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Chamaepinnularia thermophila (Bacillariophyceae): synonymy with *Navicula tongatensis* Hustedt and update of its geographic distribution and ecology

by

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Abstract

Chamaepinnularia thermophila is a small and poorly known diatom species. After the first description from a hot spring in Guadalupe in 1952, its presence appeared to be limited to a few other springs of the French Antilles. The objective of this study is to report new information on aspects of taxonomy, distribution and ecology of this species. Accurate analysis under light and scanning electron microscope of the material collected on different substrates (cobbles, macrophytes and fine sediments) from a thermo-mineral spring of Sardinia (Italy) allowed us to document the first record of the species in the Mediterranean area. Furthermore, the comparison with *Navicula tongatensis* from Hustedt's original material, carried out because of their similarity, revealed identical morphological characteristics suggesting their consequent synonymy. Based on the information available in the literature and our data, *C. thermophila* is a rare species present mainly in tropical areas, in thermal springs with alkaline pH, medium to high conductivity and low to moderate nutrient content. The occurrence of the species at sites with very different environmental characteristics seems unusual, but it could indicate a broader ecological range. This study contributes to the standardization of the nomenclature used for this species so far and provides the first framework on its global geographic distribution and ecology.

Key words: *Chamaepinnularia tongatensis*, *Navicula thermophila*, species distribution, ecology, springs, thermo-mineral waters

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Introduction

The genus *Chamaepinnularia* was originally described by Lange-Bertalot & Krammer (Lange-Bertalot & Metzeltin 1996) and comprises isolated and relatively small cells (up to 25 µm in length and 4 µm in width). Slightly larger dimensions (up to 30 µm in length and 4.9 µm in width) were reported for *Chamaepinnularia gerlachei* from Antarctica (Van de Vijver et al. 2010). Representatives of the genus have linear-elliptic to linear-lanceolate valve outlines, sometimes sinuous, with rounded apices. The striae arranged in a single row are composed of large areolae interrupted by a silica line near the valve face-mantle junction along the apical plane. The openings in the areolae are covered externally by vela and divided internally by plates or silica bridges (Lange-Bertalot & Metzeltin 1996; Wetzel et al. 2013).

According to Kociolek et al. (2018), the genus currently contains 63 taxa, of which 20 are uncertain, including several species previously allocated by different authors to the genera *Navicula* or *Pinnularia* (e.g. Petersen 1915; 1928; Krasske 1929; Hustedt 1934; 1942). The genus *Chamaepinnularia* has a cosmopolitan distribution and is often an important component of diatom assemblages in pristine areas and habitats less affected by anthropogenic activities, including springs (Cantonati & Lange-Bertalot 2009; Wetzel et al. 2013). Several species are typical of aerial habitats (on/around wet mosses and soil) (Metzeltin & Lange-Bertalot 1998; 2007; Wydrzycka & Lange-Bertalot 2001; Cavacini et al. 2006; Cocquyt 2007; Van de Vijver et al. 2010; Van de Vijver & Cox 2013; Żelazna-Wieczorek & Olszyński 2016). However, different species occur in fresh waters, e.g. *C. amphiborealis* Lange-Bertalot & Werum in Werum & Lange-Bertalot, *C. begeri* (Krasske) Lange-Bertalot in Lange-Bertalot & Metzeltin, *C. schauppiana* Lange-Bertalot & Metzeltin and *C. vyvermanii* Lange-Bertalot in Lange-Bertalot & Metzeltin, in fresh to brackish waters, e.g. *C. krookii* (Grunow) Lange-Bertalot & Krammer apud Lange-Bertalot & Genkal and *C. krookiformis* (Krammer) Lange-Bertalot & Krammer apud Lange-Bertalot & Genkal and in brackish waters, e.g. *C. gibsonii* Van de Vijver in Van de Vijver et al. A few *Chamaepinnularia* species are also found in marine environments, e.g. *C. clamans* (Hustedt) Witkowski, Lange-Bertalot & Metzeltin and *C. truncata* (D.König) Witkowski, Lange-Bertalot & Metzeltin (Witkowski et al. 2000; Wetzel et al. 2013; Żelazna-Wieczorek & Olszyński 2016).

