded for 85 samples, properties from the leaves were recorded for 96 samples, and 19 axillary shoots and 15 seeds were measured.

Stem

Stems are slender with a helical leaf arrangement. They are always fragmentary, but the longest fragment is 360 mm. The leaves are inserted at a perpendicular angle or even at a downward angle, after which the leaf departs at an acute angle thus commonly forming a pouch (Fig. 2).

The 85 measurements of the stem width indicate a diameter of 2 to 36 mm (mean 11 mm). Samples from the Mont Pelé are the smallest (on average 10 mm), while samples from Lubná, Oelsnitz and Ronchamp have on average wider stems (mean respectively 13, 16 and 17 mm).

Leaf cushions

Leaf cushion length varies between 3 and 22 mm (mean 7 mm). Samples from Oelsnitz, Ronchamp and Lubná display longer leaf cushions (mean respectively 8, 9 and 12mm). Leaf cushions are between 1.3 and 6.7 times longer than wide (mean 3.5, indicating an average width of 2 mm). The Oelsnitz samples have relatively broad leaf cushions (on average only 2.3 × longer than wide).

The scar position in the present data determines the length of the basal and apical leaf cushion field (Fig. 1). On average the 20% of the total leaf cushion length represented

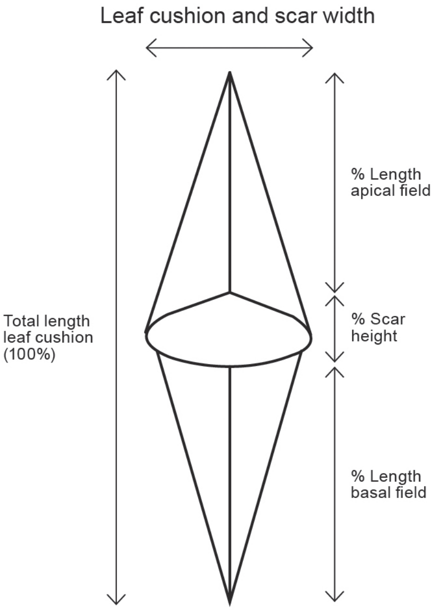

Figure 1. Schematic leaf cushion organisation: Total length and width leaf cushion, length apical and basal field leaf cushion, height and width leaf scar.

Figure 2. Side view of leaf attachment: sample 191, Mt Pelé. (Arrow indicates leaf attachment).

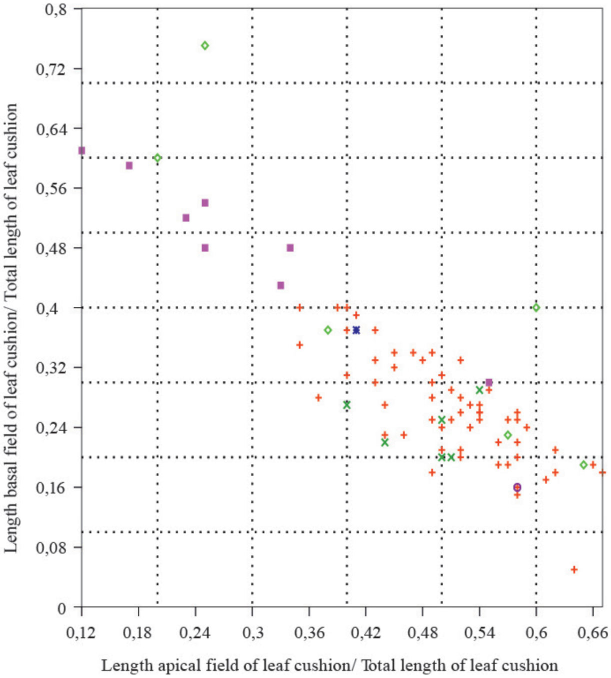

Figure 3. Diagram of the relative dominance of the basal over the apical leaf cushion field. Legend: Horizontal axis: Length apical leaf cushion field/ total length leaf cushion, vertical axis length basal leaf cushion field/ total length leaf cushion. Pink square: Lubná red cross: Mt Pelé, light green diamond: Ronchamp, dark green cross: Oelsnitz, dark blue star: St Etienne, purper circle: Kladno.

by the leaf scar is in the lower half of the leaf cushion, thus leaving 35% for the basal leaf cushion and 45% for the apical one. In plotting the size of the basal field relative to the total leaf cushion length against the relative size of the apical field to the total leaf cushion length (Fig. 3), it becomes apparent that the Lubná and two Ronchamp samples have a relatively large basal leaf cushion field (Fig. 4A), while the Mt Pelé, Oelsnitz and Kladno specimens have a small basal field and a relatively large apical field (Fig. 4B).

Leaf scars

Leaf scars are broader than height. The leaf scar is apically rhombic acute, basally rhombic obtuse, with a height of 1–3 (mean 1.5) mm and a width of 1–3.5 (mean 2) mm.

The average leaf scar density varies strongly between 1 and 34/cm^2 (mean 9/cm^2). Scar density in the Mont Pelé material is highest (10/cm ^{2}), and is lower for the Lubná, Ronchamp and Oelsnitz samples (mean respectively 3, 3 and 7/cm^2). Furthermore, as can be inferred from the scar density plotted against stem width, these properties are correlated (Fig. 5A). The scar density decreases with the increase of the stem width. At the same time leaf cushion length and width increase with stem width (Fig. 5B,C).

