1 ***Cocconeis rouxii* Héribaud & Brun a forgotten, but common benthic diatom**
2 **species from the Massif Central, France**

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12 **ABSTRACT:** *Cocconeis rouxii* was described by J.Héribaud & J.Brun from samples collected
13 in mountainous freshwater sources at the Auvergne region, France. Despite being mentioned
14 in earlier publications and classic European floristic books, this species has never been fully
15 explained. Its morphology is poorly known as its confusing and sparse citations in the
16 literature, despite being abundant in several samples from the Massif Central. Some
17 inconclusive attempts to investigate the original gatherings during the 80's, and the exclusion
18 of the taxon in major floristic works led to the almost abandon of the name. We here detail
19 with light and scanning electron microscopy one population found in the source Bernadette,
20 located nearby its type locality. The species seems to be quite common in regions of France
21 with metamorphic geological properties (i.e. crystalline rocks).

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23 **KEYWORDS:** diatoms, springs, mineral waters, epilithon, epipelon.

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Introduction

Joseph Héribaud (1841-1918) was an honorary member of the French botanical society (*Société de botanique de France*) and one of the most distinguished French diatomists from the 19th century who described hundreds of diatom taxa (see Kociolek et al. 2018). His well-known books “*Les Diatomées d’Auvergne*”, “*Les Diatomées Fossiles d’Auvergne*” and “*Les Diatomées de Travertins d’Auvergne*”, the last one a posthumous *oeuvre*, are examples of fine and detailed taxonomy carried out by him. In his first remarkable account (Héribaud 1893, in collaboration with J.Brun and M.Peragallo), Héribaud described several species that are poorly known today, or whose names remain yet rarely used. Among the taxa described by or in Héribaud work’s, several *Cocconeis* from freshwater environments are highlighted. In Héribaud (1893) several species were introduced as new, such as *Cocconeis intermedia* Héribaud & M.Peragallo, *Cocconeis intermedia* f. *minor* M.Peragallo & Héribaud, *Cocconeis pediculus* var. *rotunda* Brun & Héribaud, *Cocconeis placentula* f. *minor* Brun & Héribaud, *Cocconeis scutellum* var. *minutissima* M.Peragallo, *Cocconeis speciosa* Héribaud and *Cocconeis trilineatus* M.Peragallo & Héribaud. Moreover, two taxa that have been nowadays often registered in central France (Massif Central) and whose identity was obscure are here discussed: *Cocconeis rouxii* Héribaud & Brun and its variety *Cocconeis rouxii* f. *minor* M.Peragallo & Héribaud.

By the time of Héribaud, *Cocconeis rouxii* was recorded at many localities of the Auvergne region: Héribaud (1893, p. 45) observed it as fossil (at *Ponteix*) and as well living forms in several sources in including Puy-de-Dôme (*Source à Saint-Saturnin, Vallée de Chaudefour au Mont-Dore*) and the Cantal region (*Farges, Paulhac, Plomb du Cantal* and *Puy Mary*). The type of habitat mentioned by Héribaud is “*Eaux vives des montagnes*”. Shortly after its description, Cleve (1895, p.169) makes the first record of the species under “*Cocconeis placentula* Ehrenberg var. *rouxii* (Brun & Héribaud) Cleve”, without further details or illustrations. The variety *minor* was registered again by Héribaud (1902) in his publication concerning the *fossil* diatoms of Auvergne, from a sample collected at the *Joursac* deposit (*Cantal*). The nominate species was registered again in Héribaud (1920) at the *Travertins du Royat* (Puy de Dôme), in samples identified by the Danish phycologist Ernst Østrup.

Cocconeis rouxii has been treated as a variety under *Cocconeis placentula* since then (see Cleve 1895, Hustedt 1930, Krammer & Lange-Bertalot 1991, 2004) and its identity is somewhat obscure in the literature. The original material was investigated by Holmes et al. (1982), but his examinations of material gathered by Héribaud from Saint-Saturnin and

deposited in the British Museum (Natural History) were far inconclusive because the diatoms in this sample were badly eroded.

While observing samples from freshwater sources in the Auvergne region (Beauger et al. 2015, 2016, 2019) we have found a common freshwater *Cocconeis* that we have initially identified as an unknown species, until a deeper search in the literature led us to the name *Cocconeis rouxii*. Since there is no clear understanding or illustrations of this species in the literature, we provide here a detailed historical bibliographic revision as well as a wide morphological account of the variability of this species with LM and SEM illustrations.

