A new species and expanded distributions of freshwater *Audouinella* (Acrochaetiaceae, Rhodophyta) from Central Mexico and south-eastern Brazil

JAVIER CARMONA JIMÉNEZ¹ AND ORLANDO NECCHI JR²

 ¹ Laboratorio de Ficología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad Universitaria, A.P. 70-620, Coyoacán, 04510, México, D.F.
 ² Departamento de Zoologia e Botânica, Universidade Estadual Paulista, Rua Cristóvão Colombo, 2265–15054-000–São José do Rio Preto, SP, Brazil

(Received 15 July 2000; accepted 20 March 2001)

Eighteen collections of red-coloured Audouinella from Central Mexico and southeastern Brazil detected three species. The most common species, A. eugenea, is characterized by macroscopic thalli, the erect system consisting of filaments with cylindrical cells, undifferentiated into proximal and distal parts, and relatively large monosporangia ($\ge 12.0 \,\mu m \log \beta$). Spermatangia and possible propagules were observed in some Mexican populations. This is the third Audouinella species observed to have gametangia and the first member of the Acrochaetiales with putative propagules. The second species, from Central Mexico, was characterized by the following features: macroscopic thalli, the erect system differentiated into proximal parts with cylindrical cells, unbranched or rarely branched, and distal parts with barrel-shaped cells, abundantly branched to form dense fascicles, with alternate or dichotomous branching, some at right-angles to the axis, and relatively large monosporangia ($\ge 12.0 \,\mu\text{m}$ long). The morphologically distinct proximal and distal portions of the erect system, the latter forming dense fascicles, was a consistent character so far unknown in Audouinella; thus, we propose a new species, A. huastecana sp. nov. The third species is a microscopic epiphyte, A. meiospora, with a well-developed prostrate system composed of creeping and loosely aggregated filaments, and a short homogeneous erect system (< 15 cells) of filaments with cylindrical or barrel-shaped cells and small monosporangia ($\leq 13.0 \,\mu m$ long). A. eugenea and A. meiospora are characterized for the first time from the Southern and Northern Hemispheres, respectively, both occurring mostly in areas of tropical or subtropical rainforests. A. meiospora is reported from new macroalgal hosts. A. eugenea and A. huastecana tended to occur in warm, alkaline waters with a high ion content that were moderate to fast flowing, whereas A. meiospora was not associated with particular habitats.

Key words: Acrochaetiaceae, Audouinella, Audouinella huastecana, Brazil, Mexico, Rhodophyta, stream

Introduction

Freshwater members of *Audouinella* have recently been divided into two groups (Necchi *et al.*, 1993*a*, *b*; Necchi & Zucchi, 1995, 1997): the redcoloured and the bluish species. The reddish species are independent and capable of producing gametangia, carposporangia and tetrasporangia (Necchi *et al.*, 1993*a*; Necchi & Zucchi, 1995). The bluish representatives are commonly accepted as the alternate life-history phase of batrachospermalean taxa, called the 'Chantransia' stage, and typically have young gametophytes differentiating on some filaments (Necchi & Zucchi, 1997). However, neither sexual reproduction nor young gametophytes are often observed in freshwater acrochaetioid algae under natural conditions (Korch & Sheath, 1989;

Correspondence to: O. Necchi. Fax: +55 (17) 224 8692. e-mail: orlando@bot.ibilce.unesp.br Necchi et al., 1993a, b; Necchi & Zucchi, 1995, 1997). Four red-coloured species have been recognized in recent studies (Necchi et al., 1993a; Necchi & Zucchi, 1995): A. eugenea (Skuja) Jao, A. hermannii (Roth) Duby, A. meiospora (Skuja) Garbary and A. tenella (Skuja) Papenfuss. Sexual reproductive structures or tetrasporangia have been reported in A. hermannii (Drew, 1935; Israelson, 1942; Reis, 1961; Starmach, 1985; Korch & Sheath, 1989; Compère, 1991; Necchi et al., 1993a), A. meiospora (Skuja, 1944) and A. tenella (Necchi et al., 1993a; Necchi & Zucchi, 1995) but not in A. eugenea.

The red-coloured *Audouinella* species have been poorly documented in Mexico. Sánchez-Rodriguez (1974) reported *A. hermannii* [as *A. violacea* (Kützing) Hamel] in a high mountain river. Necchi *et al.* (1993*a*) described morphometric and environmental characteristics of two Mexican populations of *A. eugenea*, and Montejano *et al.* (1999) listed this same species as a component of the stream algal flora of the region of La Huasteca. In Brazil, the genus has been more intensively studied. Necchi & Zucchi (1995) provided data on the distribution, morphology and habitat of *A. hermannii*, *A. meiospora* and *A. tenella*. Necchi *et al.* (1998) presented additional records for the distribution of *A. meiospora* from a tropical rainforest island and Necchi *et al.* (1999) listed *A. eugenea* from São Paulo State, including environmental data but without any morphological description.