Chamaepinnularia thermophila (Manguin) C.E.Wetzel & Ector was originally described from a hot saline spring in Guadalupe in the French Antilles as *Navicula thermophila* by Manguin in 1952 (Bourrelly & Manguin 1952). In 2007, the species was explicitly excluded from *Navicula sensu stricto* and was provisionally named *Naviculadicta thermophila* by Metzeltin & Lange-Bertalot (2007) until a more appropriate genus was defined. In 2016, based on further structural analysis of Manguin's original material in light (LM) and scanning electron microscopy (SEM), the species was moved to the genus *Chamaepinnularia* (Wetzel & Ector 2016). *Chamaepinnularia thermophila* is a small and poorly known species, rarely recorded in Europe and other continents. The available information on this species is scattered and not yet comprehensive. In some cases, the specific location and characteristics of the sites as well as the ecology of the species are not clearly defined in the literature.

The objectives of this study were as follows: 1) to highlight the synonymy of *C. thermophila* and *Navicula tongatensis* Hustedt by LM and SEM comparison; 2) to provide additional information and data after the first record in Sardinia (Italy); 3) to provide the first framework on the global geographic distribution and ecology of the species.

Materials and methods

Study site

The spring of San Giovanni Su Anzu (Fig. 1) is located in the eastern extremity of Monte S'Ospile in the Supramonte massif (central-eastern Sardinia) (Mucedda & Fancello 2002). The territory is characterized by Paleozoic granites and metamorphic rocks, limestones and dolostones of the Middle Jurassic and Upper Cretaceous, and Mesozoic carbonate outcrops (De Waele & Grafitti 2004). The spring (40°19'15.3"N, 009°37'05.6"E) is a small rheocrenic system that flows at about 151 m a.s.l. The water is partially collected in a tub, locally referred to as Lapia, inside a small covered structure, and is used by the local community and tourists for free thermal baths (Fiorentino et al. 2017). Part of the water forms a rivulet that flows in karst waters coming from the nearby cave of San Giovanni Su Anzu-Ispinigoli at a short distance from the emergence point. The water, known since the Roman times, is hypothermal, with a bicarbonate-alkaline-earth chemistry (Bacciu 2009).

Sampling and analyses

Water and diatom samples were collected simultaneously in July 2016 and February 2017 in the spring-fed rivulet. Water temperature, pH and

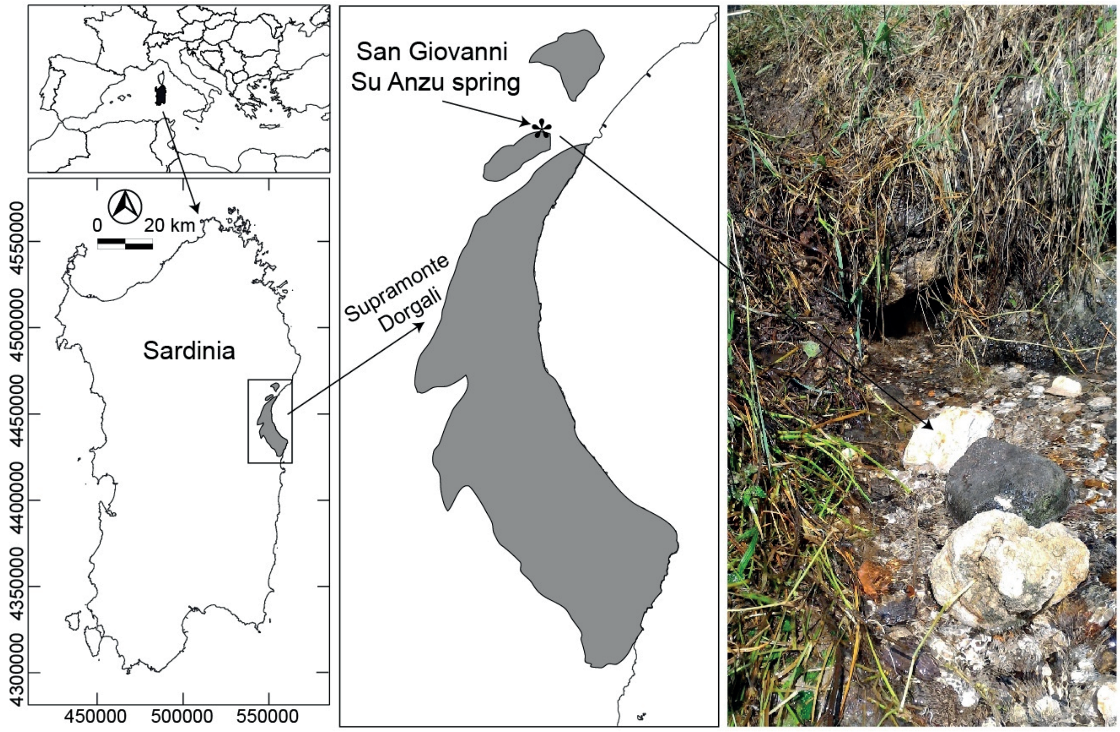

Figure 1

Geographic location and photo of the San Giovanni Su Anzu thermo-mineral spring (Sardinia, Italy)