Material and Methods

The sample here analysed in details comes from the same region where *C. rouxii* was originally described, i.e. the Auvergne region. The spring Bernadette is situated in the Cézaillier area near the city of Saint-Alyre-ès-Montagne at an altitude of 1317 m (Fig 1). The Cézaillier is located in the Massif Central. From a geological point of view, Cézaillier is made up primarily of a metamorphic Variscan basement. Two main types of rocks are present: 1) bedrock with gneiss, amphibolites, migmatites; 2) volcanic deposits of the lava plateau (Feuga, 1987; Cantagrel et al. 1987; Négrel et al. 1997). The spring is rheocrene (i.e. flowing spring) and emerges in a pasture (Fig. 1d).

Dissolved oxygen (%), pH, conductivity ($\mu\text{S cm}^{-1}$) and water temperature ($^{\circ}\text{C}$) were measured using a WTW Multiline P4. Water samples were collected for further chemical analysis in the laboratory. Water samples from the sources in France were filtered using Whatmann GF/F filters before ionic chromatography (Dionex ICS 1500) analysis. The concentrations in lithium, sodium, ammonium, potassium, magnesium, calcium, fluoride, chloride, bromine, nitrate, phosphate, sulphate and carbonate were measured (mg l^{-1}) (Table 1).

The terminology recommended in Ross et al. (1979), Holmes et al. (1982) and Round et al. (1990) was used for the description of frustule features. The sternum and raphe–sternum valves are identified as SV and RSV, following Romero & Jahn (2013). Striae density was counted at the center of the valve face and, if the striae were markedly radiate, also at the margin opposite the center of the valve. In the species amendment description, AA is used for the apical axis, TA for the transapical axis.

94 Table 1: Values of physical and chemical parameters from the Bernadette spring on 19 April 2017.

Parameter	
Altitude (m)	1317.82
Br ⁻	-
Conductivity ($\mu\text{S cm}^{-1}$)	73
pH (pH units)	6.78
Temperature ($^{\circ}\text{C}$)	6.10
Oxygen (%)	85
Li ⁺ (mg L^{-1})	-
Na ⁺ (mg L^{-1})	3.38
NH ₄ ⁺ (mg L^{-1})	0.07
K ⁺ (mg L^{-1})	1.43
Mg ²⁺ (mg L^{-1})	1.98
Ca ²⁺ (mg L^{-1})	6.42
F ⁻ (mg L^{-1})	0.09
Cl ⁻ (mg L^{-1})	2.74
NO ₃ ⁻ (mg L^{-1})	4.34
NO ₂ ⁻ (mg L^{-1})	<0.05
PO ₄ ³⁻ (mg L^{-1})	0.04
HCO ₃ ⁻ (mg L^{-1})	31.20
SO ₄ ²⁻ (mg L^{-1})	3.07

Results

Cocconeis rouxii Héribaud & Brun *emend.* C.E.Wetzel & Ector (Figs 2–39)

Héribaud (1893, *Les Diatomées d'Auvergne*, pg. 45, plate 1, fig. 3)

Heterotypic synonyms: $\equiv$ *Cocconeis rouxii* f. *minor* M. Peragallo & Héribaud in Héribaud 1893, p. 46; $\equiv$ *Cocconeis rouxii* var. *minor* (M. Peragallo & Héribaud in Héribaud) Héribaud 1903, p. 4; $\equiv$ *Cocconeis placentula* var. *rouxii* Cleve 1895, Synopsis of the naviculoid Diatoms, part. II, pág. 169.

Heterotypic synonym: = *Cocconeis grosii* Héribaud (1920, pl. 7, fig. 43).

Amended description:

