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***Fontina* gen. nov. (Bacillariophyta): a new diatom genus from a thermo-mineral spring of the French Massif Central (France)**

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**Abstract**

Light and scanning electron microscope observations on the genus *Fontina* gen. nov. from a thermo-mineral spring of the Massif Central (France) are presented. Based on morphology, the new genus shows features that have not been described previously, such as the stria pattern, interrupted at the valve face/mantle junction and composed of one long, slit-like areola on both valve face and mantle. Externally, areolae are closed by hymenes. *Fontina arverna* sp. nov. is described as the *typus generis* of *Fontina*. This new genus was compared with some similar freshwater genera such as *Adlafia*, *Chamaepinnularia*, *Genkalia*, *Germainiella*, *Microfissurata* and *Nupela*. So far, we are unable to establish an evolutionary link or cladistic association with currently known genera. The new genus is described from a sampling site characterized by high conductivity and high carbonate concentration, brackish conditions and whose water originates deep in the crust (high lithium concentration).

**Keywords:** *Fontina arverna*, *mineral springs*, *new genus*, *raphid diatom*, *taxonomy*

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## Introduction

Mineral and thermal springs are formed by hydro-geological processes, linked to volcanic and tectonic activities. A significant portion of rain water feeds shallow aquifers, while elsewhere it slowly infiltrates faults up to several kilometers deep. Indeed, mineral springs coincide with the fault zones (Risler 1974). It is well known that “fracturing the platform promotes the circulation of fluids (water and gas) including those of carbon dioxide (CO<sub>2</sub>) and helium (He), which may be hampered by the presence of clay or marl” (Gal et al. 2012). The rainwater infiltrates the soil by gravity and capillarity to the hydrostatic level, then rises through hydrostatic or gaseous pressure. At several kilometers deep, warming promotes progressive destruction by hydrolysis of minerals such as feldspar rocks, through which constituents such as sodium, calcium and potassium come into solution. Before reaching the surface where the fractures have a tree-like aspect, water can be mixed, in varying proportions, with the surface water layers (Labernardière, personal communication). It is during this journey that they acquire their different characteristics (Risler 1974). Thus, mineral and thermal springs present waters characterized by their gaseous properties, with significant mineralization and sometimes high temperatures.

Depending on their abiotic properties, different ecosystems may develop. Some springs create inland saline areas under the influence of saline waters that accompany the salt deposits, or as areas exposed to water deficit in dry climates (Reimold & Queen 1974, Poljakoff-Mayber & Gale 1975). These environments are relatively widespread throughout the world and cover ca. 10% of the land (O’leary & Glenn 1994, Piernik 2012). Inland salt environments occur in limited areas, mostly on “fossil salt deposits and around salty springs” (Piernik 2012). Other springs containing carbonates can induce the formation of travertine, i.e. a limestone rock, and are known as Limestone-Precipitating Springs (LPS) (Cantonati et al. 2016). Depending on the geology, some springs can be both LPS and salty. Springs have been studied by diatomists all over the world, often leading to the discovery of new taxa (Werum & Lange-Bertalot 2004, Cantonati & Lange-Bertalot 2006, 2011, Reichardt 2006, Wojtal 2009, 2013, Żelazna-Wieczorek 2011, Lai et al. 2018).

The French Massif Central (over 85,000 km<sup>2</sup>) is composed of mountain reliefs, plateaus and volcanoes (quiescent), where the Hercynian platform appears at the surface, surrounded by different sedimentary basins. It is well known that the many faults in the massif allow the circulation of water in the rocks and the emergence of water after a more or less long travel across the earth’s crust. Thus, in the French Massif Central, and more

precisely in the Puy-de-Dôme department, Truchot (1878) described more than 200 springs. Due to the history of the massif, a high variety of habitat conditions are present, including high altitude springs (>1000 m a.s.l.) but also the hottest spring in Europe (80 °C). Previous studies conducted on springs from the Massif Central have revealed the high algal biodiversity (Héribaud 1893, 1920, Chaouite & Romagoux 1989, Tudesque 1996, Cordonnier 2008, Beauger et al. 2015, 2016, 2017, 2019).

During a biodiversity survey of mineral springs around the city of Saint-Nectaire, a new genus was observed in one of them. This paper describes the new genus and species, *Fontina arverna*, using light (LM) and scanning electron microscopy (SEM). Based on the available literature, a morphological comparison is made with the most similar genera and together with information on their ecology.