conductivity were measured *in situ* with a multiparameter probe (YSI ProPlus). Repeated measurements of discharge (Q) and water depth were made respectively by the volumetric method using a 1 l bottle, a chronometer and a graduated metric rod.

Water samples were collected using 1 l polyethylene bottles. Samples for dissolved oxygen were collected in 150 ml glass bottles and immediately fixed in situ for the laboratory analyses by the Winkler method (Winkler 1888). Biochemical Oxygen Demand (BOD_5) was determined by direct titration of the samples after aeration up to saturation and incubation for five days at a temperature of 20°C and dark conditions. Physical and chemical analyses, including ions and trace elements, were carried out following standard methods (Strickland & Parsons 1972; APAT-IRSA & CNR 2003).

Diatom samples were collected from three different substrates (cobbles, macrophytes and fine sediments), following the methods described in Kelly et al. (1998) and ISPRA (2014). Epilithic diatoms were collected from five cobbles randomly selected with a hard-bristled toothbrush. Epiphytic diatoms were collected from submerged parts of *Mentha insularis* Req., *Lotus rectus* L. and *Typha* cf. *domingensis* (Pers.) Steudel. The material collected from macrophytes was integrated into a composite sample. Epipelic diatoms were collected from fine surface sediments by glass tubes. All diatom samples were immediately fixed with formaldehyde to a final concentration of 4%.

Diatom subsamples were treated with hydrogen peroxide (30% v/v) on a heating plate. Diluted hydrochloric acid (37% v/v) was added on the cooled material to remove carbonates according to ISPRA (2014).

LM observations, measurements and counts were carried out on slides mounted by Styrax® resin (refractive index = 1.59) using a Leica® DMR microscope with a 100x oil immersion objective. The count data were converted into percentage relative abundance (RA) in respect to the total count (~400 valves) for each sample. Micrographs were taken with a Leica® DFC 500 high-resolution digital camera using Leica Application Suite software (v. 3.7.0, Leica Microsystems©).

For SEM observations, subsamples on aluminum stubs sputtered with platinum were observed with a Hitachi SU-70 field emission scanning electron microscope.

Hustedt's original material of *Navicula tongatensis* (Hustedt's collection, material No. AT341, corresponding to lectotype slide No. 345/57. Nuku'alofa, Tonga-Ins., aL 9. Well. Specimen ID H46586, year 1954) was used for LM and SEM comparison.

LM and SEM images were manipulated using CorelDraw X6.

Results

Chamaepinnularia thermophila (Manguin) C.E.Wetzel & Ector 2016

Basionym: ≡ *Navicula thermophila* Manguin in Bourrelly & Manguin 1952

Synonyms: = *Navicula tongatensis* Hustedt 1962; = *Chamaepinnularia tongatensis* (Hustedt) Lange-Bertalot in Lange-Bertalot & Metzeltin 1996; ≡ *Naviculadicta thermophila* Metzeltin & Lange-Bertalot 2007.

The main characteristics and the type locality of *N. thermophila* and *N. tongatensis* reported in the original descriptions are summarized in Table 1.

Specimens from the San Giovanni Su Anzu spring (Sardinia): main morphological characteristics

The specimens observed show ends subcapitate and rounded. Slightly radiate striae are more widely spaced in the center of the valve but difficult to resolve with LM. The central area is very small. The raphe is filiform and straight with distal ends bent toward the same side and a central silica nodule is present. They are composed of three large areolae interrupted by the silica deposition along the apical plane clearly visible with SEM.

LM. Fig. 2(a–t). Valve outline linear-lanceolate. Ends subcapitate and rounded. Length 6.5–9.0 µm, width 2.5–3.0 µm. Raphe filiform, very small central area.