The present investigation was carried out to evaluate the taxonomic characters, the environment of occurrence and the geographic distribution of red-coloured populations of *Audouinella*, along with previous reports from the central region of Mexico (La Huasteca) and southeastern Brazil (São Paulo State). The two regions are situated in similar latitudes in North and South Americas and have been surveyed using standardized sampling procedures, allowing comparisons.

Materials and methods

Eighteen red-coloured collections of freshwater Audouinella were analysed in this study. Eleven samples were collected from the region of La Huasteca, central Mexico (21-22 °N, 98-100 °W) from 51 sites with red algae (Carmona, 1997) at altitudes of 100-1000 m (Fig. 1). Seven samples were collected from São Paulo State, southeastern Brazil (22-25 °S, 45-51 °W) from 104 stream segments containing red algae (Necchi et al., 1999) at altitudes of 40-740 m (Fig. 1). The sampling programs aimed to include the main biomes (basically rainforest and Cerrado 'Brazilian savanna' areas) and geological regions (hard-water areas, draining calcareous rocks) particularly in the best-preserved areas. Sites were visited at least once and were 10-40 km apart. Each sampling site consisted of a 10 m length reach in streams of different sizes (first to fifth order), which was thoroughly examined for the presence of macroscopic red algal representatives and abundance estimated in terms of percentage cover (Necchi et al., 1999). At each site, one mixed algal sample was collected, including at least five specimens (tufts in the case of Audouinella species) of each visually recognizable macroalgal morphological type. Samples were fixed immediately after collection in 4% formaldehyde and included in the herbaria FCME and SJRP (Holmgren et al., 1990; Holmgren & Holmgren, 1993). The following environmental variables were recorded for each sampling site (according to procedures described in Carmona, 1997 and Necchi et al., 1999): temperature, specific conductance, current velocity, pH, depth and type of substratum.

Wedocumented all morphological characters previously considered to be of taxonomic importance in this genus, and microscopic analyses followed the procedures described by Necchi *et al.* (1993*a*) and Necchi & Zucchi (1995). For the algae in populations 8–10, with differentiated proximal and distal parts, we described separ-



Fig. 1. Location of the study regions in Central Mexico (La Huasteca) and southeastern Brazil (São Paulo State) with indication of the sites with red-coloured populations of freshwater *Audouinella*: circles, *A. eugenea*; squares, *A. huastecana*; triangles, *A. meiospora*.

ately the characters from the axis and fascicles. From each sample, five plants were taken, from which observations were made and morphometric characters measured in replicates of 20. Student's *t*-test was applied to some data for monosporangia, spermatangia and vegetative cells. A key was constructed for all freshwater *Audouinella* species from the Americas, using data from Necchi *et al.* (1993*a*), Necchi & Zucchi (1995) and information from this study.

Results and discussion

Morphological analysis

Three distinct groups of red-coloured freshwater *Audouinella* collections were recognized from Central Mexico and southeastern Brazil (Table 1, Figs 1–15). The first group (Figs 2–7), of 11 samples

(seven from Central Mexico and four from southeastern Brazil), fits within the circumscription of *A*. *eugenea* as described by Skuja (1934) and Necchi *et al*. (1993 *a*). It is characterized by macroscopic thalli, the erect system undifferentiated into proximal and distal parts, filaments with cylindrical cells and relatively large monosporangia ($\ge 12.0 \,\mu m \log n$).

Two important morphological features were observed in some Mexican populations of A. eugenea. Branches contained fascicles with two or three hyaline, elliptical or obovoidal terminal spermatangia (Table 1, Figs 3-4). These characteristics agree with the general spermatangial arrangement for the Acrochaetiaceae described by Woelkerling (1983). Interestingly, we found no structures that could unequivocally be described as carpogonia. This is only the third freshwater species of Audouinella reported with gametangia and it supports the contention that this entity is not a 'Chantransia' stage. Spermatangia were significantly smaller (p < 0.001) than the monosporangia from the same populations (Table 1). On the other hand, they were considerably larger than those reported for another freshwater species, A. hermannii (2.8-6.0 µm in diameter, as summarized by Necchi et al., 1993a).

The second novelty was the presence of possible propagules (Table 1, Figs 3, 5-7). They are pear- to club-shaped or irregular in shape, and consist of one to three cells with thickened cell walls and granulated and vacuolated cytoplasm. They are formed in mid-cells of filaments or less often terminally, from vegetative cells which undergo a special division resulting in the complete development of the propagule. Propagules have been described in the Gigartinales and Ceramiales (Guiry, 1990) and the Batrachospermales (Sheath & Whittick, 1995) but this is the first report for the Acrochaetiales. The occurrence of structures resembling propagules suggests that they possibly represent an alternative mode of vegetative reproduction, which might be important to population maintenance in stream habitats, but we have not observed germination, and further cytological studies are necessary to clarify development and function.

