Systematics and distribution of *Thorea* (Thoreaceae, Rhodophyta) from central Mexico and south-eastern Brazil

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SUMMARY

Thirteen populations of Thorea were analyzed from central Mexico and south-eastern Brazil. All populations were considered as belonging to a single species [Thorea hispida (Thore) Desvaux], with wide variation of morphological features. Secondary branches varying in frequency were observed in several populations with an overlapping in the range of branch density for Thorea violacea Bory and T. hispida (0-9 and 11-41 per 30 mm, respectively). As this is the most distinguishing character and on the basis of the overlapping (within a same population or even a single plant), we regarded T. violacea as a synonym of T. hispida. 'Chantransia' stage in culture, as well as gametophyte and carposporophyte were described in detail. We confirmed the coexistence of asexual monosporangia with sexual reproductive structures (carpogonia and spermatangia) and carposporangia. Size, content, arrangement and chromosome number were the most distinctive characteristics among spermatangia, carposporangia and monosporangia. Monosporangia can be promptly differentiated from spermatangia by their granulated content and larger size but they are similar to carposporangia in shape and size; however, monosporangia are not arranged in fascicles. Structures resembling bisporangia were observed in female plants of some populations. Chromosome numbers were n = 4 for spermatangia and fascicle cells, and 2n ca 8 for gonimoblast filaments, carpospores and the 'Chantransia' stage cells. The populations of *Thorea* from central Mexico and south-eastern Brazil corroborated the known world distribution for T. hispida, consisting dominantly of tropical to subtropical rainforests, sometimes extending into warm temperate areas. Thorea hispida occurred in warm (temperature 17.6-28.0°C), neutral to alkaline (pH 7.0-8.0), high ion content (specific conductance 59–2140 µS cm⁻¹), moderate flowing (current velocity 17-43 cm/s) and shallow waters (depth < 50 cm); these data are essentially similar to previous reports.

Key words: Batrachospermales, Brazil, Mexico, Rhodophyta, stream, systematics, *Thorea*, Thoreaceae

INTRODUCTION

The freshwater red algal family Thoreaceae is distinguished from the other members of the Batrachospermales basically by having multiaxial thalli (Starmach 1977; Sheath et al. 1993). The sequence data from the large subunit of ribulose 1,5-bisphosphate carboxilase/ oxygenase (rbcL) gene and 18S ribosomal DNA (small subunit) showed that Thorea does not appear to be a natural grouping within the Batrachospermales (Vis et al. 1998). The authors suggested that Thoreaceae should be elevated to ordinal status but still considered it as 'incertae sedis' in the Florideophyceae. Sheath et al. (2000) proposed the order Thoreales to accommodate the two recognized genera: Thorea and Nemalionopsis. Thorea is distinguished by having assimilatory filaments not contained in a common gelatinous matrix with monosporangia at their base, whereas in *Nemalionopsis* they are embedded in a gelatinous matrix with monosporangia at their apex (Skuja 1934). Sheath et al. (1993) continued to recognize the separation of the two genera based on spore-bearing branches and assimilatory filament density: lower ratio (≤ 0.3) of sporangial branch to assimilatory filament length and loose aggregation in Thorea and higher ratio (≥ 0.6) and compressed assimilatory filaments in Nemalionopsis.

Members of the family are worldwide in distribution but tend to be more common in tropical and subtropical regions or warm temperate waters (Sheath and Hambrook 1990; Sheath *et al.* 1993). *Thorea* has been reported from several continents, whereas *Nemalionopsis* is known only from a few localities in Asia and North America (Sheath *et al.* 1993). These authors recognized only four species of *Thorea* worldwide: *Thorea clavata* Seto et Ratnasabapathy, *T. hispida* (Thore) Desvaux, *T. violacea* Bory and *Thorea zollingeri* Schmitz; then *Thorea conturba* Entwisle et Foard (1999) was described from Australia. Taxonomic characters used for species delineation include essentially

*To whom correspondence should be addressed. Email: orlando@bot.ibilce.unesp.br Communicating editor: H. Kawai Received 22 November 2000; accepted 9 May 2001. vegetative features: plant length, branching (copious or sparse secondary branches), shape of assimilatory filaments (clavate or non-clavate), size of assimilatory filaments and frequency of monosporangial clusters. This fact brings some problems for species circumscriptions in the genus, which are still not satisfactorily resolved. Sexual reproduction, as well as the presence of juvenile gametophytes, have also been observed under natural conditions (Yoshizaki 1986; Necchi 1987; Sheath *et al.* 1993; Necchi and Zucchi 1997a; Entwisle and Foard 1999).