Table 1

Main characteristics and the type locality of *Navicula thermophila* and *Navicula tongatensis* reported in the original descriptions of the species

	Navicula thermophila Manguin in Bourrelly & Manguin 1952	*Navicula tongatensis* Hustedt 1962
Valve outline	elliptic	linear-elliptic
Ends	capitate	sub-capitate
Raphe		straight, filiform
Striae	radiate, more spaced in the middle	slightly radiate, more spaced in the middle
Central area	sub-quadratic	
Length (µm)	7.2–8.0	6.0–8.0
Width (µm)	2.5–3.0	2.5
Striae/10 µm	29–30	26–28
Type locality	hot-salt spring	thermal well

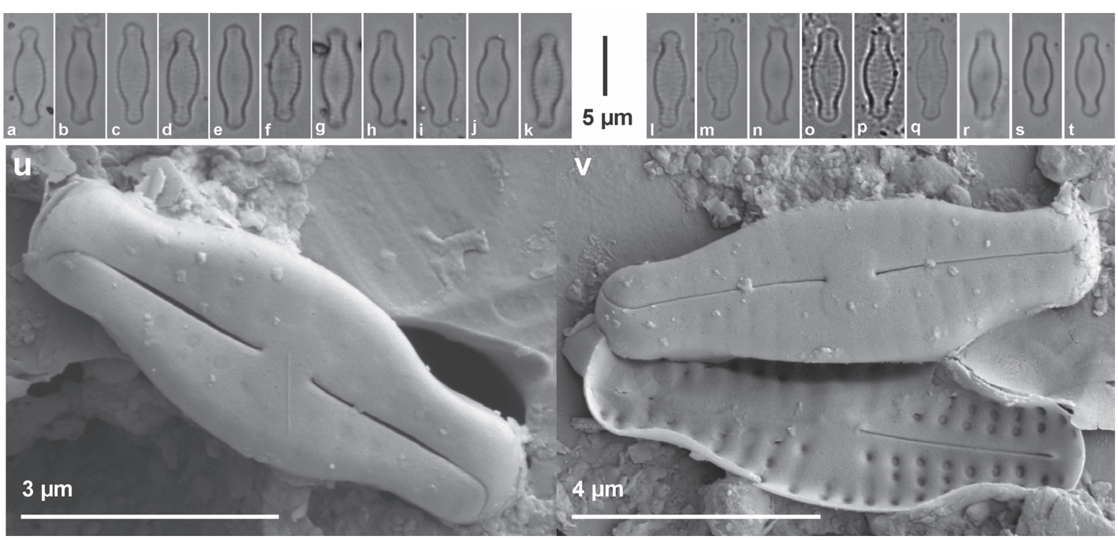

Figure 2(a–v)

Fig. 2(a–t). Light microscopy (LM). *Chamaepinnularia thermophila* from the San Giovanni Su Anzu spring. Fig. 2(u–v). Scanning electron microscopy (SEM). *Chamaepinnularia thermophila* from the San Giovanni Su Anzu spring. Fig. 2(u–v): external views. Valves showing the straight raphe, with distal ends bent toward the same side, the central silica nodule and striae slightly radiate. Fig. 2v: internal view. Valve showing three large areolae interrupted by the silica deposition along the apical plane

Striae difficult to resolve with LM.

SEM: External views. Fig. 2(u–v). Valve showing the straight raphe, with distal ends bent toward the same side and the central silica nodule. Striae slightly radiate (26–28 in 10 µm), more widely spaced in the center of the valve and composed of areolae occluded by thin closing membranes.

SEM: Internal view. Fig. 2v. Valve showing three large areolae interrupted by silica deposition along the apical plane.

Comparison with *Navicula tongatensis* Hustedt 1962

The LM and SEM observations of *Chamaepinnularia thermophila* from Sardinia in Figure 2(a–v) revealed valve outlines, structure of the raphe and striae pattern identical with *Navicula tongatensis* Hustedt reported in Figure 3(a–u). Our specimens of *C. thermophila* show slightly longer and wider valves compared to the original description by Hustedt.

New finding in Sardinia (Italy)

Chamaepinnularia thermophila was found in summer 2016 (July) and winter 2017 (February) in samples collected from three substrates (cobbles, macrophytes and fine sediments) in the San Giovanni Su Anzu spring. In general, the RA ranged from 0.9 to 10.8% and was higher on cobbles (10.8%) and sediments (4.1%) in summer. The seasonal and spatial distribution of the species (winter/summer, substrates) is presented in Figure 4.