The second group, of three collections from Central Mexico (Table 1, Figs 8–13), is characterized as follows: thalli macroscopic, the erect system differentiated into proximal and distal parts, the proximal with cylindrical cells, unbranched or rarely branched, the distal with barrel-shaped cells, abundantly branched to form dense fascicles, with alternate or dichotomous branches, some at rightangles to the axis, and relatively large monosporangia ($\ge 12.0 \,\mu$ m long). Cells of proximal and distal parts were significantly (p < 0.001) different. The presence of proximal and distal portions in the erect system, the latter forming dense fascicles, was a consistent character so far unknown in *Audouinella*. We considered it of sufficient taxonomic importance to propose a new species. '*In situ*' monospore germination was often observed in this species (Figs 12–13). The occurrence of '*in situ*' monospore germination has not been reported in Acrochaetiaceae and seems to represent a reproductive strategy to enhance the probability of new filament growth, which is particularly important for survival under the high current velocities ($\geq 90 \text{ cm s}^{-1}$) in the species' habitat.

The third group (of one Mexican and three Brazilian collections; Table 1, Figs 14-15) is characterized by microscopic thalli, with a well-developed prostrate system composed of creeping and loosely aggregated filaments, and a short erect system, of up to 15 cells, undifferentiated into proximal and distal parts, filaments with cylindrical or barrel-shaped cells, branch angles $< 25^{\circ}$ and small monosporangia ($\leq 13.0 \,\mu\text{m}$ long). The characters for these populations agree with the descriptions of A. meiospora by Skuja (1944) and Necchi & Zucchi (1995). The species was also observed on hosts other than those previously reported (Table 2): Blennothrix ganeshii (Cyanophyta), Compsopogon coeruleus (Rhodophyta) and Vaucheria spp. (Xanthophyta).

Descriptions and taxonomic proposals

Audouinella eugenea (Skuja) Jao, *Sinensia*, **10**: 362, 1941 (Basionym: *Chantransia eugenea* Skuja, *Beih. Bot. Cbl.*, **52**: 177, 1934). Figs 2–7

Plants macroscopic, up to 10 mm high, and consisting of > 50 cells, red-coloured; basal system composed of an irregular prostrate mass with aggregated filaments; erect system with no differentiation into proximal and distal parts, composed of filaments with cylindrical vegetative cells, 11.5-60·0 μm long, 7·5–16·0 μm in diameter; branch angles $\leq 25^{\circ}$; chloroplast reticulate, covering most of the cell volume; monosporangia arranged in fascicles, obovoidal to subspherical, 12.0-18.0 µm long, 7.5–18.0 µm in diameter. Spermatangia 2 or 3 per branch, elliptical to obovoidal, hyaline, 8.0- $12.0 \,\mu\text{m}$ long, $6.0-12.0 \,\mu\text{m}$ in diameter. Putative propagules consisting of 1-3 cells, pear- to clubshaped or irregular, 22.0-48.0 µm long, 16.0-38.0 µm in diameter. Carpogonia, carposporangia and tetrasporangia not observed.

SPECIMENS EXAMINED: MEXICO: (1) San Luis Potosí, Tamasopo, Puente de Dios, coll. G. Montejano, 17.i.1984 (FCME PA1799); (2) Ciudad Valles, Micos, coll. G. Montejano, 26.iii.1987 (FCME PA2693); (3) Puente de Dios II, coll. J. Carmona, 8.ix.1989 (FCME PA3154); (4)

