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

3
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11
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).

22
23 **KEYWORDS:** diatoms, springs, mineral waters, epilithon, epipelon.

24
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26 **Introduction**

27 Joseph Héribaud (1841-1918) was an honorary member of the French botanical
28 society (*Société de botanique de France*) and one of the most distinguished French diatomists
29 from the 19th century who described hundreds of diatom taxa (see Kociolek et al. 2018). His
30 well-known books “*Les Diatomées d’Auvergne*”, “*Les Diatomées Fossiles d’Auvergne*” and
31 “*Les Diatomées de Travertins d’Auvergne*”, the last one a posthumous *oeuvre*, are examples
32 of fine and detailed taxonomy carried out by him. In his first remarkable account (Héribaud
33 1893, in collaboration with J.Brun and M.Peragallo), Héribaud described several species that
34 are poorly known today, or whose names remain yet rarely used. Among the taxa described
35 by or *in* Héribaud work’s, several *Cocconeis* from freshwater environments are highlighted.
36 In Héribaud (1893) several species were introduced as new, such as *Cocconeis intermedia*
37 Héribaud & M.Peragallo, *Cocconeis intermedia* f. *minor* M.Peragallo & Héribaud, *Cocconeis*
38 *pediculus* var. *rotunda* Brun & Héribaud, *Cocconeis placentula* f. *minor* Brun & Héribaud,
39 *Cocconeis scutellum* var. *minutissima* M.Peragallo, *Cocconeis speciosa* Héribaud and
40 *Cocconeis trilineatus* M.Peragallo & Héribaud. Moreover, two taxa that have been nowadays
41 often registered in central France (Massif Central) and whose identity was obscure are here
42 discussed: *Cocconeis rouxii* Héribaud & Brun and its variety *Cocconeis rouxii* f. *minor*
43 M.Peragallo & Héribaud.

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

56 *Cocconeis rouxii* has been treated as a variety under *Cocconeis placentula* since then
57 (see Cleve 1895, Hustedt 1930, Krammer & Lange-Bertalot 1991, 2004) and its identity is
58 somewhat obscure in the literature. The original material was investigated by Holmes et al.
59 (1982), but his examinations of material gathered by Héribaud from Saint-Saturnin and

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

62

63 While observing samples from freshwater sources in the Auvergne region (Beauger et al.
64 2015, 2016, 2019) we have found a common freshwater *Cocconeis* that we have initially
65 identified as an unknown species, until a deeper search in the literature led us to the name
66 *Cocconeis rouxii*. Since there is no clear understanding or illustrations of this species in the
67 literature, we provide here a detailed historical bibliographic revision as well as a wide
68 morphological account of the variability of this species with LM and SEM illustrations.

69

70 **Material and Methods**

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

79 Dissolved oxygen (%), pH, conductivity ($\mu\text{S cm}^{-1}$) and water temperature ($^{\circ}\text{C}$) were
80 measured using a WTW Multiline P4. Water samples were collected for further chemical
81 analysis in the laboratory. Water samples from the sources in France were filtered using
82 Whatmann GF/F filters before ionic chromatography (Dionex ICS 1500) analysis. The
83 concentrations in lithium, sodium, ammonium, potassium, magnesium, calcium, fluoride,
84 chloride, bromine, nitrate, phosphate, sulphate and carbonate were measured (mg l^{-1}) (Table
85 1).

86

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

93

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

95

96 **Results**

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

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

99

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

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

104

105 **Amended description:**

106 The valves are usually elliptic (Figures 2–6) with smaller specimens showing slightly cuneate
107 apices (Figures 8–11); AA: 18.0–55.0 µm, TA: 12.5–37.5 µm. The SV (Figures 2–12, 25–29)
108 is convex near the margin but depressed towards the sternum (Figures 26, 27). It bears about
109 five to seven apical striae with strongly irregular zigzag longitudinal pattern on each
110 hemivalve, concave toward the relatively wide, linear sternum. Striae (14–16 in 10 µm) are
111 uniseriate, mostly radiate and are slightly curved towards the valve apices (Figure 6), and
112 consist of alveoli with roundish internal foramina (Figure 29). Externally the areolae show
113 high variability including transapical slightly elongated but rounded (Figure 25) to
114 transapically elongated areolae with the outer openings single foramina but a few constricted
115 to various degrees (Figures 26–28). The areolae in the SV mantle are thinner and always
116 elongated showing higher density and regular space between them (i.e. rounded/elongated to
117 almost linear). Sometimes the lack of areolae is visible in the circumference of the SV valve
118 (Figures 2, 25 and 28). The valvocopula bears irregularly distributed fimbriae (Figures 13, 15,
119 20, 29 and 33–38). The fimbriae are thickened, sometimes bulbous projections of the
120 valvocopula, which is closed at the apex (Figures 35 and 36). These vary in length and do not
121 always reach the broad thickened region lying inward from the edge of the valve (Figures 33
122 and 38). Those that do reach this thickened region have not been observed to extend inward
123 beyond the mid-point of this inner ridge. The concave RSV (Figure 30) has a rectilinear
124 raphe, which ends on the internal side of the submarginal hyaline area (Figures 13 and 15). A
125 small elliptical central area is observed (Figures 16–19). Striae are uniseriate, 17–23 in 10 µm,
126 parallel in the middle, radiate toward the valve apices, slightly curved (Figures 11 and 16),
127 interrupted by a submarginal hyaline area (Figures 16–19). Areolae from the valve face are
128 sometimes missing (Figures 17 and 30) giving an aspect of irregular distribution. Straight
129 raphe with external drop-like shape ends (proximal and terminal) are conspicuous (Figures 30
130 and 31). Two to three marginal areolae are slightly separated from those of the valve face by a