## **Material and methods**

In summer 2016, a survey was performed around the former thermal city of Saint-Nectaire. The granitic horst of Saint-Nectaire, flanked on the east and west by two Oligocene compartments and divided by N.S. and E.W. faults, is closely related to the Limagne fracture system (Risler 1974). More than 40 springs were listed by Truchot (1878) emerging from this granitic context. Currently, some springs are used for petrification craft industry due to the hardness of the water. The sample was collected in the thermal (32.2 °C) and carbonate (3240 mg L<sup>-1</sup>) spring (according to the classification of Glazier 2014) of Antonia in Saint-Nectaire (French Massif Central) (Fig. 1). Due to their former therapeutic use, many springs were modified by drilling to increase their discharge. It was the case for the Antonia spring. Thus, the actual outlet is a former borehole dug in 1980. The spring has a low radium content (0.7 millimicrocurie, Jacquet 1928).

The diatoms were sampled on travertine, a sedimentary rock by brushing the stone. The geographical position of the sampling site was taken using a DGPS Trimble Geo7x, in Lambert 93. Samples were cleaned using hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>, 35%) and hydrochloric acid (HCl), and rinsed several times. Cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides and mounted in Naphrax®. LM and morphometric measurements were performed using a Leica® DMRX bright field microscope with 100x oil immersion objective, and light photographs were taken with a Leica® DC500 camera. For scanning electron microscopy (SEM), parts of the oxidized

suspensions were filtered and filters were mounted on aluminium stubs and coated with platinum. An ultrahigh-resolution analytical field emission (FE) scanning electron microscope Hitachi SU-70 (Hitachi High-Technologies Corporation, Japan) operated at 5 kV and 10 mm distance was used for the analysis. SEM images were taken using the lower (SE-L) and upper (SE-U) detector signal and sometimes tilted up to an angle of 28 degrees. Conductivity ( $\mu\text{S}\cdot\text{cm}^{-1}$ ), pH (pH units), and water temperature ( $^{\circ}\text{C}$ ) were measured at the sampling site, using a WTW Multiline P4. The oxygen was measured using an oximeter Ysi ProODO. A water sample was collected for further chemical analysis in the laboratory and was analysed using the high-pressure ion chromatography technic. Spring water radioactivity (radon) was measured using gamma-spectrometry with a well Germanium detector and a gamma survey was conducted at spring site using a Myrion Colibri VLD instrument.

## Results

### ***Fontina* Beauger, C.E. Wetzel & Ector gen. nov.**

*Description:* it is a small-celled diatom. No girdle views were observed. Valves are from narrowly elliptical, linear-elliptical, lanceolate-elliptical to broadly elliptical with endings broadly rounded to slightly capitate or cuneate. The valve face appears hyaline with any structure other than the raphe and the axial area. Valves are slightly asymmetric to the apical axis. Under SEM, the axial area is narrow and enlarged near the central area. Striae are interrupted at the valve face/mantle junction and composed of one long, slit-like areola on both valve face and mantle. Externally, areolae are closed by hymenes. External distal raphe fissures are slightly deflected to the same side and internally, they end in small raised helictoglossa. Girdle bands are perforated.

*Generitype:* *Fontina arverna* Beauger, C.E. Wetzel & Ector sp. nov. (Figs 2–34)

The term *Fontina* refers to the Latin word “*Fons*”= spring, the habitat where the new genus was observed.

*Fontina arverna* Beauger, C.E. Wetzel & Ector sp. nov. (Figs 2-39)

*Description:* Length 3.5–14  $\mu\text{m}$ , breadth 1.5–3.5  $\mu\text{m}$ , stria density 60–70 in 10  $\mu\text{m}$ .

LM: Raphe filiform conspicuous. Valves appear hyaline and are slightly transapically curved. The axial area is narrow.

SEM: The axial area is narrow and enlarged near the central area. Thin striae are interrupted near the valve face/mantle junction, continuing onto the mantle (Figs 21–39). Valve face striae are composed of elongated areolae (Figs 35–37), one on the valve face and the other on the mantle. Depending on the valve shape, the valve face areola is sometimes shorter than the one on the mantle (Fig. 28), which is relatively deep. Moreover, the lengths of the areolae, decreasing from the apex to the central area, are not the same on each side of the valve face, emphasising the asymmetry of the frustule. Internally, the virgae can sometimes be bifurcated near the valve face/mantle junction, randomly along the valve (usually near the valve centre). The areolae are closed externally by hymenes and internally are composed of small pores that are difficult to observe (Fig. 38). Externally, the proximal raphe endings are straight, slightly expanded, or pore-like and slightly deflected to the same side (Figs 21–34) while internally, they are expanded and slightly deflected to the same side (Figs 35–39). Distal endings of raphe externally slightly deflected and reaching the valve mantle at the apex. Both endings are deflected to the same side (Figs 21–34). Internally, the distal raphe fissures end in small raised helictoglossae (Figs 35–37, 39). Girdle bands appeared perforated at the apex with two rows of areolae near the valve apices (Fig. 39).