	Plant longth		Pranch angla	Vegetat	ive cell	Fascio	cle cell	Monos	porangia	Sperm	atangia	Propa	agules?
Populations	(mm)	Basal system	(degrees)	Length	Diameter	Length	Diameter	Length	Diameter	Length	Diameter	Length	Diameter
Mexican populations													
Audouinella eugenea													
1. PA1799	2	IP	< 25	28.1-52.0	11.3-17.6	_	_	13.3-22.6	7.5-15.3	_	_	_	_
Puente de Dios				39.2 ± 4.8	13.9 ± 1.4			17.0 ± 1.8	11.9 ± 2.1				
2. PA2693	10	IP	≤ 25	11.5-45.9	7.5-14.8	_	_	12.0-28.0	10.0-20.0	8.0-12.0	6.0-12.0	22.0-44.0	16.0-38.0
Micos				27.8 ± 10.7	9.8 ± 1.6			17.6 ± 4.8	13.6 ± 3.39	10.1 ± 1.7	8.9 ± 1.9	31.7 ± 4.9	22.6 ± 6.31
3. PA3154	2	IP	≤ 25	24.1-60.1	9.3-18.0	_	_	13.5-24.8	9.7-18.0	_	_	26.0-48.0	18.0-30.0
Puente de Dios II				44.8 ± 9.6	13.0 ± 2.2			19.1 ± 1.9	15.1 ± 1.7			33.5 ± 6.1	23.9 ± 3.3
4. PA3215	1	IP	< 25	13.0-36.0	7.5-15.2	-	_	14.5-24.2	7.9–16.6	_	_	_	_
Tancuilín				22.7 ± 5.4	$11 \cdot 2 \pm 2 \cdot 0$			19.9 ± 2.6	14.0 ± 2.2				
5. PA3356	3	IP	< 25	16.0-46.0	8.0-13.0	_	_	14.0-18.0	8.0-12.0	8.0-12.0	6.0-12.0	22.0-36.0	18.0-22.0
Santa Anita				$29 \cdot 1 \pm 7 \cdot 6$	10.1 ± 1.3			16.6 ± 1.9	10.8 ± 1.3	10.8 ± 1.3	8.5 ± 1.8	$29{\cdot}0\pm 5{\cdot}0$	19.5 ± 1.6
6. PA3435	1	IP	< 25	15.0-55.0	7.3-11.5	-	_	16.0-26.0	10.0-16.0	_	_	_	_
Nacimiento del Mante				35.6 ± 14.2	7.4 ± 3.3			19.7 ± 3.2	11.9 ± 1.6				
7. PA3490	1	IP	< 25	9.5-34.6	8.4-12.4	-	_	13.0-20.0	7.5-11.2	_	_	_	_
La Media Luna				16.6 ± 3.4	9.2 ± 1.6			17.0 ± 2.4	$10{\cdot}8\pm0{\cdot}6$				
Audouinella huastecana													
8. PA3163	5	IP	≤ 25	20.0-28.0	10.0-16.0	6.0-16.0	6.0-12.0	12.0-16.0	10.0-14.0	_	-	_	_
Choy A				23.7 ± 2.9	12.8 ± 1.8	8.8 ± 2.9	8.6 ± 2.1	14.0 ± 1.6	12.6 ± 1.8				
9. PA3261	5	IP	≤ 25	16.0-28.0	10.0-12.0	6.0-14.0	6.0-10.0	12.0-20.0	10.0-14.0	_	_	_	_
Choy B				22.4 ± 3.2	10.7 ± 0.9	8.0 ± 2.3	7.0 ± 1.5	17.1 ± 2.8	12.1 ± 1.5				
10. PA3584	7	IP	≤ 25	18.0-36.0	10.0-16.0	7.0-20.0	6.0-10.0	12.0-22.0	8.0-14.0	_	_	_	_
Choy C				26.6 ± 5.1	11.5 ± 1.9	10.5 ± 4.3	7.8 ± 1.0	16.0 ± 2.9	11.0 ± 2.0				
Audouinella meiospora				—	—	—	—	—	—				
11. PA3622	100 µm	CF	< 25	8.0-16.0	6.0-11.0	_	_	8.0-13.0	7.0-11.0	_	_	_	_
Tampaque				11.2 ± 2.2	8.8 ± 1.1			10.7 ± 1.4	8.8 ± 1.1				

Table 1. Characteristics of freshwater red-coloured populations of Audouinella from Central Mexico and south-eastern Brazil

Audouinella eugenea													
12. MA20	1	IP	< 25	27.5-40.0	$10 \cdot 0 - 12 \cdot 5$	I	Ι	12.5-17.0	$8 \cdot 0 - 10 \cdot 0$	Ι	I	Ι	Ι
Ilhabela				33.5 ± 4.3	10.8 ± 0.9			14.7 ± 2.2	9.0 ± 1.0				
13. SP12	1	IP	< 25	34.0-52.0	12.0 - 15.0	I	I	$14 \cdot 0 - 21 \cdot 0$	$12 \cdot 0 - 16 \cdot 0$	I	I	Ι	Ι
Apiaí (km 15)				$43 \cdot 1 \pm 5 \cdot 1$	$13 \cdot 1 \pm 0.9$			$17 \cdot 1 \pm 1 \cdot 8$	$13 \cdot 0 \pm 1 \cdot 0$				
14. SP13	1	IP	< 25	19.0 - 34.0	11.0-16.0	I	I	14.0 - 16.0	$12 \cdot 0 - 14 \cdot 0$	I	I	I	I
Apiaí (km 30)				$24 \cdot 2 \pm 4 \cdot 1$	$14\cdot 2\pm 1\cdot 4$			15.2 ± 0.97	12.8 ± 0.7				
15. SP14	1	IP	< 25	32.0-51.0	12.0 - 16.0	I	Ι	17.0-20.0	10.0-14.0	I	I	Ι	Ι
River Betari				$41 \cdot 5 \pm 4 \cdot 8$	13.9 ± 1.3			18.8 ± 1.2	12.7 ± 1.4				
Audouinella meiospora													
16. SP20	375 µm	CF	< 25	$12 \cdot 0 - 13 \cdot 0$	$8 \cdot 0 - 10 \cdot 0$	I	Ι	Ι	I	I	I	Ι	Ι
Juquiá				$11 \cdot 3 \pm 2 \cdot 1$	$9 \cdot 1 \pm 1 \cdot 0$								
17. SP49	100 µm	CF	< 25	9.5–18.0	$7 \cdot 0 - 10 \cdot 0$	I	Ι	I	Ι	I	I	I	I
Echaporã				13.6 ± 3.0	$8 \cdot 1 \pm 0 \cdot 8$								
18. SP72	100 µm	CF	< 25	12.0 - 18.0	8.0–12.0	I	I	13.0	8.0	I	I	Ι	I
Conchas				$15 \cdot 1 \pm 2 \cdot 1$	9.7 ± 1.5								
Measurements are in microm	netres (unless other	rwise specified)	and represent	range, mean an	d standard dev	iation.							
CF. Creeding Infaments: 1F. II	Tegular Di Usulare	mass.											