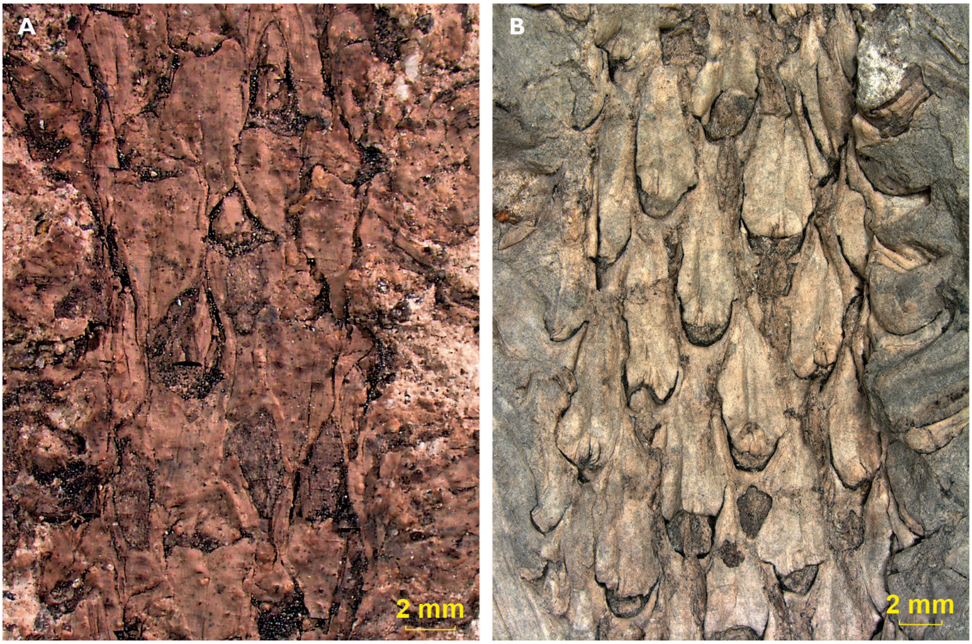

Figure 4. Variations in leaf cushion organisation: **A** Leaf cushion organisation in a specimen with a relatively dominant basal leaf cushion field, Sample E 06944, Lubná **B** Leaf cushion organisation in a specimen with relatively dominant apical leaf cushion field, Specimen 223, Mt Pelé.

Leaves

The angle of bifurcation in leaf specimens ranged from 2 to 41 degrees for the first bifurcation, and 18 to 68 degrees for the second. The second angle is generally larger than the first (Fig. 6A).

As most leaves were incomplete, only the length of the middle segment could be measured. The length of the middle leaf segment varied between 1.4 and 87.0 mm (mean 18.2). The Mont Pelé samples had the smallest middle segment (mean of 8.4 mm), while Ronchamp, Lubná and Sperberbach second leaf fragments were larger (mean respectively 15.7, 19.7 and 19.9 mm).

The width of all three leaf fragments could be measured varying between 1.0 and 4.6 mm (mean 2.3 mm). While the width of the first non-bifurcated segment of Mt Pelé samples was relatively small (mean 1.9 mm), those of Ronchamp, Lubná and Sperberbach was relatively large (mean respectively 2.1, 2.9 and 2.9 mm). The width of the second segment varied between 0.6 and 2.5 mm (mean 1.4 mm) while, again, the width of the second segment of Mt Pelé samples was relatively small (mean 1 mm), and that of Ronchamp, Sperberbach and Lubná samples was relatively large (mean respectively 1.3, 1.8 and 2.0 mm). Finally the same was the case for the width of the third segment that varied between 0 and 2.1 mm (mean 0.5 mm). While the width of the third segment of the Mt Pelé samples was smallest (mean 0.2 mm), that of Ronchamp, Sperberbach and Lubná samples was relatively large (mean respectively 0.5, 0.9 and 1.4 mm).

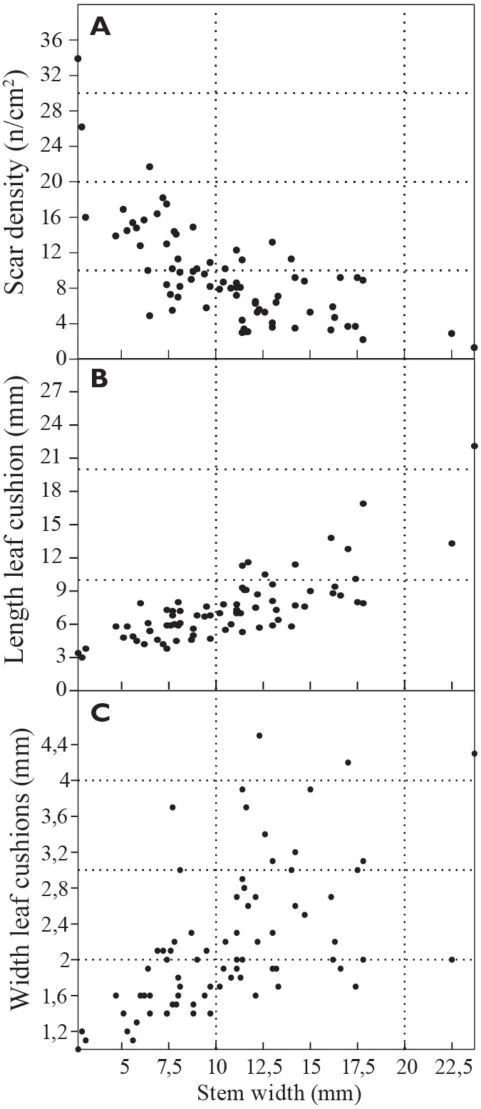

Figure 5. Changing properties with changing stem width: **A** Diagram of the scar density (in n/cm^2) to the stem width (in mm) **B** Diagram of leaf cushion length (in mm) to stem width (in mm) **C** Diagram of leaf cushion width (in mm) to stem width (in mm).

Leaf structure

Two rather distinct cuticular patterns on *D. gallicum* leaves can be observed on the different sides of the leaf. In a few specimens, two furrows were very clearly pronounced as protrusions on the impressed surface and no midvein was apparent (Fig. 6B); instead, we observed several thin striae between the furrows. As the furrows are documented to be located on the abaxial side of the leaf (Barthel 1977, Meyen