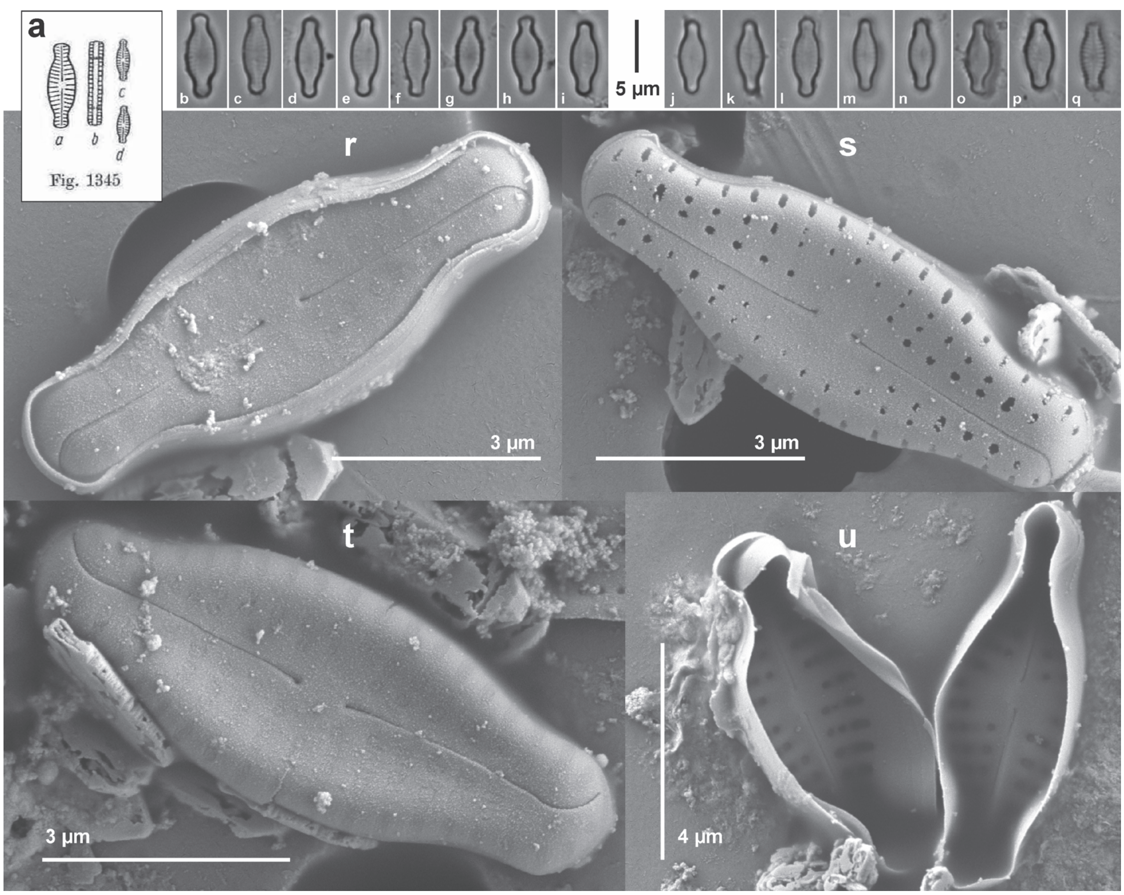

Figure 3(a–u)

Fig. 3a: Reproduction of the holotype material illustrated in Hustedt (1962) – Fig. 1345: a, b 2000/1, c, d 1000/1. Fig. 3(b–q): Light microscopy (LM). *Navicula tongatensis* Hustedt 1962 from his original material. Fig. 3(r–u): Scanning electron microscopy (SEM). *Navicula tongatensis* Hustedt 1962 from his original material. Fig. 3r: external view. Frustule showing unperforated girdle bands. Fig. 3(s–t): external views. Valves showing the radiate striae composed of three or four areolae and the straight raphe, with distal ends bent toward the same side. Fig. 3u: internal views. Valves showing the areolae interrupted by the silica deposition along the apical plane