The valves are usually elliptic (Figures 2–6) with smaller specimens showing slightly cuneate apices (Figures 8–11); AA: 18.0–55.0 μm , TA: 12.5–37.5 μm . The SV (Figures 2–12, 25–29) is convex near the margin but depressed towards the sternum (Figures 26, 27). It bears about five to seven apical striae with strongly irregular zigzag longitudinal pattern on each hemivalve, concave toward the relatively wide, linear sternum. Striae (14–16 in 10 μm) are uniseriate, mostly radiate and are slightly curved towards the valve apices (Figure 6), and consist of alveoli with roundish internal foramina (Figure 29). Externally the areolae show high variability including transapical slightly elongated but rounded (Figure 25) to transapically elongated areolae with the outer openings single foramina but a few constricted to various degrees (Figures 26–28). The areolae in the SV mantle are thinner and always elongated showing higher density and regular space between them (i.e. rounded/elongated to almost linear). Sometimes the lack of areolae is visible in the circumference of the SV valve (Figures 2, 25 and 28). The valvocopula bears irregularly distributed fimbriae (Figures 13, 15, 20, 29 and 33–38). The fimbriae are thickened, sometimes bulbous projections of the valvocopula, which is closed at the apex (Figures 35 and 36). These vary in length and do not always reach the broad thickened region lying inward from the edge of the valve (Figures 33 and 38). Those that do reach this thickened region have not been observed to extend inward beyond the mid-point of this inner ridge. The concave RSV (Figure 30) has a rectilinear raphe, which ends on the internal side of the submarginal hyaline area (Figures 13 and 15). A small elliptical central area is observed (Figures 16–19). Striae are uniseriate, 17–23 in 10 μm , parallel in the middle, radiate toward the valve apices, slightly curved (Figures 11 and 16), interrupted by a submarginal hyaline area (Figures 16–19). Areolae from the valve face are sometimes missing (Figures 17 and 30) giving an aspect of irregular distribution. Straight raphe with external drop-like shape ends (proximal and terminal) are conspicuous (Figures 30 and 31). Two to three marginal areolae are slightly separated from those of the valve face by a

submarginal hyaline area (Figures 30–32). The internal areola openings are occluded (Figure 39), with small struts extending from the virgae, overlying the internal faces of the vimines (Figures 38 and 39). A small helictoglossa reaches the internal border of the submarginal hyaline area (Figures 32 and 39). Proximal raphe endings (deflected to opposite directions) are located in a conspicuous central silica nodule (Figures 32, 33 and 35).

Discussion and conclusions

After its initial findings in the Auvergne region, France (Héribaud 1893, 1902), the species was found in Austria by Handmann (1914) who first expanded its geographical range. This author had his material identified by M. Peragallo who specifically highlighted *Cocconeis rouxii* and its appearance as a “poorly known diatom” in the Danube area in the vicinity of Linz, the reason why the species was treated in more detail in this publication. Héribaud (1920) in the third publication concerning diatoms from the Auvergne focused on the diatom flora from calcareous rocks deposited from mineral springs (i.e. known as travertines, “*Les Diatomées des Travertins d’Auvergne*”), and has signalled *Cocconeis rouxii* at the *Travertin de Royat*. In the same publication he described *Cocconeis grosii* Héribaud (1920, pl. 7, fig. 43) explaining that the new species only differed from *C. rouxii* by not having the fimbriate valvocopulae: “*Se distingue de notre Cocconeis rouxii, par l’absence de nodules sur l’anneau marginal, par ses stries moins serrées, par l’aire axiale plus développée, surtout autour du nodule central et par la ponctuation des stries transversales*” (Héribaud 1920).

As demonstrated by Holmes, Crawford, and Round (1982) this characteristic is not a fixed element and can be observed separately from the valves (i.e. Figures 13, 20, 23, 29 and 33–38). Thus, since the species has been described without details of the SV (only the RSV is shown) and this being the only criterion to separate both species, we consider *C. grosii* to be a heterotypic (taxonomic) synonym.

Hustedt (1930, 190), followed the concept defined by Cleve (1895), i.e. that **C. rouxii** should be considered a variety of *Cocconeis placentula* Ehrenberg, and lists the species in the freshwater flora of Europe, noting that the striations in both valves are less clearly marked (deutlicher) on the rapheless valve. In the following years the species was observed by several other prominent diatomists such as Amossé (1932) and Manguin (1954) who observed the species in France at the mouth of the Brivet River near Saint-Nazaire (Loire-Atlantique department, Pays de la Loire region) and in the mud from the bottom of Lake Pavin (Puy-de-Dôme department, Auvergne-Rhône-Alpes region). In the following years, Hustedt (1942)

and Cleve-Euler (1953) mentioned the species for Sweden, Margalef (1953) observed *C. rouxii* in the Balears Islands (Mallorca), while Messikommer (1954, 16) found *C. placentula* var. *rouxii* in Switzerland at high altitude small mountain rivers.