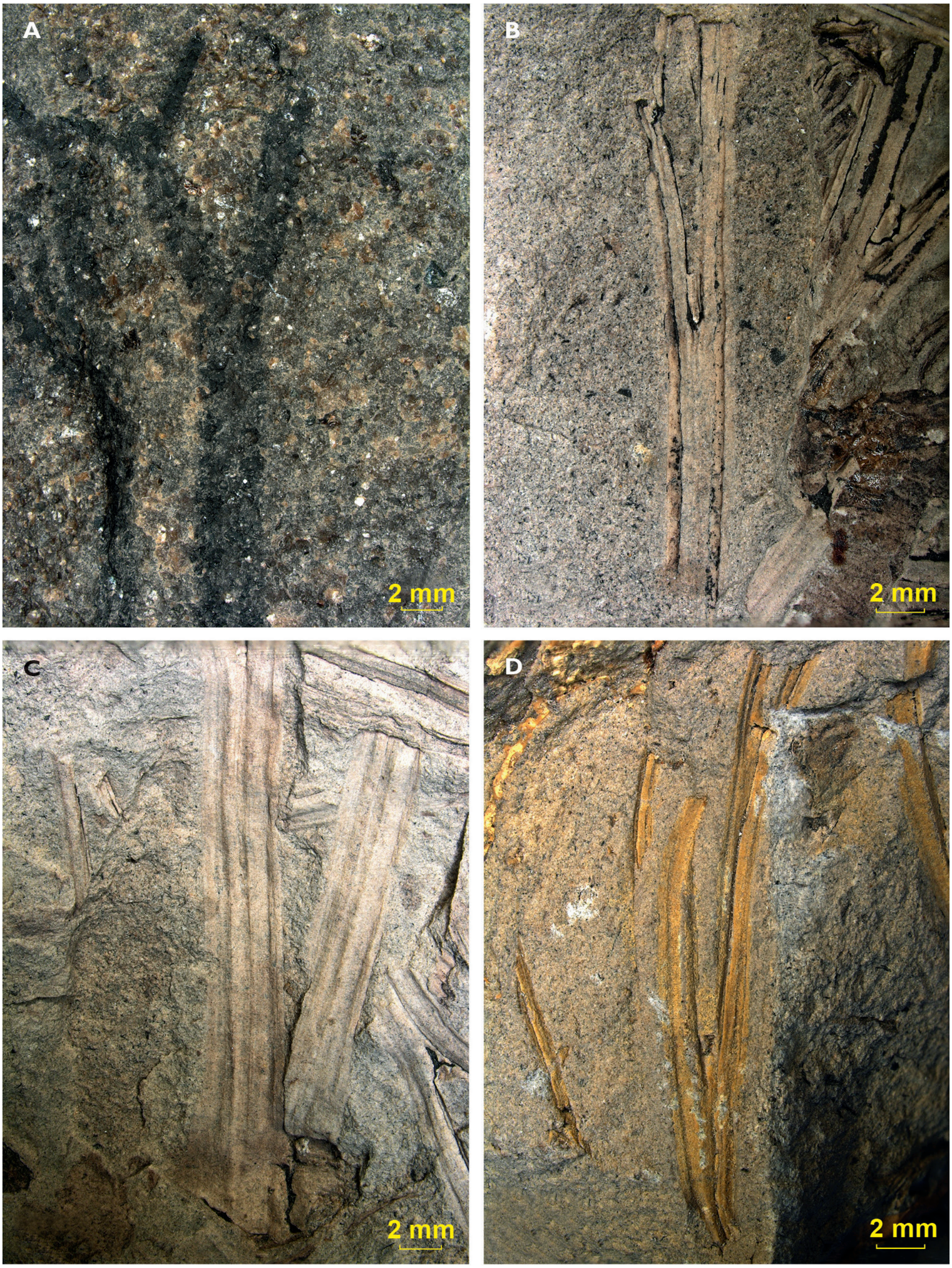

Figure 6. Leaf structures: **A** Leaf displaying two consecutive bifurcation angles, the second angle is larger than the first, sample 30, Ronchamp **B** Stomatal furrows as pronounced protrusions on the adaxial side of the leaf surface, note several thin striae between the furrows, sample 220 Mt Pelé **C** Stomatal furrows as pronounced depressions on the abaxial side of the leaf surface, note the midvein depression, sample 225 Mt Pelé **D** Venation in a *Dicranophyllum gallicum* leaf, note the trajectory of the midvein from the inner edge of the second leaf segment, gradually back to the centre position before the second bifurcation, sample 157, Mt Pelé.

and Smoller 1986), these leaves are identified as impressions of the abaxial side of the leaf. Impressions of the adaxial side of the leaf form the second leaf pattern that consists of a narrow midvein intrusion and two wide depressions which indicate the location of the underlying furrows pushing the adaxial leaf surface upwards (Fig. 6C). The furrows are between 0.3 and 0.4 mm (mean 0.35 mm). After its first bifurcation the midvein was observed to follow a distinct trajectory into the second leaf segment (Fig. 6D). It splits some distance before the actual bifurcation of the leaf and then follows the inner edge of the second segment while gradually returning to the centre position in the leaf sheet. Simultaneously, a new furrow appears alongside it.

Based on present observations of the adaxial and abaxial sides of the leaves of *D. gallicum* (Fig. 6B, C), it was possible to reconstruct the cross section of the leaf (Fig. 7A, B). As the furrows are visible on both sides of the leaf, the leaf of *D. gallicum* is expected to have been rather thin. The furrows on the underside of the leaf push the upper leaf surface upwards, causing the depressions in impressions of the adaxial leaf surface.

On some compression fossils marginal microdenticulation is preserved (Fig. 8A).

Attachment of the leaves to the stem

Reconstructing the attachment of leaves to the stem is difficult, as these two organs are commonly found separated from each other. Several specimens of *D. gallicum* do show a stem fragment with remnants of attached leaves, in which the leaf follows a specific curve as it escapes from the stem. There is little information on how this trajectory appears on leaf remains, as most leaves with clear venation are broken off and left their basal portion behind. An exception was found on specimen 1529 of Mt Pelé (Fig. 8B): this is an impression of the abaxial side of a leaf. The basal part of the leaf shows that the two furrows do not run all the way down in the leaf base, but find their origin more centrally to the leaf scar. Extrapolation of the orientation of the two furrows relative to the midvein indicates an origin for the two furrows near the basal portion of the leaf scar.

Axillary shoots

Well-preserved axillary shoots were found in the collections of the Museum of Natural History in Prague. Various shoots are attached to the stem of *Dicranophyllum gallicum* specimens from the Lubná locality (Fig. 9A–D). They are composed of elongated scales of 6 mm in length and 2 mm in width and are commonly positioned in the leaf axil. Although they have a general conical shape, their apical end is often widened (Fig. 9A). Their length varies between 4.0 and 14.0 mm (mean 8.0 mm), and their width varies between 2.5 and 7.0 mm (mean 4.0 mm) (Suppl. material 4). A cross

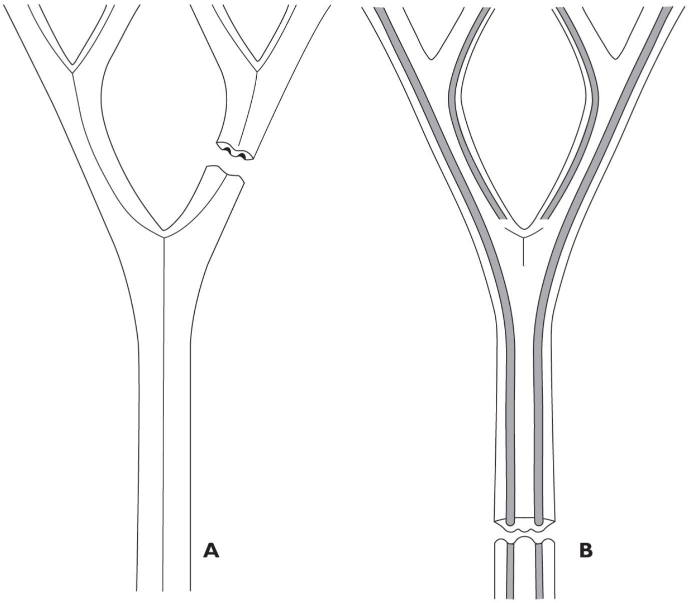

Figure 7. Diagram of leaf structure: **A** Reconstruction of the adaxial leaf side of *Dicranophyllum gallicum*, note the path of the midvein in the second segment of the leaf **B** Reconstruction of the abaxial leaf side of *Dicranophyllum gallicum*, note the prominent furrows and the absence of a clear midvein.