Populations of Thorea have been poorly documented in Mexico. Carmona and Montejano (1993) reported T. violacea from a tropical calcareous spring. Sheath et al. (1993) described morphometric and environmental characteristics of two Mexican populations of T. violacea and T. hispida, whereas Montejano et al. (1999) listed T. violacea as a component of the stream algal flora of the region of La Huasteca. In Brazil, the genus has been more intensively studied. Necchi (1987) described in detail the sexual reproduction in T. violacea (as Thorea bachmannii Pujals). Necchi and Zucchi (1997a) reported the occurence of T. violacea with descriptions, as well as environmental and geographical information, whereas Necchi et al. (1999) listed T. violacea from hard water regions in São Paulo State, including environmental data.

Considering the relatively poor knowledge on stability of taxonomic characters and distributional aspects for *Thorea* species worldwide, the present investigation was carried out. We aimed to evaluate the variability of taxonomic characters, the environment of occurence and the geographic distribution of *Thorea* populations, in addition to previous reports from the central region of Mexico and south-eastern Brazil (São Paulo State). The two regions are situated in similar latitudes in North America and South America.

MATERIALS AND METHODS

Thirteen populations of Thorea were analyzed in this study. Nine were collected from central Mexico (17-23°N, 98–102°W) from 51 sites with the presence of red algae (Carmona 1997) in altitudes of 10-500 m (Fig. 1). Four populations were collected from São Paulo State, southeastern Brazil (23-24°S, 47-48°W) from 104 stream segments containing red algae (Necchi et al. 1999) in altitudes of 190-680 m (Fig. 1). The samples were preserved in 4% formaldehyde and included in the herbaria FCME and SJRP (Holmgren et al. 1990; Holmgren and 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. In addition, percentage cover of the alga on the substratum was estimated for each sampling site.



Fig. 1. Location of the study regions in central Mexico and south-eastern Brazil (São Paulo State) with indication of the sites with *Thorea* populations.

We included all morphological characters previously considered to be of taxonomic importance, and the microscopical analyzes followed the same procedures described by Sheath *et al.* (1993) and Necchi and Zucchi (1997a). To examine the frequency of secondary branches, we evaluated the branch density for the whole plant (dense *vs* sparse branching), and also enumerated the branches in a 30 mm length (Sheath *et al.* 1993), in order to avoid problems for not uniformly branched plants.

Chromosome countings were made for two populations, both under natural conditions (fertile gametophytes, population 12) and from plants grown in culture ('Chantransia' stage, population 13, isolate no. 64). Isolation into culture followed procedures described in a previous study (Necchi and Zucchi 1997b). 'Chantransia' stage was produced from carpospore germination. This isolate was kept in 20:1 water-soil culture medium in a RI 12–555 Revco incubator with illumination from above supplied by cool-white fluorescent lamps (Phillips 15 W) under the following conditions: temperature 20°C; irradiance 65–85 µmol $m^{-2} s^{-1}$; photoperiod 12:12 h light:dark). Plants were preserved in Carnoy's solution and stained according to Wittmann's hematoxylin technique according to procedures described in Necchi and Sheath (1992) and Sheath and Cole (1993). To obtain the chromosome counts a minimum of 10 countings were made for each cell type.

RESULTS AND DISCUSSION

Morphological analysis

Only one group of *Thorea* populations, with relatively wide variation of morphological features (Table 1,2, Figs 2-14), was recognized from Central Mexico and south-eastern Brazil. Plants were multiaxial, moderately mucilaginous, with reproductive structures situated at the basal region of the assimilatory filaments and nonclavate (mean upper-to-lower cell diameter ratio 0.4-1.2) and sparsely branched (0-3, rarely 4 branchings) assimilatory filaments. Plant length (0.8-80.0 cm), plant diameter (138.5–1929.0 µm), medulla diameter (112.2-625.0 µm), assimilatory filament length (61.3-686.7 µm), monosporangium diameter (7.0–18.0 µm) and clustering overlapped for most morphometric features measured. We found no clear correlation of morphological characters with the environmental variables analyzed but this aspect deserves a more detailed analysis (e.g. microhabitat) in future studies.