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

136

137 *Discussion and conclusions*

138 After its initial findings in the Auvergne region, France (Héribaud 1893, 1902), the
139 species was found in Austria by Handmann (1914) who first expanded its geographical range.
140 This author had his material identified by M. Peragallo who specifically highlighted
141 *Cocconeis rouxii* and its appearance as a “poorly known diatom” in the Danube area in the
142 vicinity of Linz, the reason why the species was treated in more detail in this publication.
143 Héribaud (1920) in the third publication concerning diatoms from the Auvergne focused on
144 the diatom flora from calcareous rocks deposited from mineral springs (i.e. known as
145 travertines, “*Les Diatomées des Travertins d’Auvergne*”), and has signalled *Cocconeis rouxii*
146 at the *Travertin de Royat*. In the same publication he described *Cocconeis grosii* Héribaud
147 (1920, pl. 7, fig. 43) explaining that the new species only differed from *C. rouxii* by not
148 having the fimbriate valvocopulae: “*Se distingue de notre Cocconeis rouxii, par l’absence de*
149 *nodules sur l’anneau marginal, par ses stries moins serrées, par l’aire axiale plus développée,*
150 *surtout autour du nodule central et par la ponctuation des stries transversales*” (Héribaud
151 1920).

152 As demonstrated by Holmes, Crawford, and Round (1982) this characteristic is not a fixed
153 element and can be observed separately from the valves (i.e. Figures 13, 20, 23, 29 and
154 33–38). Thus, since the species has been described without details of the SV (only the RSV is
155 shown) and this being the only criterion to separate both species, we consider *C. grosii* to be a
156 heterotypic (taxonomic) synonym.

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

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

168

169 Hustedt (1959) and subsequently Krammer and Lange -Bertalot (1991) vaguely mention *C.*
170 *rouxii* still as a variety of *C. placentula*. The long-lasting discussions (see Monnier et al.
171 2007) about the identity of *C. placentula* and its varieties have only recently been settled
172 following the typification proposed by Jahn, Wolf–Henning, and Romero (2009) and Romero
173 and Jahn (2013), but in none of these publications has *C. rouxii* appeared to be circumscribed
174 or deeply investigated. Romero and Jahn (2013, 6) asserts that *Cocconeis rouxii* var. *euglypta*
175 (Ehrenberg) Héribaud is a homotypic synonym of *C. euglypta* Ehrenberg. Based on our
176 ultrastructural analysis from populations coming from the Auvergne region, this is not
177 sustainable and *C. rouxii* seems to be an independent species, mainly concerning the features
178 already used by Héribaud to separate the species (i.e. coarse areolae and conspicuous
179 valvocopulae).

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

199 Pomazkina, Rodionova, and Makarevich 2013a, 296, 2013b, 206; Petrovska and Stojanovski
200 2007, 286; Yatsenko-Stepanova, Ignatenko, and Nemtseva 2014, 6; Yatsenko-Stepanova et al.
201 2015a, 50, 2015b, 84; Antsiferova 2018, 275; Niyatbekov and Barinova 2008, 305). In none
202 of the mentioned publications could we confirm the presence of the species.

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

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

224 In the Auvergne, *C. rouxii* was also observed in the wildlife reserve of Chastreix-Sancy in
225 different rheocene springs (Bladanet, Bois de la Tège) situated at an altitude > 1200 m. With
226 regard to the spring Bernadette, the water was poorly mineralized (conductivity < 120
227 $\mu\text{S}\cdot\text{cm}^{-1}$), well oxygenated and contained low nutrient levels (nitrates and phosphates
228 concentrations) (Table 1). Due to the geological context, the pH is acidic in all springs. In the
229 spring Bernadette and in two other springs of the wildlife reserve, *Cocconeis rouxii* was living
230 as epilithic. The dominant co-occurring species (>5%) were *Crenotia thermalis* (Rabenhorst)
231 Wojtal, *Planothidium lanceolatum* (Brébisson ex Kützing) Lange-Bertalot, *Planothidium*
232 *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.
236

237 **Disclosure statement**

238 No potential conflict of interest was reported by the authors.

239

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243

244 **Notes on contributors**

245

246 *Carlos E. Wetzel*: Botanist and Research Associate at the Luxembourg Institute of Science
247 and Technology. Contribution: conceived the idea, preparation of images, bibliographic
248 research, writing and edition of the manuscript.