Hustedt (1959) and subsequently Krammer and Lange -Bertalot (1991) vaguely mention *C. rouxii* still as a variety of *C. placentula*. The long-lasting discussions (see Monnier et al. 2007) about the identity of *C. placentula* and its varieties have only recently been settled following the typification proposed by Jahn, Wolf-Henning, and Romero (2009) and Romero and Jahn (2013), but in none of these publications has *C. rouxii* appeared to be circumscribed or deeply investigated. Romero and Jahn (2013, 6) asserts that *Cocconeis rouxii* var. *euglypta* (Ehrenberg) Héribaude is a homotypic synonym of *C. euglypta* Ehrenberg. Based on our ultrastructural analysis from populations coming from the Auvergne region, this is not sustainable and *C. rouxii* seems to be an independent species, mainly concerning the features already used by Héribaude to separate the species (i.e. coarse areolae and conspicuous valvocopulae).

Outside Europe, the taxon was first cited in Chile by Frenguelli (1936), who worked with fossil material from the Atacama Desert. Frenguelli l.c. transferred *Cocconeis intermedia* Héribaude & M.Peragallo in Héribaude to a varietal level under *Cocconeis rouxii* var. *intermedia* Frenguelli, besides describing its own variety from the Calama Desert: *Cocconeis rouxii* var. *calamae* Frenguelli, another name that has rarely been used. Further research by Frenguelli (1945) in Argentina (Platense deposit) and by Orlando (1966) has also mentioned *C. rouxii* for South America. In the USA the species has been identified in the Great Lakes region (Kreis and Stoermer 1979; Stoermer, Schelske, and Wolin 1990; Stoermer, Kreis, and Andresen 1999), Alaska (Foged 1981) and Hawaii Islands (Fungladda, Kaczmarska, and Rushforth 1983). The illustrations provided by Kingston (2003, 624, fig. 14D) of *Cocconeis placentula* var. *rouxii* seem to correspond to yet another species. The only Asian record of the species is from Japan (Koba-Yashi 1957, 72). The species has been cited to Lake Tanganyika by Caljon and Cocquyt (1992, pl. 3, p. 147, fig. 16), Cocquyt (1998, 44) and Cocquyt (2000, 144), however the provided illustrations do not seem to correspond with the populations found in the Auvergne region. Doubtful records are also mentioned in Egypt (El Shoubaky and Amin 2007, 280; Shaaban-Dessouki, Deyab, and Mofeed 2004, 26). Although most of the recent records are from the Holarctic region (Russia mainly), most of its citations are without comprehensive illustrations making these records unverifiable or doubtful (e.g. Antsiferova and Borisova 2009, 91; Chekryzheva 2012, 64; Makarevi 2012, 35; Antsiferova 2013, 110;

Pomazkina, Rodionova, and Makarevich 2013a, 296, 2013b, 206; Petrovska and Stojanovski 2007, 286; Yatsenko-Stepanova, Ignatenko, and Nemtseva 2014, 6; Yatsenko-Stepanova et al. 2015a, 50, 2015b, 84; Antsiferova 2018, 275; Niyatbekov and Barinova 2008, 305). In none of the mentioned publications could we confirm the presence of the species.

Cocconeis rouxii has not been included in the last version of the freshwater diatoms from Europe by Lange-Bertalot et al. (2017), but our own observations have confirmed the species frequently (sometimes dominant) present in samples from France, namely the Limousin and Auvergne regions, but also in parts of Languedoc-Roussillon, Midi-Pyrenees and Rhone-Alpes. All regions are in the general area of the Massif Central, showing that the species seems to be restricted to this type of geological formation (at least in France). To date, we could not find in the literature images that would correspond to *C. rouxii* except from the original drawings made by Héribaude himself in 1893, and the recent illustrations provided by Peeters and Ector (2018, 90, figs. 1–14, as *Cocconeis* sp.1) from the Morvan mountainous massif, Nièvre department, Bourgogne-Franche-Comté Region, France.

The coarse areolae pattern is similar to the ones found in *Cocconeis pseudolineata* (Geitler) Lange-Bertalot in Werum and Lange-Bertalot (2004, 133). The typical zigzag areolar arrangement can be recognized as a constant feature among different species, and in *C. rouxii* the areolation patterns are quite constant, with coarse rounded areolae and valvocopulae with thick irregularly distributed and conspicuous fimbriae. Few similar *Cocconeis* species are comparable to *C. rouxii*. One of them is *Cocconeis egregia* Gerd Moser, Steindorf, and Lange-Bertalot (1995, 60, 61, pl. 13, figs. 1–9) which shows the same coarse areolae pattern on the SV. However, its RSV are quite distinct having longer areolae surrounding the valve and distinct valvocopulae with more regular smaller fimbriae. Héribaude (1893) described a variety minor for *C. rouxii* which we here consider to belong to the same species following the cell diminution series.