*Holotype*. Deposited in Herbiers Universitaires de Clermont-Ferrand, France (CLF 104889), shown here in Figs 2–20 (LM) and 21–39 (SEM).

*Isotypes*. Deposited in Herbiers Universitaires de Clermont-Ferrand, France (CLF 104890) and in Botanic Garden Meise, Belgium (BR-4517).

*Type locality*. Saint-Nectaire, Anthonia spring, France (altitude: 691m, E 699358.66, N6498243.64 - Lambert 93). Sample NE10-23072016-AN collected the 23th of July 2016 by A. Beauger.

*Etymology*. The epithet “*arverna*” refers to the Auvergne region (part of the Massif Central near Saint-Nectaire) and the name of the Gallic people in this part of France.

*Ecology and associated diatoms species:* The type population of *F. arverna* was found in the Anthonia spring where it represents 14% of the epilithic diatom flora. The dominant taxa were *Halamphora coffeaeformis* (C. Agardh) Levkov (43%), *Navicula sanctamargaritae* Beauger in Beauger et al. (26%), *Crenotia thermalis* (Rabenhorst) Wojtal (9%) and *Nitzschia valdecostata* Lange-Bertalot & Simonsen (5%).

*Physical and chemical variables:* The conductivity of this thermo-mineral spring is high with mainly bicarbonates, chlorides and sodium (Table 1). The concentration in dissolved oxygen is low and the lack of anthropogenic impact is revealed by the concentrations of nitrates, nitrites and phosphates. The concentration of lithium and bromine (respectively 14.1 and 5.2 mg L<sup>-1</sup>) underline the deep origin of the water and its circulation through the granite (Michard 1990). Spring water radioactivity was measured resulting in radon activity of 11.3 +/- 0.2 Bq/l. It appears that the dissolved radium content has been ignored for this estimate. Gamma, dose rates up to 1100 nSv/h, have been measured on top of the travertine where diatoms were sampled, revealing significant but low radioactivity in the sediment.

## **Discussion**

The precise taxonomic position of this taxon is unclear. The ultrastructural analysis revealed that its combination of morphological characters made it difficult to establish relationships with currently described diatom genera, although it probably belongs in the family Naviculaceae.

*Fontina* is characterized by the peculiar stria ultrastructure and valve asymmetry. Table 2 documents other genera that show some similar combinations of morphological features: *Adlafia* Gerd Moser, Lange-Bertalot & Metzeltin in Lange-Bertalot et al. (1996), *Chamaepinnularia* Lange-Bertalot & Krammer Metzeltin in Lange-Bertalot & Metzeltin (1996), *Genkalia* Kulikovskiy, Lange-Bertalot & Metzeltin in Kulikovskiy et al. (2012), *Germainiella* Lange-Bertalot & Metzeltin in Metzeltin et al. (2005), *Microfissurata* Lange-Bertalot, Cantonati & Van de Vijver in Cantonati et al. (2009) and *Nupela* Vyverman & Compère.

The most similar genus to *Fontina* is *Nupela* (Table 2) as both taxa can be asymmetric, without a conopeum and striae that cannot be resolved with LM. However, they differ in several morphological features. Thus, while the striae of *Fontina* are briefly interrupted near the valve face/mantle junction, continuing onto the mantle with only a single slit-like areola

on the valve face, *Nupela* is characterized by many elliptical slit-like areolae per stria (Vyverman & Compère 1991, Siver et al. 2007, Sala et al. 2014, Miscoe et al. 2016). The areolae in *Nupela* are covered internally by hymenes perforated at the centre; some species also have external hymenate areola occlusions. While the external distal raphe endings of *Fontina* are slightly deflected, those of *Nupela* are sharply curved. The internal proximal raphe endings of *Nupela* can be T-shaped or hook-shaped. The girdle bands of *Fontina* are perforated near the apex which is not the case for *Nupela*. Finally, *Nupela* is widespread and present in freshwater environments with low conductivity and in aerial habitats (Vyverman & Compère 1991, Siver et al. 2007, Spaulding & Edlund 2008, Kulikovskiy et al. 2009, Sala et al. 2014, Falasco et al. 2015, Miscoe et al. 2016).