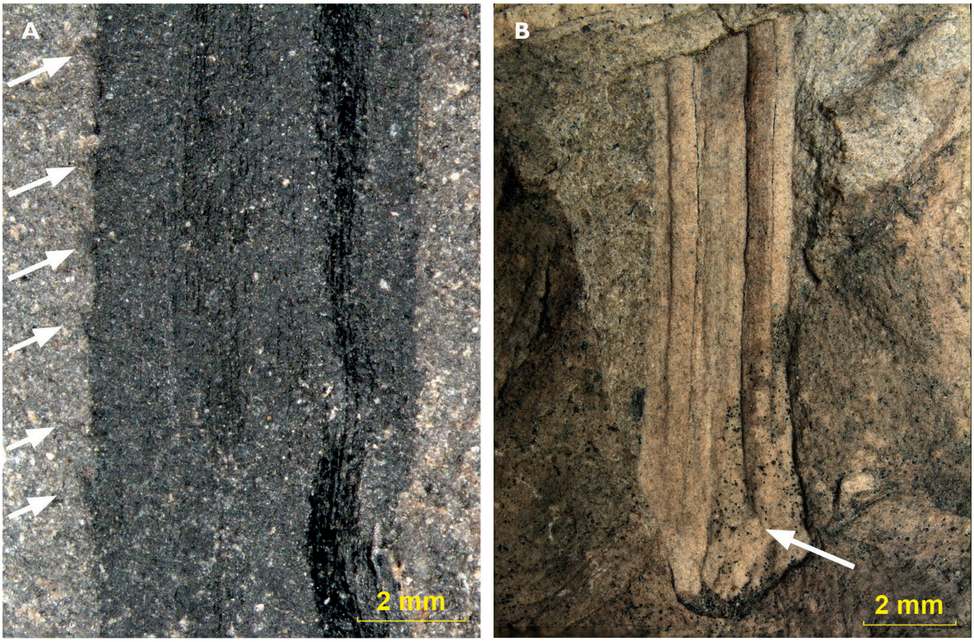

Figure 8. Leaf details: A Marginal microdenticulation, sample 34, Ronchamp (arrows indicate microdenticulation). B. Basal part of the leaf showing that the two stomatal furrows do not run all the way down in the leaf base, sample 1529, Mt Pelé (arrow indicates origin of furrow).

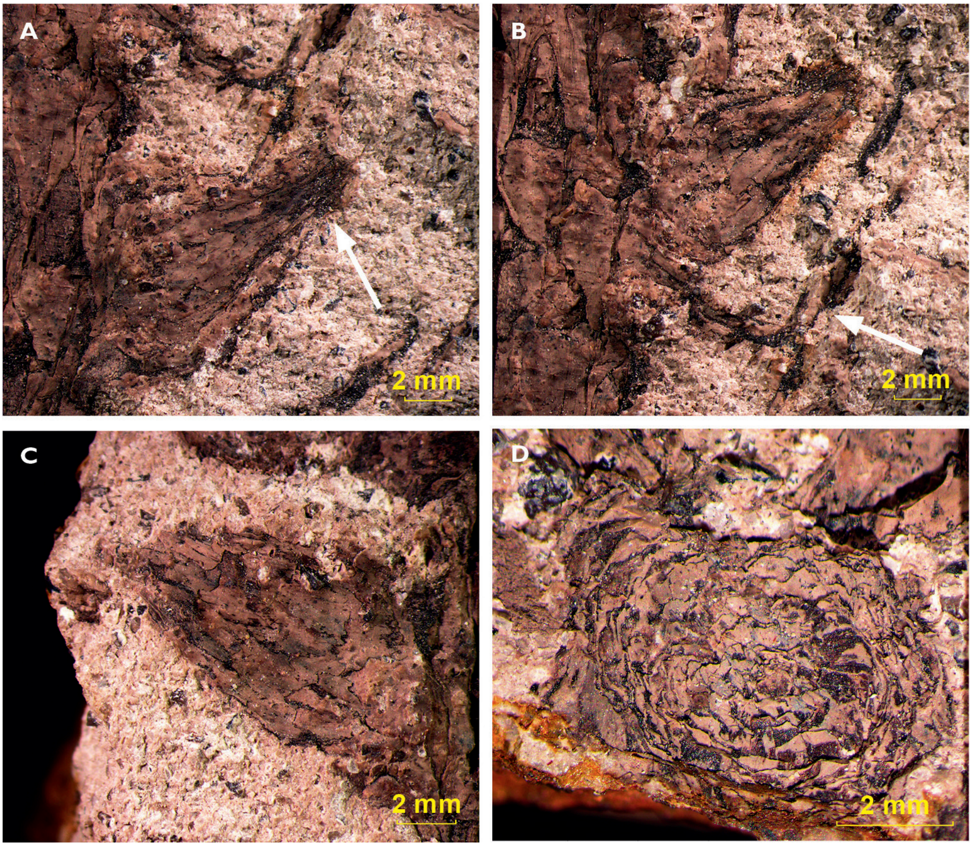

Figure 9. Axillary shoots: **A** Axillary shoot with apical widening (indicated by arrow), E 06946, Lubná **B** Axillary shoot with subtending leaf (indicated by arrow), sample E 06946, Lubná **C** Axillary shoot without broad apical widening, sample E 06950, Lubná **D** Cross section of axillary shoot, sample E 06946, Lubná.

section of one of these structures (Fig. 9D) could also be observed. It clearly displays the helical arrangement of the scales forming it. Some specimens from the Mont-Pelé locality also show axillary shoots.