Brazilian populations

creeping filaments; IP, irregular prostrate mass.

Tamazunchale, Tancuilín, coll. J. Carmona, 5.xi.1990 (FCME PA3215); (5) Aquismón, Santa Anita, coll. G. Montejano, 20.ii.1992 (FCME PA3356); (6) Rio Verde, La Media Luna, coll. C. Candelaria, 23.v.1993 (FCME PA3490); (7) Tamaulipas, Ciudad Mante, nacimiento del Mante, coll. J. Carmona, 27.v.1993 (FCME PA3435). BRAZIL: (12) Ilhabela, Ilha de São Sebastião, road towards north, Ponta das Canoas, coll. O. Necchi Jr and C.C.Z. Branco, 21.viii.1993 (SJRP MA22); (13) Apiaí, Route SP-165, 15 km from the town, coll. O. Necchi Jr and C.C.Z. Branco, 9.x.1996 (SJRP SP12); (14) Iporanga, Route SP-165, 30 km from Apiaí, coll. O. Necchi Jr and C.C.Z. Branco, 9.x.1996 (SJRP SP13); (15) Iporanga, Route SP-165, 5 km from the town, Betari River, coll. O. Necchi Jr and C.C.Z. Branco, 9.x.1996 (SJRP SP14).

Audouinella huastecana Carmona et Necchi, sp. nov. Figs 8-13

DIAGNOSIS: Frons heterotricha, macroscopica, ad 7 mm alta. Partes proximales et distales systematis erecti dissimiles; fila proximalia cellulis cylindraceis, non vel raro ramosa; fila distalia cellulis doliiformibus, abundanter ramosa fasciculos densos facientesque; rami alternati dichotomive, interdum ab axe ad angulum 90° divergentes.

Monosporangia elliptica vel obovoidea, in filis distalibus terminalia, solitaria, 12.0–22.0 µm longa, 10.0-14.0 µm diametro.

Plants macroscopic, up to 7 mm high, and consisting of > 50 cells, red-coloured; basal system composed of an irregular prostrate mass with aggregated filaments; erect system differentiated into proximal and distal parts; proximal filaments with cylindrical vegetative cells, 16.0-36 µm long, $10.0-16.0 \,\mu\text{m}$ in diameter, unbranched or rarely branched; distal filaments with barrel-shaped cells $6.0-20 \,\mu\text{m}$ long, $6.0-12.0 \,\mu\text{m}$ in diameter, abundantly branched to form dense fascicles; branches alternate or dichotomous, some at right-angles to the axis: chloroplast reticulate, covering most of the cell volume; monosporangia elliptical or obovoidal, 12.0–22.0 µm long, terminal on distal filaments, single, 10.0-14.0 µm in diameter. Gametangia, carposporangia and tetrasporangia not observed.

HOLOTYPE: (8) coll. J. Carmona and G. Montejano, 9.ix.1989 (FCME PA3261).

TYPE LOCALITY: MEXICO: San Luis Potosí, Ciudad Valles, Choy.

ETYMOLOGY: The specific epithet is based on the pre-Hispanic culture called 'Huasteca' of the people inhabiting the region where the type locality is located.

ADDITIONAL SPECIMENS EXAMINED, FROM SAME LO-CALITY: (9) coll. J. Carmona and G. Montejano,



Figs 2–15. Morphological features of red-coloured freshwater species of *Audouinella*. Figs 2–7. *A. eugenea*. Fig. 2. Filament with a monosporangium (**FCME** PA3215). Fig. 3. Initial apparent propagule (arrow) and spermatangia (arrowhead) (**FCME** PA2693). Fig. 4. Detail of spermatangia (**FCME** PA2693). Figs 5–7. Details of possible propagules (**FCME** PA2693). Fig. 5. Pear-shaped propagule. Fig. 6. Irregular-shaped propagule. Fig. 7. Two-celled propagule. Figs 8–13. *A. huastecana*. Fig. 8. General view showing dense fascicles in distal parts (arrow) and unbranched proximal parts (arrowhead) (**FCME** PA3584). Fig. 9. Detail of an erect branch showing a dense fascicle (arrow) and an unbranched proximal part (arrowhead). Fig. 10. Detail of distal filaments from a fascicle (**FCME** PA3261). Fig. 11. Detail of a monosporangium (**FCME** PA3261). Figs 12–13. '*In situ*' monospore germination (**FCME** PA3261). Fig. 12. Initial stage. Fig. 13. Germinating filament with rest of monosporangium cell wall (arrow). Figs 14–15. *A. meiospora* (**FCME** PA3622). Fig. 14. Erect filaments with monosporangia (arrows). Fig. 15. Creeping filaments developing epiphytically around a filament of *Blennothrix ganeshii*. Scale bars represent: Figs 1, 8, 1 cm; Fig. 9, 5 mm; Figs 2, 5–7, 10–15, 20 μm; Figs 3–4, 10 μm.

1.v.1991 (**FCME** PA3261); (10) coll. J. Carmona, 7.vii.1995 (**FCME** PA3584).