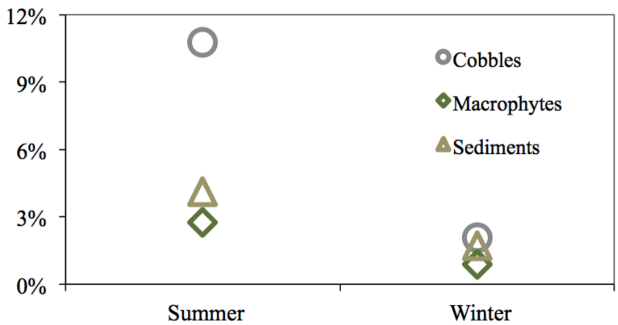

Figure 4

Seasonal abundance of *Chamaepinnularia thermophila* on the three investigated substrates from the San Giovanni Su Anzu spring (Sardinia, Italy)

The species composition based on five most abundant taxa associated with *C. thermophila* for each substrate and season is presented in Figure 5. Among these, the presence of *Cocconeis feuerbornii* Hustedt is interesting as it is considered a pantropical species (Pringle et al. 2016).

The spring was characterized by a constant temperature with a seasonal variation of 0.7°C. The

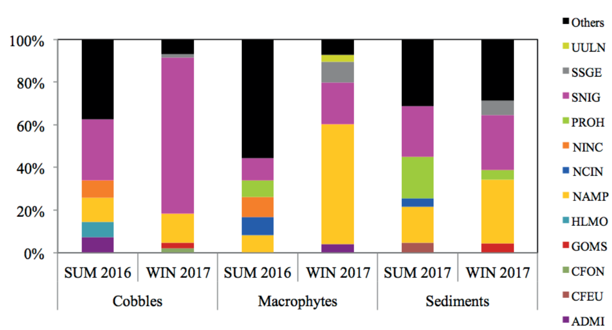

Figure 5

Species composition based on five most abundant taxa associated with *Chamaepinnularia thermophila* for each substrate and season. Acronyms of the species: ADMI = *Achnanthidium minutissimum* (Kützing) Czarnecki; CFEU = *Cocconeis feuerbornii* Hustedt; CFON = *Caloneis fontinalis* (Grunow) Cleve-Euler; GOMS = *Gomphonema* sp.; HLMO = *Halamphora montana* (Krasske) Levkov; NAMP = *Nitzschia amphibia* Grunow; NCIN = *Navicula cincta* (Ehrenberg) Ralfs; NINC = *Nitzschia inconspicua* Grunow; PROH = *Planothidium rostratoholarcticum* Lange-Bertalot & Bąk; SNIG = *Sellaphora nigri* (De Notaris) C.E.Wetzel & Ector; SSGE = *Sellaphora saugerresii* (Desmazières) C.E.Wetzel & D.G.Mann; UULN = *Ulnaria ulna* (Nitzsch) Compère

water discharge and depth were low. The conductivity was medium to high and consistent with the prevalent carbonate bedrock. In general, the nutrient content, in particular the inorganic nitrogen compounds, was low. However, considering the phosphorus and BOD_5 values, the spring San Giovanni Su Anzu seems to be affected by agricultural activities and livestock breeding existing in the surrounding area. Physical and chemical variables of the site are presented in Table 2.

Geographic distribution

The type locality of the species *Navicula thermophila* is a spring from the Bouillante geothermal area on Basse-Terre Island, in Guadalupe, the French Antilles (Bourrelly & Manguin 1952). After its description, the species was reported at the following sites: 1) the spring of Chutes du Carbet on Basse-Terre Island, Guadalupe, the French Antilles; 2) the spring of La Lise on Basse-Terre Island, Guadalupe, the French Antilles; 3) the spring of Sucrerie in the Anses-d'Arlet sector, Martinique, the French Antilles (ASCONIT Consultants 2015; Eulin-Garrigue et al. 2017).

The type locality of the species *Navicula tongatensis* is a well located near Nuku'alofa on the Tonga Islands (Hustedt 1962), in the Polynesian archipelago, the southwestern Pacific Ocean (Hustedt 1962). After its description, the species was reported from three thermal springs at the southern border of the Kaokoveld region in Namibia, Southwest Africa (Cholnoky 1966) and in freshwater diatom assemblages from Quaternary sections collected in the Pay-Khoy region (Moreyu River basin) in Russia (Loseva 1997).