One important morphological feature was observed in several Mexican and Brazilian populations: sparse or dense branching, with secondary branches (Table 1, Fig. 2) varying in frequency from 0–22 per 30 mm. This overlaps in the range of branch density for *T. violacea* (mean 2.6 per 30 mm, range 0–9 per 30 mm) and *T. hispida* (mean 20.7 per 30 mm, range 11–41 per 30 mm), according to Sheath *et al.* (1993). Considering that this is the most distinguishing character and on the basis of this considerable overlapping, within the same population (e.g. populations 3, 5, 8, 10–13) or even a single plant (Fig. 2), we concluded that the two species are synonymous and they are referred to the oldest epithet (*T. hispida*).

The 'Chantransia' stage (Fig. 4) was observed in culture with the following characteristics: brownish tufts; basal portion composed of prostrate filaments densely aggregated forming a mass; erect portion composed of filaments with cylindrical cells, abundantly branched; vegetative cells $28.0-54.0 \,\mu\text{m}$ in length and $8.0-12.0 \,\mu\text{m}$ in diameter; monosporangia $12.0-21.0 \,\mu\text{m}$ in length and $10.0-14.0 \,\mu\text{m}$ in diameter. These features agreed with a previous description in Necchi (1987).

Plants were dioecious, with male plants distinguished from the female ones by their slender thalli. Both gametophytes had assimilatory filaments variable in length on young and old parts. Spermatangia (Table 2, populations 5, 8, 10–13, Fig. 8) were hyaline, elliptical or obovoidal, $6.0-14.0 \,\mu\text{m}$ in length, $3.0-10.0 \,\mu\text{m}$ in diameter. They were borne in pairs, terminally or subterminally on fascicles situated near the basis of short assimilatory filaments.

Carpogonia (Table 2, populations 4, 9, 12, Figs 3,6 and 7) were formed in abundance on the younger parts of primary and secondary branches. They were conical, 3.0-7.0 µm in diameter, each having an elongate filiform and straight or slightly curved trichogyne (Figs 6 and 7), which was up to 280.0 µm long, extending above the assimilatory filaments (Fig. 3). Carpogonial branches were borne laterally on short vegetative filaments and were sessile, one or two-celled. Their position in the thallus was the same as those of the spermatangia. In population 12 several abnormal carpogonia, with branched trichogyne, were observed (Fig. 7). Spermatia adhered to the distal end of the trichogynes and their nuclei presumably migrated to the base of the carpo-gonium. Early phases of carposporophyte development were not observed.

The mature carposporophyte (Table 2, populations 4, 12, Figs 9 and 10) had a simple arrangement in clusters without any kind of envoltorium. Carposporangia were borne in clusters of up to eight, terminally or subterminally on gonimoblast filaments. They were clubshaped or obovoidal, with a granulated and dense content, 8.0-18.0 µm in length and 7.0-12.0 µm in diameter. Size, arrangement and chromosome number were the most distinctive morphological characteristics of carposporangia, in addition to the production of the 'Chantransia' stage in culture from their germination. Gonimoblast filaments were composed of cylindrical cells of two kinds: (i) long, prostrate and loosely arranged cells, with a diffuse growth among and resembling medullary filaments (Fig. 9); (ii) short, erect, compactly arranged cells, with a definite growth, forming fascicles and producing carposporangia (Fig. 10).

The characteristics described above agreed with the general descriptions of spermatangia, carpogonia and carposporophytes for *Thorea* given by Yoshizaki (1986), Necchi (1987), Necchi and Zucchi (1997a), Sheath *et al.* (1993) and Entwisle and Foard (1999).