Seeds

A total of 15 seeds was observed on the specimens in our study (Supplementary File 5). They were found dispersed on specimens from the Mont-Pelé locality, with one exception from the Ronchamp locality (specimen 1362). Seeds have a conical to ovate shape, 2.6–3.8 mm long (mean 3.4 mm) and 2.8–3.8 mm wide (mean 3.1 mm), usually longer than wide. A nucellus can often be observed and is 1.0–1.5 mm long (mean 1.2 mm) and 0.7–1.2 mm wide (mean 1.0 mm). The seed base is rounded, the chalaza part is flat-

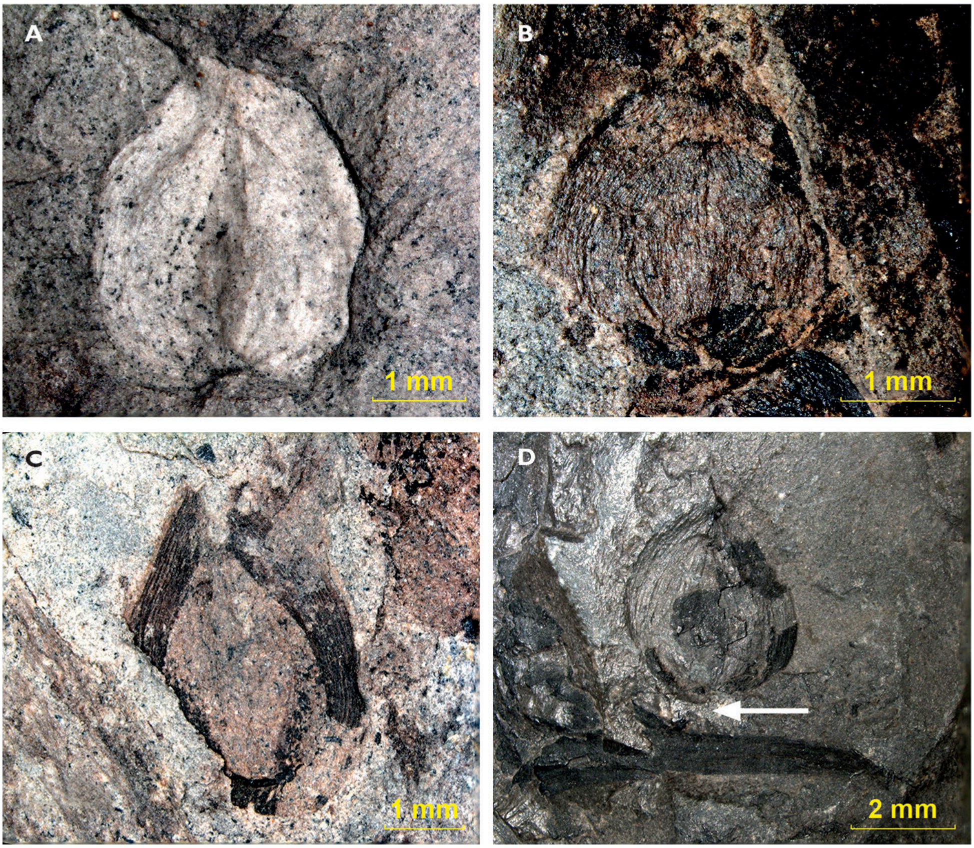

Figure 10. Seeds: **A** Seed with notched chalaza, sample 1529, Mt Pelé **B** Striate seed with visible pollen chamber, sample 75, Mt Pelé **C** Seed with visible micropyle, sample 75, Mt Pelé **D** Seed possibly on first leaf segment, sample 1362, Ronchamp (arrow indicates interrupted organic bridge).

tened to notched or cordate (Fig. 10A). The seed surface is striate (Fig. 10B). The apex is notched with what appears to be a (sometimes wide) micropyle (Fig. 10C). In a single seed (Fig. 10B) a triangular cavity which could be interpreted as a pollen chamber is seen in the seed. The integumentary coat is thick (200 μm), apically slightly thicker than basally. Two seeds are positioned next to a *Dicranophyllum gallicum* leaf, one of which shows an organic bridge between the leaf and the seed, but the bridge is interrupted (see Fig. 10D).

Discussion

Stem

The stem diameter recorded in the literature hovers around the mean values of 11 mm recorded here such as 9.0 mm for *D. gallicum* var. *parchemineyi* (Renault and Zeiller

1888), 10 mm for the German *D. gallicum* described by Barthel (1977) and 8 to 14 mm for the 7 samples from La Magdalena (Castro Martínez, 2005). Samples from Lubná, Oelsnitz and Ronchamp are wider, sample 10472 from Ronchamp being 36 mm wide. This indicates that the variability in the present European stem selection is much higher than what was recorded until now.

Leaf persistence and growth patterns

Leaves were found attached to stems of various sizes, implying that the plant had leaves covering most of the stem. Nonetheless, stem 221 in our study material shows a transition from large, well-developed leaf cushions to small, poorly defined leaf cushions. This transition gives an indication that the more apical part of these stems was still developing, while the more basal part was mature. Periodic growth patterns have not been observed on any stems, not even on the longest stem fragments of *D. gallicum*. This suggests that stem growth in *D. gallicum* never halted, that is, it was more or less continuous.

Many stem fragments are gently curved. Although we have not analysed this character in detail, it makes sense to expect that thicker stems are more resistant to bending, while slender stems are more flexible (also being younger). The majority of stems in the *Dicranophyllum gallicum* material is slender and curved to some extent, indicating that during its life the plant was probably flexible.

Grand'Eury (1877), Renault and Zeiller (1888) and Barthel (1977) considered the leaves to be persistent. The density of attached leaves appears to have been the largest in the apical regions, where establishing the details of the leaf morphology was often difficult as the leaves were preserved on top of each other. In the present material specimens with thick stems still had leaves attached (e.g. specimen 223), while other stems were completely devoid of leaves, suggesting leaf persistence related to an ecological factor.

Leaf cushion

Leaf cushion length and width from literature, respectively 4–7 mm and 2–3 mm (Zeiller 1880, Renault and Zeiller 1888, Castro Martínez 2005), is shorter than the mean values found in the data set described here (respectively 7 to 2 mm). However, it has been said to vary considerably (Renault and Zeiller 1888, Barthel 1977).

The dominant leaf cushion organisation with a large apical field is in contrast with the leaf cushion organisation given in Grand'Eury (1877). He described the leaf scar as positioned in the upper third of the leaf cushion, thus resulting in a very small apical field. Renault and Zeiller (1888) even placed the leaf scar in the upper quarter of the leaf cushion. Scrutiny of the illustrations of Grand'Eury (1877, plate XIV, fig 10, in particular) confirms a position of the leaf scar in the upper half of the leaf cushion, yet in Zeiller (1880, plate CLXXVI, fig 1) it cannot be established. In Renault and Zeiller (1888, plate LXX, fig 8 and plate LXXI, fig. 5), on the contrary, the scar is illustrated as either positioned basally or centrally in a similar way as for the bulk of the collections described herein.