Audouinella meiospora (Skuja) Garbary, Bibl. Phycol., 77: 112, 1987 (Basionym: Balbiania meiospora Skuja, Acta Hort. Bot. Univ. Latv., 14: 10, 1944). Figs 14–15

Plants microscopic, up to 400 µm high, and consisting of ≤ 15 cells, red-coloured; basal system well developed, composed of creeping and loosely aggregated filaments with cylindrical or barrelshaped cells, 5·0–18·0 µm long, 4·0–10·0 µm in diameter; erect system composed of filaments with barrel-shaped to cylindrical vegetative cells, 8·0– 18·0 µm long, 6·0–12·0 µm in diameter; branch angles $< 25^{\circ}$; chloroplast reticulate, filling most of the cell volume; monosporangia obovoidal to spherical, 8·0–13·0 µm long, 7·0–11·0 µm in diameter. Gametangia, carposporangia and tetrasporangia not observed.

SPECIMENS EXAMINED: MEXICO: (11) San Luis Potosí, Aquismón, Tampaque, coll. G. Montejano, 25.xi.1995 (FCME PA3622). BRAZIL: (16) Juquiá, Route to Sete Barras, coll. O. Necchi Jr and C.C.Z. Branco, 11.x.1996 (SJRP SP20); (17) Echaporã, Faz Rancho dos Ipês, Route SP-333, coll. O. Necchi Jr *et al.*, 16.vii.1997 (SJRP SP49); (18) Conchas, Ribeirão Muquém, 2 km from Route SP-300, coll. O. Necchi Jr *et al.*, 18.ix.1997 (SJRP SP72).

REMARKS: This species was originally described within the genus *Balbiania*, whose type species [*B. investiens* (Lenormand) Sirodot] was recently transferred to the new order Balbianiales (Sheath & Müller, 1999). The major distinguishing morphological feature of the genus *Balbiania* is the production of spermatangia on the tips of specialized, elongate cells, which are cut off in a cluster. In contrast, the spermatangia of *A. meiospora* are produced terminally on unspecialized filaments, singly or in pairs (Skuja, 1944) and, thus, it should be kept in *Audouinella* as proposed by Garbary (1987).

Key to freshwater species of Audouinella from the Americas

1. Plants microscopic ($\leq 400 \ \mu m$ high, $\leq 30 \ cells$ long), with a well-developed basal system composed of creeping filaments *A. meiospora* 1. Plants macroscopic ($\geq 1 \ mm$ high, $< 50 \ cells$ long), with basal system composed of an irregular prostrate mass with aggregated filaments 2 2. Erect system differentiated into proximal and distal parts; proximal part with cylindrical cells, unbranched or rarely branched; distal part with barrel-shaped cells, profusely branched and forming dense fascicles *A. huastecana* 2. Erect system undifferentiated into proximal and distal parts, composed exclusively of cylindrical cells 3

3. Mean diameter of vegetative cells $< 6.0 \ \mu m$ A. tenella

- 3. Mean diameter of vegetative cells $> 7.0 \ \mu m$ 4
- 4. Mean diameter of monosporangia > $12.0 \,\mu\text{m}$ A. eugenea
- 4. Mean diameter of monosporangia < 12·0 μm *A. hermannii*

Distribution

This is one of the first unequivocal records of Audouinella eugenea in the Southern Hemisphere, following that of Necchi et al. (1999). Although Cribb (1965) reported its occurrence in a semimarine cavern from Queensland, Australia, that description and habitat are in disagreement with previous records. A. meiospora is reported for the first time from the Northern Hemisphere. On the basis of these new findings one may suspect that the two species have a much wider geographical distribution than the original records suggested. However, they are not so widely distributed as A. hermannii in temperate to boreal regions in the Northern Hemisphere (Israelson, 1942; Necchi et al., 1993a). The regions from which they were collected and previously reported (Skuja, 1934, 1944; Jao, 1941; Necchi et al., 1993a; Necchi & Zucchi, 1995) consist of tropical to subtropical rainforests. The occurrence of A. meiospora on hosts other than Rhodophyta suggests it may be more widespread than existing records indicate. The species of Audouinella occurred together with a variety of other stream algae, with no clear association (Table 2).

In terms of environmental characteristics (Table 2), A. eugenea and A. huastecana tended to occur in warm, alkaline waters with a high ion content that were moderate to fast-flowing: temperature 16.3-29.0 °C, specific conductance $128-1,357 \ \mu S \ cm^{-1}$, pH 7.0-8.5 and current velocity $27-130 \text{ cm s}^{-1}$. These data are similar to those reported for A. eugenea environments in North America by Necchi et al. (1993a). Most streams and rivers containing populations of A. eugenea in Central Mexico and southeastern Brazil had rocky substrata (bedrock or boulders) and were shaded or heavily shaded. It occurred in shallow streams (typically < 50 cm in depth), but in two sites it was collected in much deeper habitats (3-12 m). A. huastecana was collected exclusively on the bedrock of a spring with fast-flowing waters emerging from a cave. On the other hand, the records for A. meiospora revealed no clear trend for environmental occurrence, and its distribution seems to be more closely related to the presence of suitable hosts than to water quality.