Reproductive structures resembling bisporangia were observed in female plants (Table 2, populations 1, 4, 11, 12, Figs 11 and 12) at the tips of short assimilatory filaments. They were uninucleated with 12.0–24.0 μ m in length and 8.0–18.0 μ m in diameter. We could not confirm the status of these structures because they were not seen to be released or to germinate. The bisporangia resemble the structures described as seirosporangia by Sheath *et al.* (1993) and Entwisle and Foard (1999). Thus the two terms seem to have been applied with

Table 1. Vegetative chare	acteristics of Thorea p	opulations from ce	ntral Mexico and south	ı-eastern Brazil				
Populations	Plant length (cm)	Branches per 30 mm	Plant diameter	Medulla diameter	Assimilatory filaments length	Assimilatory c Distal	ell diameter Proximal	Ratio distal /proximal diameter
Mexican populations								
1. PA3346	10.0-60.0	0-5	466.9-1079.1	156.9-362.9	156.9-618.0	3.0-6.0	4.0-7.0	0.6-1.0
Puente de Dios	22.7±21.5	3.2±2.0	762.5±213.4	263.5±66.3	328.9±88.3	4.8±0.9	5.8±0.7	0.8 ± 0.1
2. PA2284	11.0-80.0	6-19	561.2-1490.0	166.6-409.5	199.0-583.2	3.0-6.0	5.8-8.0	0.5-1.0
Tamasopo	30.4±22.2	11.6 ± 4.4	844.6±201.5	265.8 ± 61.6	342.2±109.9	4.4±0.9	6.2±0.8	0.6 ± 0.1
3. PA2261	11.0-19.0	0-11	505.1-877.0	251.6-407.8	112.2-315.7	3.1-5.5	4.5-7.5	0.5-1.1
Río Gallinas	14.5 ± 2.4	3.7±3.5	621.5±126.7	319.9 ± 48.2	194.3 ± 57.1	3.9 ± 1.1	5.7±0.8	0.8 ± 0.1
4. PA3337	5.5-28.5	0-4	309.5-1010.7	200.8-506.9	68.4-311.3	2.0-5.0	4.0-7.0	0.4-1.0
Río Gallinas	17.0±7.3	0.8 ± 1.4	542.5±167.3	297.0±73.5	142.5 ± 62.8	3.4±0.9	5.2±1.0	0.6 ± 0.1
5. PA3268	2.5-10.0	0-15	266.8-1079.1	169.7-382.5	121.0-686.7	2.9-5.8	4.0-7.0	0.6-1.2
Nacimiento El Salto	5.0±2.2	3.8±4.9	702.3±203.7	266.0±63.3	315.5 ± 122.1	4.6±0.8	5.5±0.7	0.9 ± 0.1
6. PA3648	2.0-10.0	6-16	138.5-750.7	112.2-552.5	61.3-233.2	3.1-6.8	4.0-7.0	0.6-1.0
Micos	5.3±3.3	10.5 ± 3.7	479.5±135.4	230.5±107.9	145.6 ± 48.7	5.0±1.0	5.6±0.8	0.8 ± 0.1
7. PA3325	2.5-8.5	0-10	270.7-573.5	150.0-394.6	90.9-249.7	3.0-5.0	5.0-7.0	0.6-1.0
Santa Anita	5.5±2.1	3.3 ± 3.1	394.9±64.0	262.6±59.2	154.0±37.6	4.2±0.6	5.8±0.6	0.7 ± 0.1
8. PA3358	6.0-27.0	1-12	493.5-1000.0	138.0-625.0	161.2-275.0	3.0-5.0	4.0-7.0	0.6-1.0
Tambaque	15.0 ± 6.2	4.4±3.6	603.6±100.4	258.1 ± 103.6	201.2±33.2	4.4±0.5	5.4±0.8	0.7 ± 0.1
9. BALE875	13.0-48.0	4-16	775.2-1929.4	140.3-589.3	294.6-613.9	4.0-8.0	5.0-9.0	0.5-1.0
San Francisco	25.5±13.5	10.0±3.7	1118.9 ± 326.4	345.4±132.1	433.0±103.9	5.4 ± 1.0	6.7±1.0	0.8 ± 0.1
Brazilian populations								
10. SP16	3.0-13.0	1-22	420.0-1060.0	112.0-288.0	176.0-480.0	6.0-8.0	6.0-10.0	0.7-1.0
Iporanga km 7	5.6±3.3	10.5 ± 6.9	813.0±184.8	221.2 ± 46.4	327.0-106.0	6.9 ± 1.1	7.7±1.3	0.9 ± 0.1
11. SP17	0.8-4.3	0-14	400.0-1000.0	140.0-280.0	136.0-400.0	5.0-8.0	6.0-8.0	0.6-1.0
Iporanga km 4	2.3±1.2	4.1±4.5	760.0±128.2	192.1 ± 53.4	262.8±60.8	6.4±0.8	7.2±0.9	0.9 ± 0.1
12. SP72	2.8-6.5	0-17	340.0-640.0	180.0-280.0	100.0-240.0	5.0-8.0	6.0-9.0	0.7-1.1
Conchas	4.2 ± 1.1	6.9±5.3	508.0±78.8	218.0±25.2	169.0±28.6	6.7±0.8	6.6±0.8	1.0 ± 0.1
13. SP75	1.3-14.5	0-16	640.0-900.0	140.0-300.0	160.0-340.0	5.0-8.0	5.0-9.0	0.6-1.2
Jumirim	8.2±3.5	2.9±4.5	758.0±101.5	231.0±54.2	252.3±59.9	6.3±0.9	6.9 ± 1.0	0.9 ± 0.1