In the Auvergne, *C. rouxii* was also observed in the wildlife reserve of Chastreix-Sancy in different rheocene springs (Bladanet, Bois de la Tège) situated at an altitude > 1200 m. With regard to the spring Bernadette, the water was poorly mineralized (conductivity < 120 $\mu\text{S}\cdot\text{cm}^{-1}$), well oxygenated and contained low nutrient levels (nitrates and phosphates concentrations) (Table 1). Due to the geological context, the pH is acidic in all springs. In the spring Bernadette and in two other springs of the wildlife reserve, *Cocconeis rouxii* was living as epilithic. The dominant co-occurring species (>5%) were *Crenotia thermalis* (Rabenhorst) Wojtal, *Planothidium lanceolatum* (Brébisson ex Kützing) Lange-Bertalot, *Planothidium curtistriatum* C.E.Wetzel & Ector in Wetzel et al. (in press). In the wildlife reserve of

233 Chastreix-Sancy, among the dominant species (>5%) *Cocconeis rouxii* was associated with
234 *Diatoma mesodon* (Ehrenberg) Kützing, *Navicula exilis* Kützing, *Planothidium lanceolatum*
235 and *Sellaphora atomoides* C.E.Wetzel & Van de Vijver.
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247 and Technology. Contribution: conceived the idea, preparation of images, bibliographic
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Fig. 1. Location of the Bernadette water source. a: France; b: location of the Auvergne region; c: four main Departments showing the small creek at the Bernadette spring (d), that runs into the Allier river.

Figs 2–12. *Cocconeis rouxi*, SV. Figs 2–4. Elliptical valve showing the largest specimens on the sample. Figs 5 & 7. Original drawings from Héribaud (1893, pl 1, fig. 3c). Note the straight wide axial area and the irregular round areolae on the valve face. Fig. 6. Elliptical valve with a rather regular spaced areola. Figs 8–12: Smaller specimens showing slightly cuneate apices.

Figs 13-24. *Cocconeis rouxii*, RSV. Figs 13-14. Large valves that correspond to the drawings (Fig. 15) provided by Héribaud (1893, pl. 1, fig. 3d) showing the valvocopulae with irregular fimbriae and a wide space between the hyaline area and the valve border. Figs 16-24: Valve diminution series showing the size variability and shape outline. Note the lack of areolae in the central portion of the valves as well as the small central area present. Large terminal and proximal raphe end with large drop-like aperture. Fig. 20. Closed fimbriate valvocopulae.

Figs 25-29. *Cocconeis rouxii*, SV. Fig. 25. External view showing irregularly distributed areolae. Note the hyaline surrounding depression near the valve margins, commonly observed in this species. Fig. 26. Tilted view showing the groove in the axial area and slightly elongated and constricted areolae. Note the higher density of areolae near the valve mantle. Fig. 27. Valve with areolae slightly constricted. Note the variability of the areolae near the valve mantle, now showing drop-like shaped. Fig. 28. Specimen with strongly irregular spaced areolae and highly silicified valve surface. Fig. 29. Internal view showing small rounded foramina. Note the closed fimbriate valvocopulae still attached to the SV.

Figs 30-34. *Cocconeis rouxii*, RSV. Figs 30-31. External view showing strongly silicified valves. Wide hyaline area interrupting the hymenate areolae. Number of areolae near the margins varying from 2 to 3. Terminal and proximal raphe ends drop-like shaped. Fig. 32. Internal view showing the helictoglossae and the proximal raphe ends deflected to opposite sides. Fig. 33. Internal view showing surface with attached valvocopula with and irregular and thickened fimbriae. Note the expanded central area. Fig. 34. Upside-down view of the closed valvocopula showing the negative mold of the mantle areolae, which are highlighted in Héribaude's drawings.

Figs 35-39. *Cocconeis rouxii*, RSV and valvocopulae. Figs 35-36. Internal view of RSV and valvocopulae. Fig. 37. Fimbriate valvocopula. Fig. 38. Internal view showing small rounded foramina. Note the strongly silicified fimbriae still attached to the RSV. Fig. 39. Internal view showing the helictoglossae.