Sampling site no.	Temp- erature (°C)	Specific conductance (µS cm ⁻¹)	Shading ^a	Current velocity (cm s ⁻¹)	pH	Depth (cm)	Sub- stratum ^b	Associated species	% cover
Mexican streams									
Audouinella eugenea									
1. PA1799, Puente de Dios	25.0	-	D	—	-	10	1	Cladophora glomerata (Linnaeus) Kützing, Oedogonium sp.	10
2. PA2693, Micos	25.0	900	С	35	7.0	6	1	Cladophora sp., Oscillatoria spp., Lyngbya spp.	20
3. PA3154, Puente de Dios II	27.0	900	В	50	7.2	30	2	Cladophora sp., Lyngbya spp.	10
4. PA3215, Tancuilín	25.0	455	С	35	7.5	5	1	Cladophora sp.	10
5. PA3356, Santa Anita	23.0	1,237	В	35	7.5	40	2	Sirodotia huillensis (West et West) Skuja, Thorea violacea Bory, Hildenbrandia angolensis West et West	5
6. PA3435, Nacimiento del Mante	26.8	1,367	С	60	7.0	300	1	Spirogyra sp., Phormidium sp.	15
7. PA3490, La Media Luna	29.0	_	В	35	7.5	1,200	3	Chamaesiphon confervicola Rabenhorst, Lyngbya spp.	5
Audouinella huastecana									
8. PA3163, Choy A	26.0	900	D	130	7.6	50	1	Audouinella pygmaea (Kützing) Weber-van Bosse, Hyella fontana Huber et Jardin, H. angolensis	25
9. PA3261, Choy B	27.0	1,128	D	120	7.2	55	1	A. pygmaea, H. angolensis, H. fontana	25
10. PA3584, Choy C	26.0	1,100	D	90	7.0	20	1	A. pygmaea, H. angolensis, H. fontana	30
Audouinella meiospora	• • •	10.0	~				_		
11. PA3622, Tampaque	24.0	400	С	35	7.5	5	1	Blennothrix ganeshii Watanabe et Komárek (basiphyte)	—

Table 2. Physical and chemical characteristics of streams containing freshwater red-coloured populations of Audouinella in Central Mexico and south-eastern Brazil

		\sim		15	\sim		Ι	Ι			I		
	Pleurocapsa fluviatilis Langerheim, Pleurosira laevis (Ehrenberg) Compère	Microcoleus subtorulosus Gomont, Phormidium aerugineo-caeruleum	(Gomont) Anagnostidis et Komárek	Phormidium cebennense Gomont, Vaucheria sp.	Lyngbya subconfervoides Borge, M. subtorulosus, Melosira lineata (Dillwyn) C. Agardh		Compsopogon leptocladus Montagne (basiphyte), Spirogyra sp.	Compsopogon coeruleus (C. Agardh) Montagne (basiphyte), Vaucheria sp. (basiphyte),	Phormidium cf. retzii (C. Agardh) Gomont, Rhizoclonium hieroglyphicum	(C. Agardh) Kützing	C. coeruleus (basiphyte), Thorea violacea, Batrachospermum vogesiacum Skuja, Vaucheria bursata (Müller) C. Agardh (basiphyte)	· · · · · · · · · · · · · · · · · · ·	
	7	0		0	0		ε	0			7		
	7	19		30	26		11	6			14		
	8.0	8·2		8.0	8.6		7·0	7.5			7.8		
	27	54		65	108		58.5	42			33		
	D	D		в	C		в	C			C		
	128.6	168		286	218		65	80			435		
	17.3	16.3		18·7	19-7		20.9	22.6			17.6		
Audouineud eugened	12. MA20, Ilhabela	13. SP12, Apiaí (km 15)		14. SP13, Apiaí (km 30)	15. SP14, River Betari	Audouinella meiospora	16. SP20, Juquiá	17. SP49, Echaporã			18. SP72, Conchas		

Brazilian streams

1, predominantly bedrock; 2, predominantly boulder; 3, predominantly fallen tree trunks

A, open; B, partly shaded; C, shaded; D, heavily shaded.

υ

Acknowledgements

This research was supported by a DGAPA (UNAM) Postdoctoral Fellowship to J.C.J. and CNPq (300379/86-2) Research Grant to O.N.J. The authors are indebted to: James R. Coleman, for reviewing the English; Carolyn Bird, for reviewing the Latin diagnosis; and Maria Helena Carabolante, for help in the preparation of the photographs.