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Measurements are in µm (unless if otherwise specified) and represent range, mean and standard-deviation.

Table 2. Reproductive cl	haracteristics	of <i>Thorea</i> populatio	ns from centra	I Mexico and south-e	astern Brazil					
Populations	Spern Length	latangia Diameter	Carpo Length	gonia Diameter	Carpospo Length	orangia Diameter	Monospor Length	angia Diameter	Bisporal Length	ıgia Diameter
Mexican populations										
I. FA3340	I	I	I	I	I	I	10.0-20.0	12.U-10.U	10.0-24.0	0.U-13.U
Puente de Dios							20.2±1.9	I4./±I.9	1/.8±2.8	11.3±1.1
2. PA2284	I	I	I	I	I	I	14.4-21.0	18.1 ± 1.8	I	I
Tamasopo							9.9-12.6	11.2 ± 1.1		
3. PA2261	I	I		I	I	I	12.2-17.3	8.4-11.5	I	1
Río Gallinas							14.2 ± 1.3	9.4±0.8		
4. PA3337	I	I	30.0-220.C	3.0-5.0	8.0-16.0	7.0-9.0	10.0-16.0	7.0-10.0	15.0-18.0	10.0-18.0
Río Gallinas			66.3±59.2	3.6±0.6	14.3 ± 2.1	8.3±1.0	13.6 ± 1.6	8.7±0.8	15.0 ± 1.6	14.0±2.3
5. PA3268	6.0-10.0	3.0-6.0	I	I	I	I	10.6-24.2	7.7-12.2	I	1
Nacimiento El Salto	7.8±0.9	4.6 ± 10.0					17.5 ± 3.9	9.6 ± 1.1		
6. PA3648	I	I	I	I	I	I	11.7-17.7	7.1-12.2	I	1
Micos							14.3 ± 1.5	9.3±1.4		
7. PA3325	I	I	I	I	I	I	10.4-19.3	7.5-11.6	I	I
Santa Anita							13.4 ± 2.2	9.2±0.9		
8. PA3358	8.0-12.0	3.0-5.0		1	I	I	14.0-20.0	9.0-13.0	I	1
Tambaque	10.1 ± 0.9	4.2±0.6					17.7 ± 1.6	10.5 ± 1.0		
9. BALE875	Ι	Ι	22.0-42.0	4.0-5.0		I	15.0-22.0	8.0-11.0	Ι	1
San Francisco			32.0±10.0	4.4 ± 0.4			18.3±1.9	9.6±0.8		
Brazilian populations										
10. SP16	8.0-14.0	6.0-10.0	I	I	I	I	14.0-18.0	10.0-14.0	I	I
Iporanga km 7	11.7 ± 1.2	8.8±1.0	I	I	I	I	15.2 ± 1.3	11.8 ± 1.0		
11. SP17	8.0-14.0	5.0-10.0			I		14.0-20.0	10.0-14.0	14.0-16.0	8.0-12.0
Iporanga km 4	10.8 ± 2.9	7.5±1.1					16.2 ± 2.4	12.0 ± 1.5	15.0 ± 1.0	10.5 ± 1.6
12. SP72	6.0-12.0	4.0-9.0	14.0-280.C	4.0-7.0	8.0-18.0	8.0-12.0	14.0-15.0	9.0-11.0	12.0-16.0	8.0-10.0
Conchas	9.1 ± 1.5	6.3 ± 1.3	115.5 ± 80.3	3 4.9±0.7	14.8 ± 3.2	9.5 ± 1.2	14.2 ± 0.4	10.2 ± 0.7	14.0 ± 1.6	9.3±0.9
13. SP75	6.0-10.0	4.0-8.0	I	I	Ι	I	12.0-18.0	8.0-12.0	I	1
Jumirim	8.2±1.0	5.7±0.9					14.6 ± 3.0	10.1 ± 0.8		
Measurements are in p	um and repre	sent range, mean an	d standard-dev	viation.						