*Adlafia* (Table 2) has similar features to *Fontina*, including the presence of external hymenes on areolae, the absence of a conopeum, and perforated girdle bands, but it differs in the striation pattern (Moser et al. 1998, Morales & Le 2005, Liu et al. 2017). In *Adlafia* striation is very dense, composed of very fine, radiate striae, resolvable with LM whereas *Fontina* valves appear hyaline. Moreover, the valves are symmetric. *Adlafia* has striae composed of round areolae occluded by a porous vola lying on the outer periphery of each areola unlike *Fontina*, whose areolae are slit-like and the striae briefly interrupted near the valve face/mantle junction, before continuing onto the mantle. Both genera have areolae occluded by hymenes. The external distal raphe endings of *Adlafia* are strongly bent and angular, but slightly deflected in *Fontina*. The internal proximal raphe endings are expanded and slightly deflected in *Fontina*, but conspicuously bent in the same direction and opposite to the distal ends in *Adlafia*. The girdle bands of both genera are perforated; *Adlafia* has two rows of poroids on the valvocopula (sometimes one row becoming two toward the valve apices; Morales & Le 2005). *Adlafia* species live in freshwater ecosystems (Moser et al. 1998, Morales & Le 2005, Spaulding & Edlund 2009, Liu et al. 2017, Van de Vijver et al. 2017, Marquié et al. 2018).

*Chamaepinnularia* has areolae closed by hymenes, a conopeum is absent and girdle bands are also perforated as in *Fontina*. This genus has symmetric valves that are usually linear-elliptic, linear-lanceolate, elliptic-lanceolate or undulate (Lange-Bertalot & Metzeltin 1996, Cantonati & Lange-Bertalot 2009, Wetzel et al. 2013). The striae are composed of up to three slit-like areolae and are irregularly subdivided by silica bridges, a characteristic never encountered in *Fontina*. Striae can also consist of two pores, one small and rounded at the valve face/mantle junction, with the other, elongated and located on the valve face (Wetzel et

al. 2013). The internal proximal raphe endings and the external distal raphe endings are unilaterally hooked and bent to the same side respectively, whereas they are slightly deflected to the same side for the new genus. *Chamaepinnularia* is widespread and inhabits mainly low-conductivity water, although *Chamaepinnularia plinskii* Żelazna-Wieczorek & Olszyński occurs in high-conductivity water. *Chamaepinnularia* species have been observed in fresh- to marine environments and in thermal springs, e.g. *Chamaepinnularia thermophila* (Manguin) C.E. Wetzel & Ector (Lange-Bertalot & Metzeltin 1996, Cantonati & Lange-Bertalot 2009, Wetzel et al. 2013, Wetzel & Ector 2016, Żelazna-Wieczorek & Olszyński 2016).

*Genkalia* has isopolar valves and asymmetric individuals are currently unknown. Valves are elliptical to linear-elliptical or linear-lanceolate with mainly rounded ends, except *Genkalia subrostrata* (Skvortzow) Kulikovskiy, Lange-Bertalot & Metzeltin which has moderately protracted ends (Kulikovskiy et al. 2012, Wojtal et al. 2014). The internal proximal raphe endings are shortly bent to the primary side and not deflected. The external distal raphe endings are strongly bent to the secondary side and extend to the smooth junction between valve face and mantle (Kulikovskiy et al. 2012). Striae are composed of a large number of round, elliptic or transapically elongated areolae unlike in *Fontina* with one slit-like areola on the valve face and another on the mantle. *Genkalia* species are observed in lakes, except for *Genkalia subprocera* that was described in a spring, from calcium-rich water and high mineral content (Hustedt 1945, Wojtal et al. 2014).

*Germainiella* differs in several morphological features from *Fontina* (Metzeltin et al. 2005, Le Cohu et al. 2016). Valves are linear to narrowly lanceolate in shape, symmetric with capitate to subcapitate apices for *Germainiella* while for *Fontina*, they are slightly asymmetric, elliptical with rounded, capitate or cuneate apices. Unlike *Fontina*, *Germainiella* has a conopeum covering both the valve face and part of the mantle. Even though valve appears hyaline and the striae are composed of one slit-like areola, the presence of the conopeum allows separation from *Fontina*. In addition, hymenes are not observed in *Germainiella*. The external distal raphe endings are hooked for *Germainiella* but slightly deflected for *Fontina*.

*Microfissurata* has lanceolate to linear-elliptical valves with more or less protracted ends, unlike *Fontina* with narrowly elliptical, linear elliptical, lanceolate elliptical, broadly elliptical valves and broadly rounded to slightly capitate or cuneate ends (Cantonati et al. 2009). Striae are open slits, which are internally completely closed by delicate hymenes, often corroded in prepared valves (Cantonati et al. 2009). The main difference between this genus

and *Fontina* is the presence of an axial area that is wide or very wide, especially the central area in *Microfissurata*. This central area is an “apically rather expanded fascia” (Cantonati et al. 2009), a characteristic never encountered in *Fontina*. Moreover, the two known species of *Microfissurata* are encountered in freshwater and intermittently wet habitats characterized by low conductivity, contrary to *Fontina* from a thermo-mineral spring of high conductivity. *Microfissurata* also appears to be mostly epiphytic, growing on bryophytes (Cantonati et al. 2009) unlike *Fontina* that is epilithic.