According to Lange-Bertalot & Metzeltin (1996), the species *Chamaepinnularia tongatensis* was recorded in Borneo, in the Malay Archipelago, Southeast Asia. These authors also indicated a conspecificity of the *C. tongatensis* population from Borneo with *N. tongatensis* Hustedt. Finally, the species was reported in some ephemeral headwater streams in the Czech Republic: 1) Suchá Bělá, 2) Písečná rokle, 3) Hluboký důl, 4) Mlýnská rokle, 5) Červený potok, 6) Vlčí potok by Veselá (2009) & Veselá & Johansen (2009). However, as pointed out by Veselá & Johansen (2009), the co-occurrence of very similar *C. soehrensis* var. *capitata* (Krasske) Lange-Bertalot & Krammer in Lange-Bertalot & Metzeltin at these sites suggests that the specimens observed may belong to a cryptic species.

A map of all sites with the confirmed presence of *C. thermophila* (considering all its synonyms) is presented in Figure 6. The most complete data sets for the sites with *C. thermophila* available in the literature are presented in Table 2.

Table 2

Physical and chemical variables of the sites with *Chamaepinnularia thermophila* (including the new site of the San Giovanni Su Anzu spring in Sardinia, Italy), relative abundance of the species and occurrence on different substrates

Variables	Units	Country			
		Guadalupe		Martinique	Sardinia
		Spring sites			
		Chute du Carbet	La Lise	Sucrerie	San Giovanni Su Anzu
Temperature	°C	44.9	44.9	26.4	29.3–30
Discharge	$l\ s^{-1}$				0.489–0.651
Mean water depth	cm				6–7.3
pH		6.51	7.33	7.92	7.26–7.30
Alkalinity	$meq\ l^{-1}$				3.8–4.7
Conductivity	$\mu S\ cm^{-1}$			1558	570–590
Dissolved Oxygen	$mg\ l^{-1}$			7.07	7.2–8.7
Oxygen saturation	% saturation			89.2	95–114
BOD_5	$mg\ O_2\ l^{-1}$				1.0–3.3
Cl^-	$mg\ l^{-1}$	368	27.5		42.5–46.1
Total hardness	$mg\ CaCO_3\ l^{-1}$				235–235
Reactive phosphorus	$\mu g\ P\ l^{-1}$				16–24
Total phosphorus					37–78
$N\text{-}NO_2^-$	$\mu g\ N\ l^{-1}$				4–6
$N\text{-}NO_3^-$		200	1140		2448–2932
$N\text{-}NH_4^+$					3–8
Total nitrogen					3743–6244
Reactive silica	$mg\ Si\ l^{-1}$	110	72		7.53–8.65
Suspended solids	$mg\ l^{-1}$				0–1.8
Br^-					< D.L.–0.4
Ca^{2+}		188	13.4		44–44
F^-					< D.L.–0.1
Fe^{2+}					0.04–0.04
HCO_3^-		125	132		254.4–274.5
K^+		24	3.89		1.7–2.2
Mg^{2+}		64.9	4.84		30.4–30.9
Mn^{2+}		n.d.	0.011		0.04–0.05
Na^+		116.2	41.9		26–27.3
SO_4^{2-}		303	5.69		8.0–9.8
% *C. thermophila*		10–50%	< 10%	55	0.9–10.8
Substrate				cob	cob/mac/sed

** D.L. = Detection Limit. Abbreviations: cob = cobbles; mac = macrophytes; sed = sediments. Source of information and data on the spring sites in the French Antilles (Guadalupe and Martinique): Brombach et al. 2000; ASCONIT Consultants 2015; Eulin-Garrigue et al. 2017

Ecological traits of the species

According to the available literature and our data, *Chamaepinnularia thermophila* was found mainly in thermal springs (20–60°C) with alkaline pH (7.26–8), medium to high conductivity (570–1558 $\mu S\ cm^{-1}$) and low content of nitrates (200–2932 $\mu g\ l^{-1}$) (Bourrelly & Manguin 1952; ASCONIT Consultants 2015; Eulin-Garrigue et al. 2017). The species was very common in a well on the Tonga Islands with water temperature of 36°C and pH 8.0 (Hustedt 1962). In general, it was abundant in two thermal springs in South Africa (RA: 84% and 20.3%) (Cholnoky 1966), in the springs of the French Antilles (RA: < 10–55%) (ASCONIT Consultants 2015; Eulin-Garrigue et al. 2017) and Sardinia (RA: 10.8%).

The presence of the species in Quaternary sections in Russia suggests, according to Loseva (1997), warmer water conditions in the past.