References

- CARMONA, J.J. (1997). Estudio florístico (taxonómico, ecológico, biogeográfico) de las rodofitas de agua dulce en la región central de México. PhD thesis, Universidad Nacional Autónoma de México, México.
- COMPÈRE, P. (1991). Rhodophytes. Flor. Prat. Alg. D'eau Douce Belg., 3: 1–55.
- CRIBB, A.B. (1965). An ecological and taxonomic account of the algae of a semi-marine cavern, Paradise Cave, Queensland. *Pap. Dept. Bot. Univ. Queensland.*, 4: 259–282.
- DREW, K.M. (1935). The life history of *Rhodochorton violaceum* (Kützing) comb. nov. (*Chantransia violacea* Kützing). Ann. Bot., 49: 439–450.
- GARBARY, D.J. (1987). The Acrochaetiaceae (Rhodophyta): an annotated bibliography. *Bibl. Phycol.*, **77**: 1–267.
- GUIRY, M.D. (1990). Sporangia and spores. In *Biology of the Red Algae* (Cole, K.M. & Sheath, R.G., editors), 347–376. Cambridge: Cambridge University Press.
- HOLMGREN, P.K. & HOLMGREN, N.H. (1993). Additions to Index Herbariorum (Herbaria), Edition 8 – second series. *Taxon*, **42**: 489–505.
- HOLMGREN, P.K., HOLMGREN, N.H. & BARNETT, L.C. (1990). *Index Herbariorum*. Part I. *The Herbaria of the World*, 8th edition. New York: New York Botanical Garden.
- ISRAELSON, G. (1942). The freshwater Floridae of Sweden: studies on their taxonomy, ecology and distribution. *Symb. Bot. Upsal.*, 6: 1–135.
- JAO, C.C. (1941). Studies on the freshwater of China. VIII. A preliminary account of the Chinese freshwater Rhodophyceae. *Sinensia*, **12**: 245–289.
- KORCH, J.E. & SHEATH, R.G. (1989). The phenology of Audouinella hermannii (Acrochaetiaceae, Rhodophyta) in a Rhode Island stream (USA). Phycologia, 28: 228–236.
- MONTEJANO, Z.G., CARMONA, J.J. & CANTORAL, U.E. (1999). Algal communities from calcareous springs and streams in La Huasteca: a synthesis. In *Aquatic Ecosystems of Mexico: Status* and Scope (Munawar, M., Lawrence, S., Munawar, I.F. & Malley, D., editors). Amsterdam: SPB Academic Publishing.
- NECCHI, O. JR & ZUCCHI, M.R. (1995). Systematics and distribution of freshwater *Audouinella* (Acrochaetiaceae, Rhodophyta) in Brazil. *Eur. J. Phycol.*, **30**: 209–218.
- NECCHI, O. JR & ZUCCHI, M.R. (1997). Audouinella macrospora (Acrochaetiaceae, Rhodophyta) is the Chantransia stage of *Batrachospermum* (Batrachospermaceae). *Phycologia*, **36**: 220–224.
- NECCHI, O. JR, SHEATH, R.G. & COLE, K.M. (1993*a*). Systematics of the freshwater *Audouinella* (Acrochaetiaceae, Rhodophyta) in North America. 1. The reddish species. *Arch. Hydrobiol.*, *Algol. Stud. Suppl.*, **70**: 11–28.
- NECCHI, O. JR, SHEATH, R.G. & COLE, K.M. (1993b). Systematics of the freshwater Audouinella (Acrochaetiaceae, Rhodophyta) in North America. 1. The bluish species. Arch. Hydrobiol., Algol. Stud. Suppl., 71: 13–21.
- NECCHI, O. JR, BRAGA, M.R.A. & MOULTON, T.P. (1998). Survey

and distribution of freshwater Rhodophyta from Cardoso Island, Sao Paulo State, southeastern Brazil. *Arch. Hydrobiol.*, *Algol. Stud. Suppl.*, **88**: 111–124.

- NECCHI, O. JR, BRANCO, C.C.Z. & BRANCO, L.H.Z. (1999). Distribution of Rhodophyta in streams from São Paulo State, southeastern Brazil. *Arch. Hydrobiol.*, **147**: 73–89.
- REIS, P. (1961). Sobre a identificação de *Chantransia violacea* Kütz. *Bol. Soc. Brot.*, **35**: 141–154.
- SÁNCHEZ-RODRÍGUEZ, M.E. (1974). Rodofíceas dulceacuícolas de México. Bol. Soc. Bot. México, 33: 31–37.
- SHEATH, R.G. & MÜLLER, K.M. (1999). Systematics and phylogenetic relationships of the freshwater genus *Balbiania* (Rhodophyta). J. Phycol., 35: 855–864.
- SHEATH, R.G. & WHITTICK, A. (1995). The unique gonimoblast propagules of *Batrachospermum breutelii* (Batrachospermales, Rhodophyta). *Phycologia*, 34: 33–38.
- SKUJA, H. (1934). Untersuchungen über die Rhodophyceen des Süsswassers. Beih. Bot. Cbl., 52: 173–192.
- SKUJA, H. (1944). Untersuchungen über die Rhodophyceen des Süsswassers. VII–XII. Acta Horti Bot. Univ. Lat., 14: 1–63.
- STARMACH, K. (1985). Chantransia hermannii (Roth) Desvaux and the systematic position of the genera Chantransia, Pseudochantransia and Audouinella. Acta Soc. Bot. Pol., 54: 273–284.
- WOELKERLING, W.J. (1983). The Audouinella (Acrochaetium-Rhodochorton) complex (Rhodophyta): present perspectives. Phycologia, 22: 59–92.