In conclusion, this study of the diatom community of a thermo-mineral spring revealed a small, slightly asymmetric taxon with a previously unknown combination of the morphological characters. The new species has a unique pattern of characteristics which precludes allocation to any known genus, hence our description of *Fontina*.

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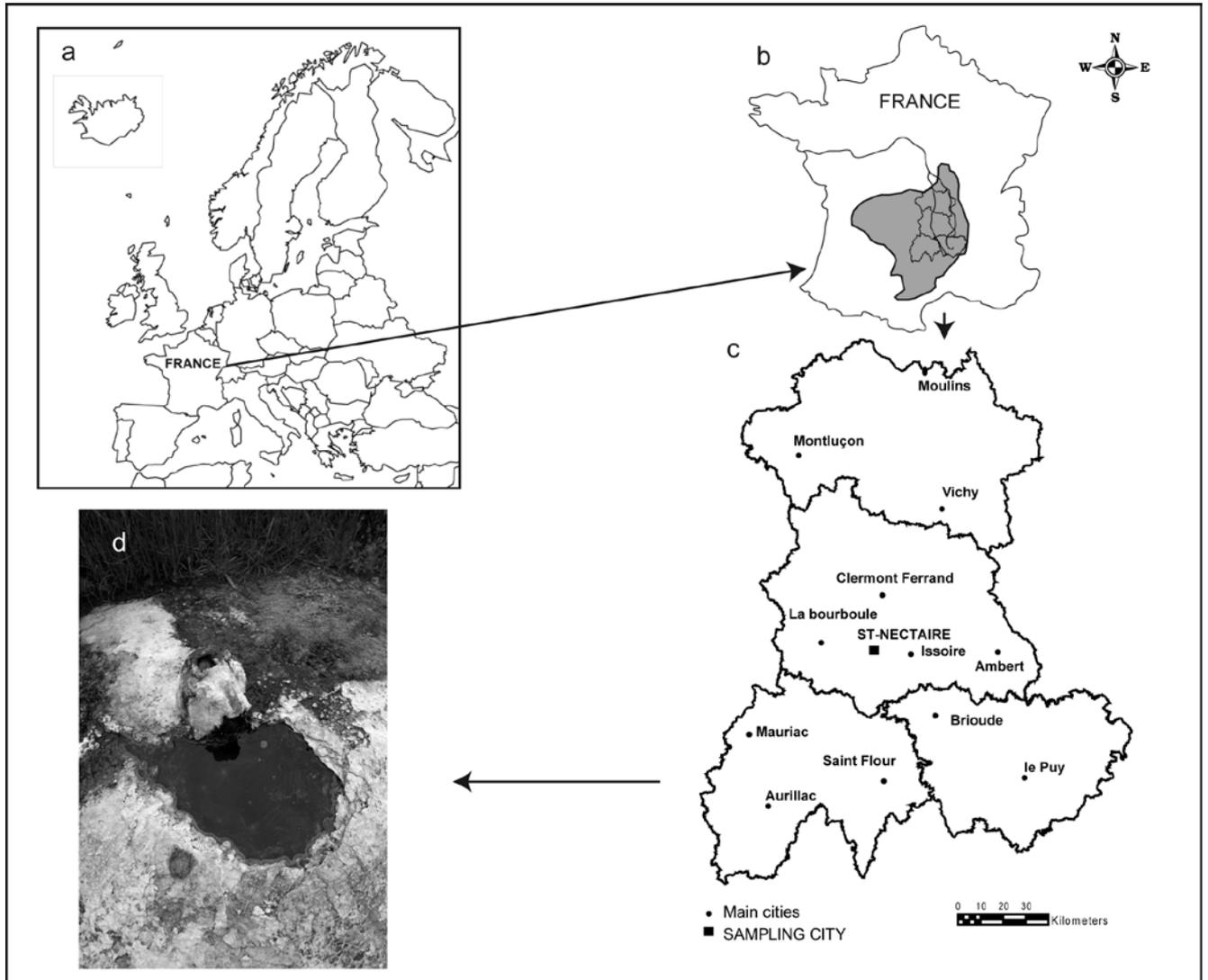
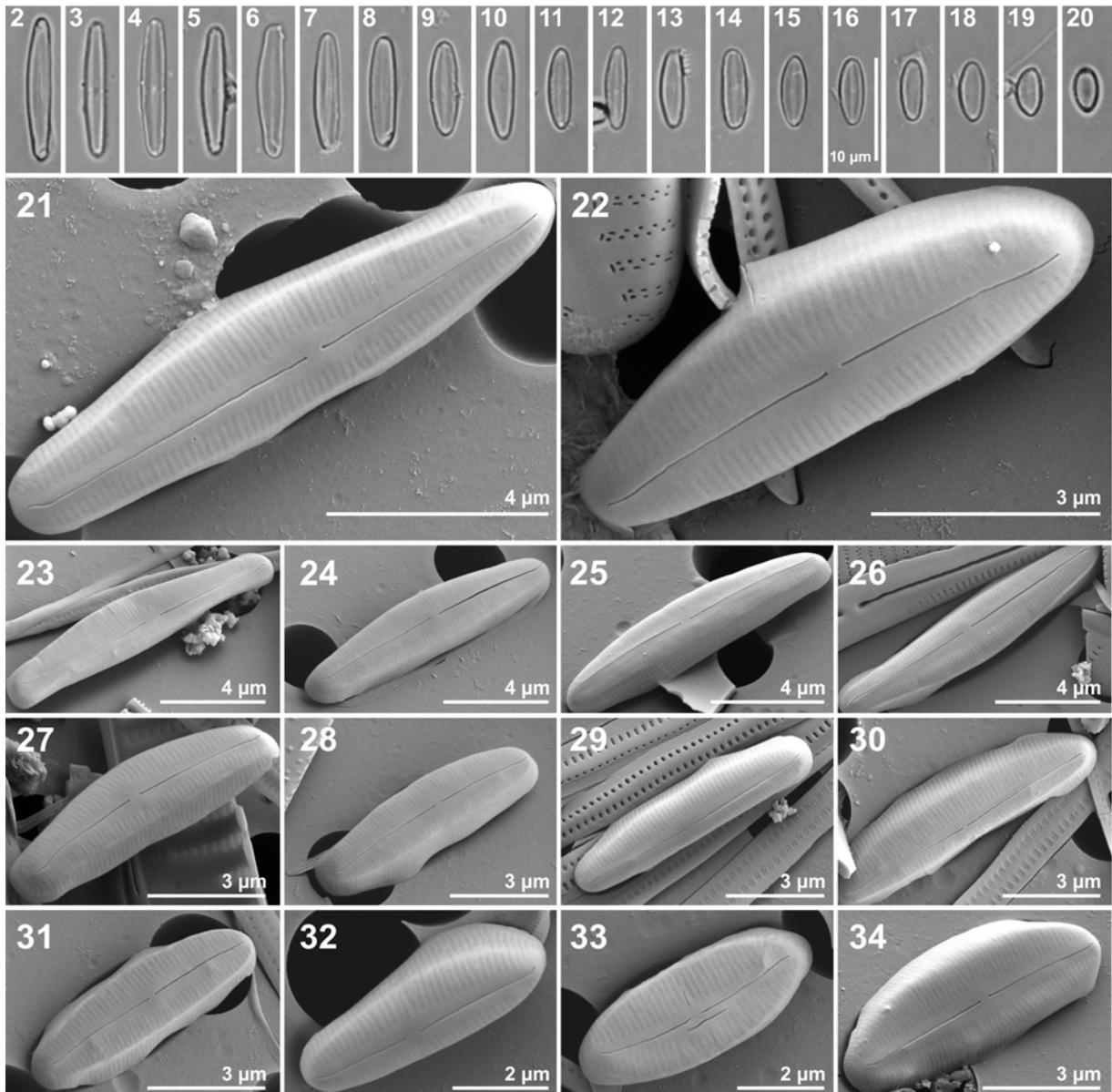
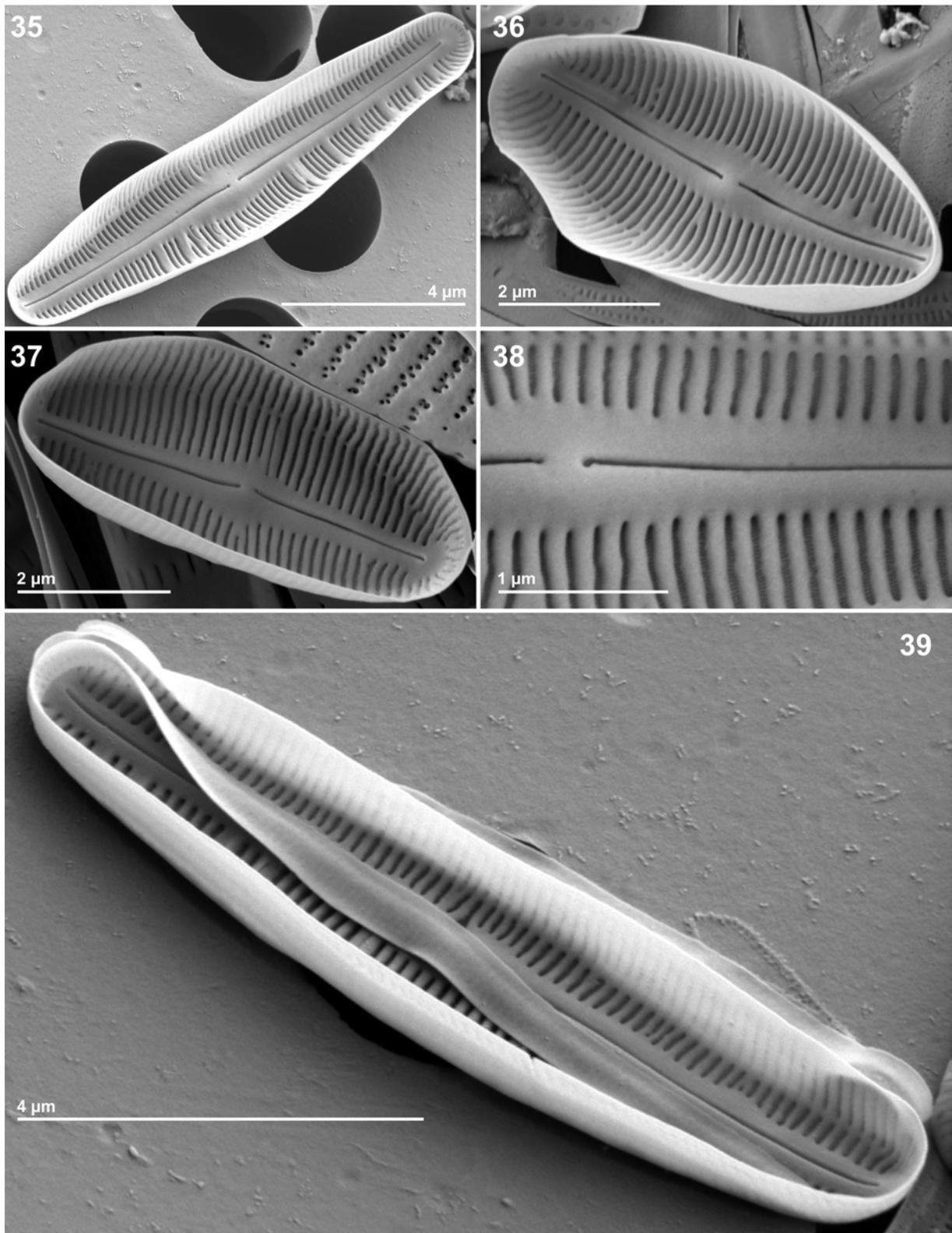