In some ephemeral headwaters of the Czech Republic, characterized by low temperatures (5.1–9.5°C), pH (3.3–7.35) and conductivity (53–181 $\mu S\ cm^{-1}$), the presumed specimens of the species were mostly rare, represented by only one or two valves in each sample (Veselá 2009; Veselá & Johansen 2009).

Figure 6

Map of *Chamaepinnularia thermophila* sites in various parts of the world. Brown circles: Quaternary sections; orange circles: thermal waters (springs and well); uncolored circles: unknown type

Discussion

The identity of *Chamaepinnularia thermophila* was clarified after structural analyses in LM and SEM on the original material of *Navicula thermophila* Manguin (Bourrelly & Manguin 1952) by Wetzel & Ector (2016).

Chamaepinnularia thermophila observed in Sardinia showed morphological features such as shape of the valves, structure of the raphe and striae pattern corresponding with those reported by Wetzel & Ector (2016). Our specimens are slightly longer than those described by Manguin (Bourrelly & Manguin 1952). The number of striae corresponds well with the specimens from the original material illustrated by Wetzel & Ector (2016), but is slightly lower compared to the original description of the species.

Chamaepinnularia thermophila from Sardinia also showed a very high morphological similarity with *Navicula tongatensis* from Hustedt's original material. The valves have identical shape and terminal raphe deflections in the same direction. In both cases, the striae are radiate and more spaced in the middle part of the valve and they are composed of three to four areolae externally occluded by hymens. The number of striae is also perfectly consistent. The valves found in Sardinia are slightly longer and wider than those described by Hustedt (1962). Based on our observations, *C. thermophila* and *N. tongatensis* can be considered synonyms of the same species.

Chamaepinnularia thermophila is a poorly known and probably rare species. In fact, in some cases, the specific location of the sites and their ecological characteristics are unclear or not available in the literature, and even considering all the synonyms of the species, the number of known sites remains limited. Furthermore, our extensive literature search revealed that *C. thermophila* is relatively abundant only at very few sites in the world, mainly in tropical areas. A limited number of sites and low abundance are frequent characteristics of rare diatoms (e.g. Noga & Rybak 2017).

Most of the known sites of *C. thermophila,* including the new site in Sardinia, are springs characterized by warm waters, alkaline pH and medium to high or high conductivity. These characteristics seem to confirm the ecological preferences initially hypothesized by Manguin: "halophilous species of salt thermal springs" (Bourrelly & Manguin 1952). For the trophic level, a comparison between sites was possible only for nitrates with La Lise and Chute du Carbet springs (Brombach et al. 2000), suggesting a possible preference of the species for low concentrations. However, our values of phosphorus and BOD_5 do not reflect the condition of pristine environments, suggesting a possible tolerance of the species to moderate levels of nutrients and organic matter. Our data provide the first information on the distribution of *C. thermophila* on a small seasonal and spatial scale (winter/summer-substrates). In general, cobbles, characterized by the highest relative abundance of the species in both seasons (summer 2016 and winter 2017), seem to be the most favorable substrate compared to macrophytes and sediments. Furthermore, in summer, the species was more abundant on all investigated substrates, probably favored by a slightly higher water temperature and greater light availability. Our data seem to confirm the preference of the species for warmer waters. The occurrence of *C. thermophila* in ephemeral headwaters of the Czech Republic (Veselá 2009; Veselá & Johansen 2009), with very different environmental characteristics compared to the spring sites, seems unusual and should be further investigated. However, the uncommon and rare presence of the species reported in these environments may suggest a possible tolerance to colder waters, acid to slightly alkaline pH and low conductivity and especially seasonal desiccation episodes. This ability to withstand a dry period could be an important biological trait, given that several *Chamaepinnularia* species are characteristic of aerial habitats (Wetzel et al. 2013).

This study highlights the synonymy of *C. thermophila* and *N. tongatensis*, considered for a long time after their description to be two different species, thus contributing to the standardization of the nomenclature used so far. It also provides the first framework on the global geographic distribution and ecology of the species based on the information available in the literature and our new data. The occurrence of this species as well as other rare diatoms in springs located in very distant and different geographic areas, especially islands, is an aspect deserving further studies in the future. In fact, springs are understudied habitats (Mogna et al. 2015). In addition, they are considered as water islands due to their scattered distribution (Werum 2001; Cantonati et al. 2012) and the diatom dispersion mechanisms are passive and limited (Vanormelingen et al. 2008).

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