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Figs 2–14. Morphological features of *Thorea hispida*. 2. General view of a male plant showing densely (arrows) and sparsely branched (arrowheads) branches (SJRP SP16). 3. Portion of a female plant showing trichogynes (arrowheads) extending above the assimilatory filaments (SJRP SP72). 4. General view of a 'Chantransia' stage (Culture isolate 64). 5. Detail of monosporangia on undifferentiated branches (FCME PA3346). 6. Carpogonium (arrowhead) developing from the base of a assimilatory filament (SJRP SP72). 7. Detail of an abnormal carpogonium with branched (arrowhead) trichogyne (SJRP SP72). 8. Spermatangia in fascicles on short assimilatory filaments (SJRP SP72). 9. Part of a carposporophyte showing carposporangia in fascicles (SJRP SP72). 10. Detail of a carposporangia fascicle (SJRP SP72). 11–12. Detail of possible bisporangia showing septum (arrowhead) (SJRP SP72). 13. Assimilatory filament cell with four chromosomes (SJRP SP72). 14. Gonimoblast filament cell with *ca* 8 chromosomes (SJRP SP72). Specimens in Figs 6,8–11,13–14 were stained with hematoxylin.

the same meaning and we found bisporangia more appropriate to the structures we observed. There is a consensus that bisporangia are homologous with tetrasporangia because they are not found on carpogonial or spermatangial plants (Guiry 1990). However, gametangial plants of *Thorea hispida* (this work) and *Audouinella dictyotae* (Collins) Woelkerling occassionally form bisporangia (Woelkerling 1971). Bisporangia

have been described in several species of Acrochaetiales, Palmariales, Gelidiales, Corallinales, Gigartinales and Ceramiales (Guiry 1990), but this is the first report for the Batrachospermales. The reproductive and ecological roles of these putative bisporangia remain uncertain and further cytological studies are necessary to explain their development and functioning.

Monosporangia were observed indistinctly on male and female plants (Table 2, Fig. 5). They are borne singly, in pairs or in clusters of up to 3 on undifferentiated branches, arising from the basal cell of the assimilatory filament (Fig. 5). They are similar in size and shape to carposporangia (Table 2) but are not arranged in fascicles. Monosporangia can be promptly differentiated from spermatangia by their granulated content and larger size. They are elliptical or obovoidal, 10.0-25.8 µm in length and 7.0–18.0 µm in diameter. The real existence of monosporangia in Thorea has been questioned (Necchi 1987; Necchi and Zucchi 1997a), as they could be spermatangia or carposporangia. Thus, it was recommended that their occurrence should be carefully studied in the light of new information concerning sexual reproduction. However, it was also noted that it is possible that monosporangia can be produced in some populations/species (Necchi and Zucchi 1997a). This study confirms the coexistence of monosporangia with sexual reproductive structures (carpogonia and spermatangia), as well as carposporangia.