As only the Lubná and the two Ronchamp samples have a well-developed basal leaf cushion field, these specimens are best comparable to the figured paratype of Grand'Eury (1877, plate XIV, fig 10). This is in contrast with the samples from Mt Pelé where, inversely, the apical field dominates over the basal field.

Leaf bifurcation angle

Renault and Zeiller (1888) described the angle of leaf bifurcation as 30° for the first bifurcation and 40° for the second. Barthel (1977) reported angles between 6° and 30°. The variation in angle size for the material described herein is much wider (2° to 68°) than what is given in the literature, yet the first angle is, indeed, commonly smaller than the second.

Leaf sizes

Earlier *Dicranophyllum gallicum* descriptions indicate that the total leaf length varied between 33 and 60 mm, with on average 15–20 mm for the first segment, 10–15 mm for the second and 8 to 10 mm for the third (Zeiller 1880, Renault and Zeiller 1888, Barthel 1977, Castro Martínez 2005). Doubinger et al. (1995) considered that the leaves can reach a length of 200 mm. The present material, based on our measurements of the second segment (mean 18.2 mm), was slightly larger than what was described earlier. Lubná, Sperberbach, Manebach and Ronchamp leaves were even larger (on average respectively 20, 17, 20 and 16 mm), while the Mt Pelé samples were, again, relatively small (8 mm).

The leaf width from earlier studies varied between 1.5 and 2.0 mm (Renault and Zeiller 1888) or between 2.0 and 3.0 mm (Barthel 1977). In the present material the leaf width varies between the same values.

Leaf structures

Dicranophyllum gallicum found in the Erzgebirge has small abaxial stomatal furrows of 0.2 to 0.25 mm wide. The furrow width in the present material was slightly larger (0.35 mm). Thin striae as found here between the two furrows have also been described earlier as five strong lineations in *D. gallicum* samples from the Goldlauterer Schichten (Barthel 1977).

The trajectory of the midvein presented above (Figs 6, 7) is one where the midvein approaches the leaf margin at the leaf bifurcation, to later diverge from the leaf margin and to again reach the central part of the leaf. This midvein pattern was not described earlier and is depicted differently in Barthel (1977) as splitting a few millimetres from the leaf margin in such a way that the two new veins always remain central to the leaf.

Leaves development

Barthel (1977) describes a process of leaf development as starting with simple unbifurcated leaves, after which the leaves produce a first, terminal bifurcation and, finally, a second bifurcation. According to De Lima (1888) a leaf can bifurcate three times.

Based on present material it is difficult to conceive such a leaf development, as no clear simple leaves on any *D. gallicum* specimen was observed. Incomplete leaves without bifurcations were observed, these could be associated to *D. gallicum* based on venation properties, that is, the clear presence of furrows, but it was not possible to make statements about whether those leaves bifurcate or are, indeed, simple leaves. A few leaves do display a size and shape that suggests an early stage of development (Fig. 11), but these already have two bifurcations. Ultimately, our material provides too little evidence to make an assumption about how the leaves developed.

Axillary shoots

Renault and Zeiller (1888), in describing a sample from Puits Forêt, indicated a charcoalified body formed by scales of 5 to 6 mm long and 2 to 3 mm wide attached to the stem. These scales are comparable in size to the scales described from the axillary shoots described above. Renault and Zeiller (1888) described the charcoalified body as seemingly forming a bud that had contained microsporangia, while the whole shoot was reminiscent in shape and size to cordaite male organs.

Dicranophyllum hallei also displays axillary shoots and Barthel and Noll (1999) suggested that these represent fertile cones (either male or female) while Noll (2011) found a dispersed female cone of *D. hallei*. In *Barthelia furcata* axillary shoots subtended by a forked bract represent ovuliferous dwarf shoots (Rothwell et al. 2005). In Anderson et al. (2007, fig. 2, p. 114), axillary shoots of *Dicranophyllum gallicum* are described as male cones, but in Meyen (1987) the axillary shoots, compared to axillary buds in *Mostotchkia*, are said to have been misinterpreted as microstrobili. From the present material and from what was described earlier, no unequivocal proof of the true nature of these axillary structures can be deducted.

Seeds

Seeds were already mentioned by Grand'Eury (1877) as very small, conical shapes positioned just above rather than at the leaf axil. Seeds have been found attached to the first leaf segment for *Dicranophyllum gallicum* var. *parchemineyi*, and described to be 4 mm long and 3 mm wide (Renault and Zeiller 1888). These sizes differ slightly from what is observed in present material (on average 3.4 long and 3.1 wide), but certainly are in the same order of magnitude. The nucellus described in the results

Figure 11. Possible juvenile leaf, sample 28, Mt Pelé.

above is smaller (mean 1.2 long and 1.0 mm wide) than what is described in Renault and Zeiller (1888) that is, 2.8 to 2.0 mm. The integumental coat, while being apically thicker in a similar way to what was described earlier, does not reach the 1 mm indicated in Renault and Zeiller (1888). These differences in size can be hypothesized to relate to the Mt Pelé material being generally smaller than was described earlier. On the other hand, because seeds are propagules and conical seeds with a nucellus and a pollen chamber are produced by numerous divergent taxa, the occurrence of these seeds in both the Ronchamp and the Mt Pelé samples and their resemblance to the seeds described by Grand'Eury (1877) and Renault and Zeiller (1888) have to be considered here as probably coincidental and further advances on *Dicranophyllum gallicum* will have to await new and better finds.

Obviously, finding and describing the original material of *Dicranophyllum gallicum* Renault & Zeiller, 1888, would give unequivocal proof of the nature and organisation of the female fertile structures, but, in spite of a specific search for it, this sample cannot be located. Here we only have the interrupted organic bridge between the leaf base and the seed (Fig. 10D). As *D. gallicum* var. *parchemineyi* was illustrated with its seeds attached to the first, non-bifurcated segment of the leaf (Renault and Zeiller 1888, plate LXXI, fig. 5), it is tempting to consider this seed to be attached to the leaf as well, given its proximity and orientation towards the leaf. However, it is not possible to find stronger evidence for any further physical connection between the leaf and seed.

Ontogenetic variability

As seen in the results, the Mt Pelé samples are relatively small in leaf and stem size, have a normal leaf cushion length, have the highest leaf scar density and have a dominance of the apical over the basal leaf cushion field. The Lubná, Ronchamp and Oelsnitz samples, in contrast, relatively have a large stem and a short leaf cushion with a large basal leaf field and low scar density.