Figure 1: Map of the studied springs. a: map of Europe; b and c: general location map of the French Massif Central (in grey) and of the study area where Anthonia spring is located (square); d: photography of the Anthonia spring.



Figs 2-34: *Fontina arverna* sp. nov. *typus generis* of *Fontina* Beauger, C.E. Wetzel & Ector sp. nov., LM. (Figs 2-20). Type population from Anthonia spring. SEM. Figs 21-34. Type population from Anthonia spring. External view of an entire valve showing the raphe structure and the striae. Scale bar = 10  $\mu\text{m}$  (Figs 2-20), 4  $\mu\text{m}$  (Figs 21, 23-26), 3  $\mu\text{m}$  (Figs 22, 27-31), 2  $\mu\text{m}$  (Figs 32-33).



Figs 35-39: *Fontina arverna* sp. nov. *typus generis* of *Fontina* Beauger, C.E. Wetzel & Ector sp. nov. SEM. Figs 35-39. Type population from Anthonia spring. Internal view. Figs 35-37, 39. Internal view of an entire valve showing the raphe structure, the striae, the helictoglossa

and girdle bands. Fig. 38. Internal detail showing the striae and the proximal raphe endings.  
 Scale bar = 4  $\mu\text{m}$  (Figs 35, 39), 2  $\mu\text{m}$  (Figs 36-37), 1  $\mu\text{m}$  (Fig. 38).

Table 1: Physical and chemical variables measured in the Anthonia spring at Saint-Nectaire on July 23, 2016.