Chromosome numbers (Figs 13 and 14) were n = 4 for spermatangia and fascicle cells and 2n ca 8 for gonimoblast, carpospores and cells of the 'Chantransia' stage filaments. These numbers are similar to those reported for several species of *Batrachospermum* in North and South Americas (n = 3-6, rarely 9, Necchi and Sheath 1992; Sheath and Cole 1993). The diploid chromosome number in gonimoblast cells confirm the identity of the carposporangia, besides the morphological characteristics and production of the 'Chantransia' stage from their germination.

Description and taxonomic proposals

Thorea hispida (Thore) Desvaux (1818: 16) emend. Sheath, Vis et Cole (1993: 238).

Basionym: Conferva hispida Thore (1799: 398).

Heterotypic synonym: *T. violacea* Bory (1808: 133) emend. Sheath, Vis et Cole (1993: 238), for a full list of synonyms see Sheath et al. (1993).

Plants densely or sparsely branched, 0.8-80 cm high, $138.5-1929 \mu m$ in diameter; secondary branches 0-22 per 30 mm; medulla $112.3-625.0 \mu m$ in diameter; assimilatory filaments non-clavate with variable branching. Spermatangia two per branch, elliptical or obovoidal, $6.0-14.0 \mu m$ long, $3.0-10.0 \mu m$ in diameter. Carpogonia conical, $3.0-7.0 \mu m$ in diameter; carpogonial branches arising laterally on short vegetative filaments, sessile or with one to two barrel-shaped

cells; trichogynes filiform, 14.0–280.0 μ m long. Carposporangia in fascicles of up to 8, 8.0–18.0 μ m long, 7.0–12.0 μ m in diameter. Putative bisporangia in isolate branches, 12.0–24.0 μ m long, 8.0–18.0 μ m in diameter. Monosporangia singly, in pairs or in clusters of up to three on undifferentiated branches, 10.0–25.8 μ m long, 7.0–18.0 μ m in diameter.

Specimens examined. Mexico:

- San Luis Potosí, Tamasopo, Puente de Dios, coll. J. Carmona, 19.ii. 1992 (FCME PA3346).
- (2) river Tamasopo, coll. G. Montejano, 17.iii. 1984 (FCME PA2284).
- (3) river Gallinas, coll. G. Montejano 17.ii. 1984 (FCME PA2261).
- (4) coll. G. Montejano, 19.ii. 1992 (FCME 3337).
- (5) Cd. Maíz, nacimiento El Salto, coll. J. Carmona, 2.v. 1991 (FCME PA3268).
- (6) Cd. Valles, Micos, coll. J. Carmona, 4.iii. 1996 (FCME PA3648).
- (7) Aquismón, Santa Anita, coll. G. Montejano, 20.ii. 1992 (FCME PA3325).
- (8) Tambaque, coll. G. Montejano, 20.ii. 1992 (FCME PA3358).
- (9) Michoacán, Lázaro Cárdenas, river San Francisco, coll. M. Gold-Morgan and L. Martinell, 21.iv. 1983 (FCME BALE875).

Brazil:

- (10) Iporanga, Route SP-165, 7 km from the town, coll. O. Necchi Jr. and C.C.Z. Branco, 10.x. 1996 (SJRP SP16).
- (11) Iporanga, Route SP-165, 4 km from the town, Córrego Soares, coll. O. Necchi Jr. and C.C.Z. Branco, 10.x. 1996 (SJRP SP17).
- (12) Conchas, Ribeirão Muquém, 2 km from Route SP-300, coll. O. Necchi Jr *et al.*, 18.ix. 1997 (SJRP SP72).
- (13) Jumirim, tributary of Sorocaba River, 2 km from the town, coll. O. Necchi Jr *et al.*, 19.ix. 1997 (**SJRP** SP75).

Remarks: The above description encompasses the characteristics of all previous records of *Thorea* from Mexico and Brazil. In addition, the expanded circumscription here proposed for *T. hispida* (considering *T. violacea* as a synonym) includes all representatives of *Thorea* with non-clavate assimilatory filaments, except the diminute Australian species *T. conturba*, which has a vegetative morphology somewhat intermediate between *Thorea* and *Nemalionopsis* (Entwisle and Foard 1999).