Such differences in features could indicate a phylogenetic differentiation, where the large Lubná samples are ancestral to smaller *Dicranophyllum gallicum* specimens, Lubná is amongst the oldest (from the Westphalian C, Table 1) localities in the present series, yet the *D. gallicum* from Kladno originates from the same Radnice Member as the Lubná samples do, yet ranges with its smaller dimensions and leaf cushion organisation with the rest of the French and German *D. gallicum*. It was demonstrated that scar density was negatively correlated to stem width (Fig. 5A), while leaf cushion length and width correlates positively to stem width (Fig. 5B, C). Lubná samples, have relatively large stems, low scar density and long and wide leaf cushions and are considered to have represented matured plants, having had the time to grow thicker stems, and longer and wider leaf cushions, thus resulting in a reduced scar density. The relative dominance of the basal over the apical leaf cushion field (Fig. 3), typifying the Lubá specimens, consequently is hypothesized here to relate to an ontogenetic development. The paratype (Grand'Eury 1877, plate VIV, fig. 10), the samples from Lubná and two samples from Ronchamp are considered to have been more mature specimen, while the Mt Pelé samples, with thin stems, relatively elongated leaf cushions and a high leaf scar density, are considered juvenile forms. As there is no systematic relation between lithology (Table 1), considered here as a reflection of the environmental setting, and specimen dimensions, ecology is not considered to play a part in the variability described herein.

Reconstruction

For the reconstruction of the habit of *Dicranophyllum gallicum* using Niklas' (1994) method, only the diameter of the plant is required. By using this method it has to be assumed that *D. gallicum* was a self-supporting plant, as the method was shown to be inapplicable to liana species (Niklas 1994, p. 1237). Indeed, *D. gallicum* shows no features like climbing hooks (see, for example, Krings and Kerp 1999 or Krings et al. 2003a).

In spite of Grand'Eury's (1877) early suggestion that a woody body formed underneath the leaf cushions and Barthel's (1977) description of *Dicranophyllum gallicum* as a woody plant, there is some uncertainty as to the true woodiness of the stem. Assuming that *D. gallicum* was, indeed, a woody plant and taking the largest stem diameters of 36 mm, it is calculated to have reached a height of at least 4.5 m (Table 2).

This expected height could increase if *D. gallicum* were shown to have branched. Grand'Eury showed a single specimen with a branching stem fragment (Grand'Eury

Table 2. Reconstruction of stem height.

Maximum width (m)	**Result (m)**	**Wood type**	**Niklas' formulas**
0.036	4.49	woody	10^(1.59+0.39 (Log 10) (Stem width))-0.18 (Log 10) (Stem width)^2)
	3.37	nonwoody	10^(2.51+1.41 (Log 10) (Stem width))-0.03 (Log 10) (Stem width)^2)
	3.37	intermediate	10^(1.81+0.7 (Log 10) (Stem width))-0.13 (Log 10) (Stem width)^2)
Average width (m)			
0.0111	1.38	woody	10^(1.59+0.39 (Log 10) (Stem width))-0.18 (Log 10) (Stem width)^2)
	0.73	nonwoody	10^(2.51+1.41 (Log 10) (Stem width))-0.03 (Log 10) (Stem width)^2)
	0.88	intermediate	10^(1.81+0.7 (Log 10) (Stem width))-0.13 (Log 10) (Stem width)^2)

1877, plate XIV, fig. 8), and reconstructed the species accordingly as a small tree (1877, tableau de végétation D, bottom left). However, no other *D. gallicum* fossils showing branching have been found since and none of the specimens in our study showed branching; Grand'Eury's (1877) figured specimen with a bifurcating branch is the only one showing this feature. This indicates that branching is either a rare occurrence in *D. gallicum* or the plant did not branch at all, thus suggesting that the specimen from Grand'Eury (1877) would be of a different species. For our reconstruction of *D. gallicum*, we propose that the plant had a simple, unbranched stem, which reached 4.5 meters in height (Fig. 12). This is comparable to the reconstruction of *Dicranophyllum hallei* by Barthel et al. (1998), in which a nearly complete, unbranched shoot of 2 m long is described. The stem widths of *D. hallei* specimens we observed were usually slightly greater than the *D. gallicum* measurements, indicating that *D. hallei* grew taller than *D. gallicum*.

Taxonomic affinity

Finding similarities between the pollination and fertilization process, and the presence of the retained motile sperms in *Ginkgo* and the Cycadales, Thomas and Spicer (1987) suggested the existence of a group of primitive pteridosperms for the common ancestor of the later. Such a group of primitive pteridosperms holding *Dicranophyllum gallicum* supports the views of Archangelsky and Cúneo (1990) of the Dicranophyllales representing an order of primitive gymnosperms. Rothwell et al. (2005) in their study of *Hanskerpia* found *Dicranophyllum hallei* to be positioned between the Cordaitales and the Voltziales at the base of the early conifers. Given that Renault and Zeiller (1888) considered *Dicranophyllum gallicum* to possibly have had male axillary shoots reminiscent of the microstrobili in Cordaitales, such a position for a member of the Dicranophyllales at the very base of the early conifers would be corroborated by an interpretation of the present axillary shoots as pollen cones, but in the absence of any unequivoval proof of them representing pollen cones, the axillary shoots are considered here as vegetative buds. As such this interpretation does not differ from the description given in

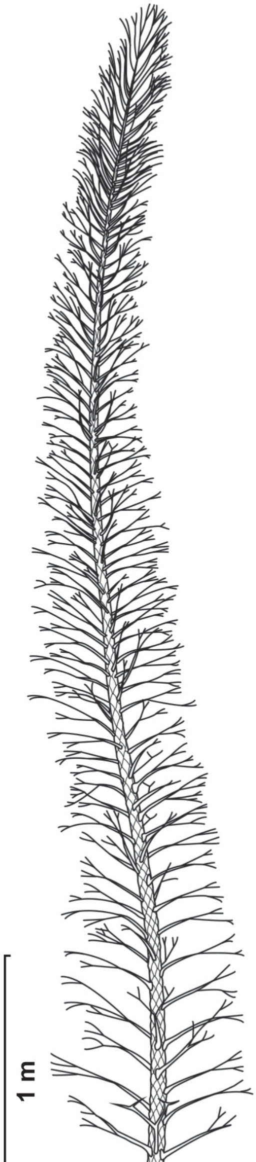

Figure 12. Reconstruction of *Dicranophyllum gallicum*.

Rothwell and Mapes (2001). They described *D. gallicum* as being represented by female fertile structures only and they considered it challenging to give a systematic assignment to early coniferophytes in general, e.g. the Dicranophyllales *sensu* Meyen (1987).