	Anthonia spring
Conductivity ( $\mu\text{S cm}^{-1}$ )	9520
pH	7.0
Temperature ( $^{\circ}\text{C}$ )	32.2
Oxygen (%)	14.9
Oxygen ( $\text{mg L}^{-1}$ )	1.1
Li <sup>+</sup> ( $\text{mg L}^{-1}$ )	14.1
Na <sup>+</sup> ( $\text{mg L}^{-1}$ )	2049.6
NH <sub>4</sub> <sup>+</sup> ( $\text{mg L}^{-1}$ )	2.6
K <sup>+</sup> ( $\text{mg L}^{-1}$ )	218.8
Mg <sup>2+</sup> ( $\text{mg L}^{-1}$ )	103.0
Ca <sup>2+</sup> ( $\text{mg L}^{-1}$ )	26.9
F <sup>-</sup> ( $\text{mg L}^{-1}$ )	0.9
Cl <sup>-</sup> ( $\text{mg L}^{-1}$ )	2195.4
NO <sub>2</sub> <sup>-</sup> ( $\text{mg L}^{-1}$ )	0.0
NO <sub>3</sub> <sup>-</sup> ( $\text{mg L}^{-1}$ )	0.4
PO <sub>4</sub> <sup>3-</sup> ( $\text{mg L}^{-1}$ )	0.1
Br ( $\text{mg L}^{-1}$ )	5.2
SO <sub>4</sub> <sup>2-</sup> ( $\text{mg L}^{-1}$ )	121.0
HCO <sub>3</sub> <sup>-</sup> ( $\text{mg L}^{-1}$ )	3240.0

Table 2: Comparison of key features among *Fontina* gen. nov. and similar genera.

Character	<i>Fontina</i> gen. nov.	<i>Adlafia</i>	<i>Chamaepinnularia</i>	<i>Genkalia</i>	<i>Germainiella</i>	<i>Microfissurata</i>	<i>Nupela</i>
Valve symmetry	slightly asymmetric	symmetric	symmetric	symmetric	symmetric	symmetric	symmetric or slightly asymmetric
Valve shape	narrowly elliptical, linear-elliptical, lanceolate-elliptical broadly elliptical	linear to linear-lanceolate	linear-elliptical, linear-lanceolate, elliptic-lanceolate or undulate	elliptic to linear-elliptic or linear-lanceolate	linear to narrowly lanceolate	lanceolate to linear-elliptical	narrowly elliptical to lanceolate
Endings	broadly rounded to slightly capitate or cuneate	blunt, rostrate, or subcapitate	rounded or rostrate	rounded or moderately protracted	capitate to subcapitate	more or less protracted ends	rostrate, capitate or apiculate
Internal proximal raphe endings	expanded and slightly deflected to the same side	conspicuously bent in the same direction and opposite to the distal ends	straight but unilaterally hooked	shortly bent to the primary side	expanded and slightly deflected to the same side	deflected to the same side or even slightly hooked	straight, simple or T-shaped or hook-shaped
Internal distal raphe endings	end in small helictoglossa	end in small raised helictoglossa	end in small raised helictoglossa	end in small raised helictoglossa	end in helictoglossa	end in small, helictoglossa	end in helictoglossa (sometimes absent)
External proximal raphe endings	straight, slightly expanded, or pore-like and slightly deflected to the same side	opposite to the other, and sometimes slightly deflected toward the same side and opposite to the distal ends	inconspicuous; opposite to the other, and sometimes slightly deflected toward the same side	proximally not expanded, curving gently to the primary side	expanded and slightly deflected to the same side	expanded, slightly deflected to the same side	inconspicuous or expanded pore-shape
External distal raphe endings	slightly deflected to the same side and reaching the valve mantle at the apex	strongly bent and angular, deflected to the same side	bent to hooked towards the same direction	strongly bent to the secondary side extended to the junction between valve face and mantle	hooked and reaching the valve mantle at the apex	deflected to the same side	sharply curved into one side of the valve
Striae/alveoli structure	uniseriate, briefly interrupted near the valve face/mantle junction, continuing on the mantle, composed of two slit-like areolae, one on	striae radial, uniseriate, composed of round areolae, occluded by a porous vola	composed of slit-like areolae (up to three), irregularly subdivided by silica bridges	uniseriate, uninterrupted from valve face to mantle, composed of round, elliptic or transapically elongated areolae	composed of one slit-like areola	open slits externally	uniseriate, 2 to 6 elliptical slit-like areolae per stria

	the valve face and the other on the mantle						
Hymenes	present externally on the striae	present externally on the areolae	present externally on the areolae	present on the areolae (in the middle)	absent	depressed in slits internally	internal hymenes perforated at the centre and external hymenes for some species
Conopeum	absent	absent	absent	absent	present, covering both valve face and a part of the mantle	absent	absent
Girdle bands	perforated	perforated, one to two rows of poroids	perforated	perforated	not perforated	not perforated	not perforated
Distribution	sinking of thermo-mineral spring; bicarbonated, sodium chloride water	species living in freshwater; widespread	low (rarely high) conductivity; oligo- or dystrophic, fresh to brackish waters and also marine; mainly aerophilic and terrestrial	most species living in freshwater, mainly in lakes but also observed in a karstic spring	most species living in freshwater (streams); widespread	most species living in freshwater: dystrophic lakes, pools, seepage springs, mires and in intermittently wet terrestrial habitats, mostly epiphytic	species living in freshwater; widespread