Distribution

The populations of *Thorea* collected in central Mexico and south-eastern Brazil corroborate the known distribution for *T. hispida* (including *T. violacea*) in Africa, Asia, Europe, North America and South America consisting dominantly of tropical to subtropical rainforests,

)						
Populations	Temperature (°C)	Specific conductance (µS cm ⁻¹)	Shading ^a	Current velocity (cms ⁻¹)	H	Depth (cm)	Sustratum ^b	Associated species	% cover
Mexican populations									
1. PA3346	23.5	1,115	В	35	7.6	10-50	1	<i>Vaucheria</i> sp.	20
Puente de Dios									
2. PA2284 	24	I	C	I	7.0	Ð	1	Cladophora sp., Zygnema sp.,	10
Tamasopo								Spirogyra sp.	
3. PA2261 Rín Gallinas	24	I	Ш	I	7.0	Ø	2	Batrachospermum globosporum, Israelson	വ
4 PA3337	22	815 8	Δ	73	¢	40	-		Ľ
Río Gallinas	77	010	C) t	5) t	H		2
5. PA3268	24	1,320	A	24	7.5	10-20	7	<i>Cladophora</i> sp.	30
Nacimiento El Salto									
6. PA3648	23	2,140	В	35	7.3	30	2	B. globosporum Israelson, Cladophora sp.	10
Micos									
7. PA3325	25	1,195	A	35	7.5	10-50	2	Sirodotia huillensis, (West et West) Skuja,	15
Santa Anita								<i>Hildenbrandia angolensis</i> , West et West,	
	С с	00 5	6	C	5	C	c	Vaucrieria sp.	
	23	1,100	'n	30	c./	30	V	b. gioposporum Israelson, <i>Spirogyra</i> sp.	CT
			ı				,		
9. BALE875	28	I	в	30	I	I	m	<i>Cladophora</i> sp.	10
San Francisco									
Brazilian populations									
10. SP16	18.7	79	C	17	7.7	2	2	Melosira lineata (Dillwyn), C. Agardh,	$^{<1}$
Iporanga km 7								Pleurosira laevis (Ehrenberg) Compère	
11. SP17	19.2	59	O	40	7.6	18	2	Compsopogon leptoclados Montagne,	2
Iporanga km 4								<i>Mougeotia</i> sp.	
12. SP72	17.6	435	C	33	7.8	14	2	<i>B. vogesiacum</i> Skuja,	2
Conchas								<i>C. coeruleus</i> (C. Agardh) Montagne, <i>Vaucheria bursata</i> (Müller) C. Agardh	
								Audouinella eugenea (Skuja) Jao,	
								<i>P. laevis</i> (Ehrenberg) Compère	
13. SP75 Jumirin	19.3	105	Ш	18	7.5	15	1	B vogesiacum Skuja, Vaucheria sp., P. laevis (Ehrenberg) Compère	1
^a A, open; B, partly s	haded; C, shaded.	1, predominantly t	bedrock; 2, pre	dominantly boulde	r; 3, pre	dominantly falle	en tree trunks.		

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sometimes extending into warm temperate areas (Sheath *et al.* 1993; Necchi and Zucchi 1997a; Entwisle and Foard 1999). Most species tend to be widespread globally, but localized regionally and our data confirm this distributional pattern. *Thorea hispida* occured together with a variety of other stream algae (Table 3), with some possible associations, such as the co-occurence in three sites with the red alga *Batra-chospermum globosporum* in Mexico and the diatom *Pleurosira laevis* in Brazil.

In terms of environmental characteristics (Table 3), *T. hispida* tended to occur in warm, neutral to alkaline, high ion content, moderate flowing and shallow waters: temperature 17.6–28.0°C, specific conductance 59–2140 μ S cm⁻¹, pH 7.0–8.0, current velocity 17–43 cms⁻¹ and depth < 50 cm. These data are essentially similar to those reported for *T. hispida* in North America by Sheath *et al.* (1993): temperature 18.0–24.0°C, specific conductance 180–500 μ S cm⁻¹, pH 7.5–8.3 and current velocity 9–99 cms⁻¹. Most streams and rivers containing populations of *T. hispida* in central Mexico and south-eastern Brazil had rocky substrata (bedrock or boulders) and were open to shaded, with more abundant growths (higher percentage covers) in the former region.

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