Environmental context

Marginal microdenticulation

Marginal microdenticulation (Fig. 8B) may indicate adaptation to a xeric environment, in which the teeth aid the plant in maintaining its internal temperature or absorb nutrients, as found in some extant xerophilic species (e.g. Benzing 1976, Benzing et al. 1976). However, marginal teeth are known to serve different functions for plants such as defence against herbivory (Krings et al. 2003b) and storage of minerals (Broadhurst et al. 2004).

Stomatal furrow

Although it was not possible with the present material to perform a cuticular analysis on the leaves of *Dicranophyllum gallicum*, Barthel's (1977) work shows that the stomata of this species occur in the embedded abaxial furrows. Jordan et al. (2008) showed that encryption of stomata in grooves (as found in *Dicranophyllum*) has evolved separately several times in a number of species of Proteaceae that are known from arid to semi-arid environments. Archangelsky et al. (1995) associated the hypostomatic leaves of the Cretaceous cycad *Pseudoctenis ornata* Archangelsky to the volcanic environment in which it occurred. The hypostomatic nature of the leaves provides no certainty about the vegetation density, which may be open as well as closed (Jordan et al. 2014). Moreover, Parkhurst (1978) explained that stomatal distribution is not primarily caused by environmental factors, but can be seen as an indicator of leaf thickness (thick leaves generally being amphistomatous).

Other plant fossils found co-occurring on the *Dicranophyllum gallicum* samples

Information about associated plant species occurring beside *Dicranophyllum gallicum* mainly comes from the tuffaceous material of the Mont-Pelé locality. The specimens from this locality had fragments of *Calamites*, *Pecopteris*, *Nemejcopteris*, *Alethopteris*, *Neuropteris*, *Sphenopteris*, *Cordaites*, and the seeds *Pachytesta* and *Samaropsis* associated with them. Also, on specimen E 06948 from the Lubná locality, a megasporangium of an *Omphalophloios* sp. was found. These genera are predominately known from the late Pennsylvanian tropical forests of Euramerica and, as *Dicranophyllum gallicum* was maximally 4.5 m high, it is suggested here that the plant stood in the shade of its taller associates. *Omphalophloios feistmantelii* is also 2–3 m in height and has been interpreted as a plant able to rapidly colonize local habitats, preferring peat and mixed peat-clastic swamps (Bek et al. 2015). *Dicranophyllum gallicum*, because of its comparable size and co-occurrence, is suggested here to have occupied the same or similar habitat.

Sediment

Dicranophyllum gallicum is as often preserved in tuffs as in shales (Table 1). Assuming the specimens preserved in tuffs are (par-) autochtonous, *D. gallicum* may have thrived in the mesic-xeric areas from a volcanic slope with active volcanism. The specimens found in shales are considered to have grown in wetter areas, as suggested in Anderson et al. (2007) for Dicranophyllaceae, in riparian or lake-side environments. Yet the occurrence in tuffs supports a more ruderal behaviour that the association with an *Omphalophloios* sp. already suggests, thus indicating an opportunistic colonization strategy. According to Wagner (2005) the paucity of *Dicranophyllum* finds may have indicated that it had ecological requirements differed from those prevailing in the 'coal measures' and rather belonged to extra basinal, well-drained soils. Considering *D. gallicum* is found both in shales and in tuff, an opportunistic colonization strategy as for *Omphalophloios* sp. is preferred here.

Conclusions

It appears that the variability of *Dicranophyllum gallicum* in stem size, leaf cushion organisation, leaf size and bifurcation angle is much wider than what was presented in earlier studies. The variability in leaf cushion organisation with either the dominance of the apical or the basal leaf cushion field is newly described herein. Dominant apical leaf cushion fields are generally found on specimens with small stems, relatively long leaf cushions and a relatively high leaf scar density, while well-developed basal leaf cushion fields commonly occur on specimens with a broad stem, relatively wide leaf cushions and relatively low scar density. As scar density and stem width are gradually and negatively correlated, while the two stem types have the same stratigraphic occurrence, but divergent lithologies, the variability they represent is considered to point towards ontogenetic rather than phylogenetic or ecologic variability. The smaller stems with higher scar density and elongated leaf scar with a dominant apical field are considered juvenile while the larger stems with lower scar density, relatively broad leaf scars with well-developed basal field are considered mature specimens. The newly described Lubná samples chiefly represent mature specimens.

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Supplementary material 1

List of samples holding the *Dicranophyllum gallicum* specimen considered in present analysis.

Authors: Jorik Van Der Pas, Linda Poppe, Isabel M. Van Waveren

Data type: Microsoft Excel Worksheet (.xlsx)

Explanation note: List of samples holding the *Dicranophyllum gallicum* specimen considered in present analysis. The samples are listed by collection, specimen number and locality.

Link: https://doi.org/10.3897/phytokeys.88.14042.suppl1

Supplementary material 2

Measurements on *Dicranophyllum gallicum* stem.

Authors: Jorik Van Der Pas, Linda Poppe, Isabel M. Van Waveren

Data type: Microsoft Excel Worksheet (.xlsx)

Explanation note: Measurements on *Dicranophyllum gallicum* stem: stem width, leaf scar length and width, leaf cushion length and width and apical and basal leaf cushion length in mm and leaf scar density in number per cm^2.

Link: https://doi.org/10.3897/phytokeys.88.14042.suppl2

Supplementary material 3

Measurements of *Dicranophyllum gallicum* leaves.

Authors: Jorik Van Der Pas, Linda Poppe, Isabel M. Van Waveren

Data type: Microsoft Excel Worksheet (.xlsx)

Explanation note: Measurements of *Dicranophyllum gallicum* leaves: length second segment, width first, second and third segment in mm.

Link: https://doi.org/10.3897/phytokeys.88.14042.suppl3

Supplementary material 4

Measurements of *Dicranophyllum gallicum* axillary shoots.

Authors: Jorik Van Der Pas, Linda Poppe, Isabel M. Van Waveren

Data type: Microsoft Excel Worksheet (.xlsx)

Explanation note: Measurements of *Dicranophyllum gallicum* axillary shoots: maximal length, maximal width, apex width in mm.

Link: https://doi.org/10.3897/phytokeys.88.14042.suppl4

Supplementary material 5

Measurements of seeds co-occurring with *Dicranophyllum gallicum*.

Authors: Jorik Van Der Pas, Linda Poppe, Isabel M. Van Waveren

Data type: Microsoft Excel Worksheet (.xlsx)

Explanation note: Measurements of co-occurring seeds: seeds length and width and nucellus length and width in mm.

Link: https://doi.org/10.3897/phytokeys.88.14042.suppl5