249 *Aude Beauger*: Botanist and Researcher at the Université Clermont Auvergne. Contribution:
250 collection of samples, performed the chemical analyses, edition of the manuscript.

251 *Luc Ector*: Botanist and Senior Researcher at the Luxembourg Institute of Science and
252 Technology. Contribution: discussion of results, bibliographic research, revision and edition
253 of the manuscript.

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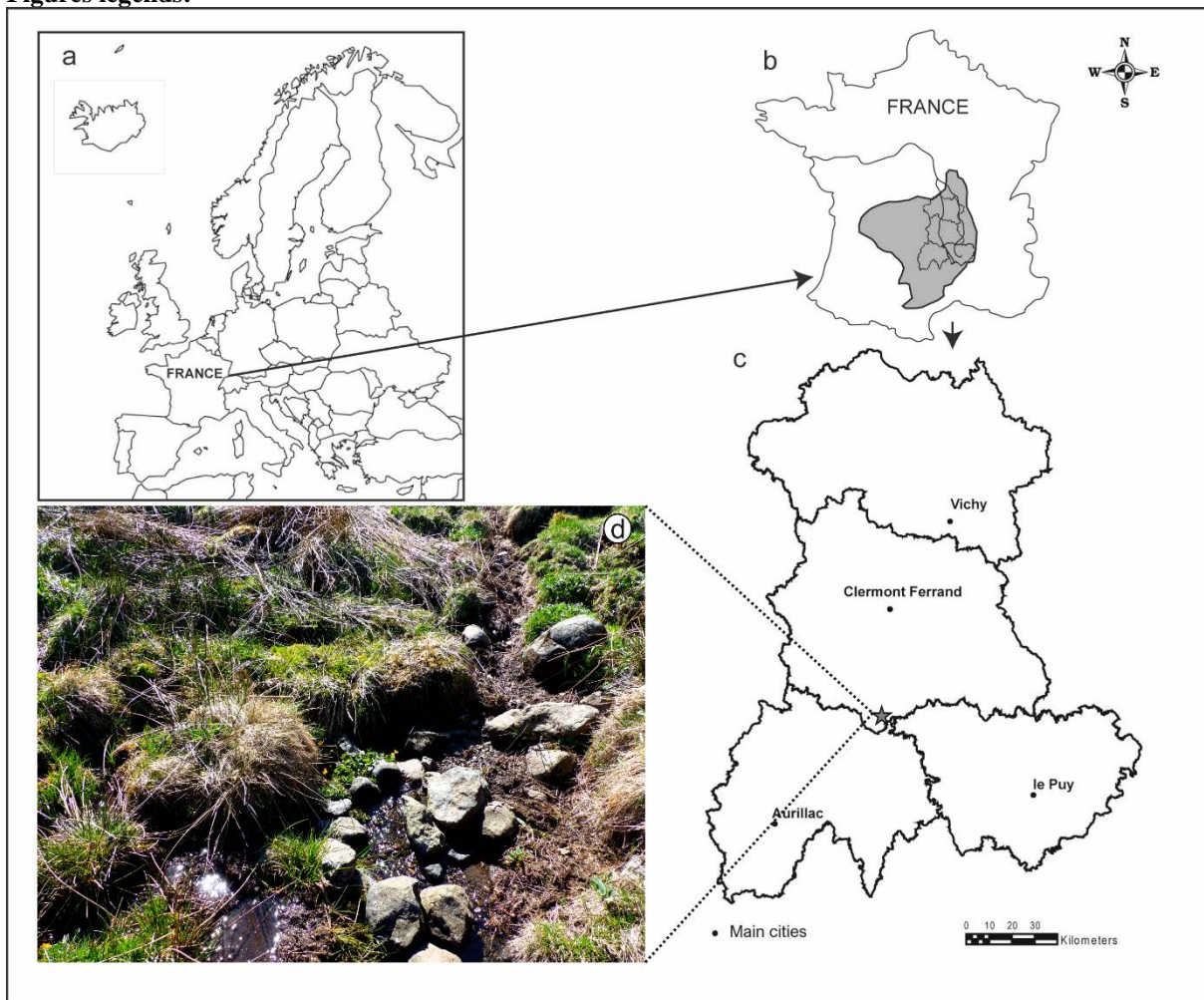
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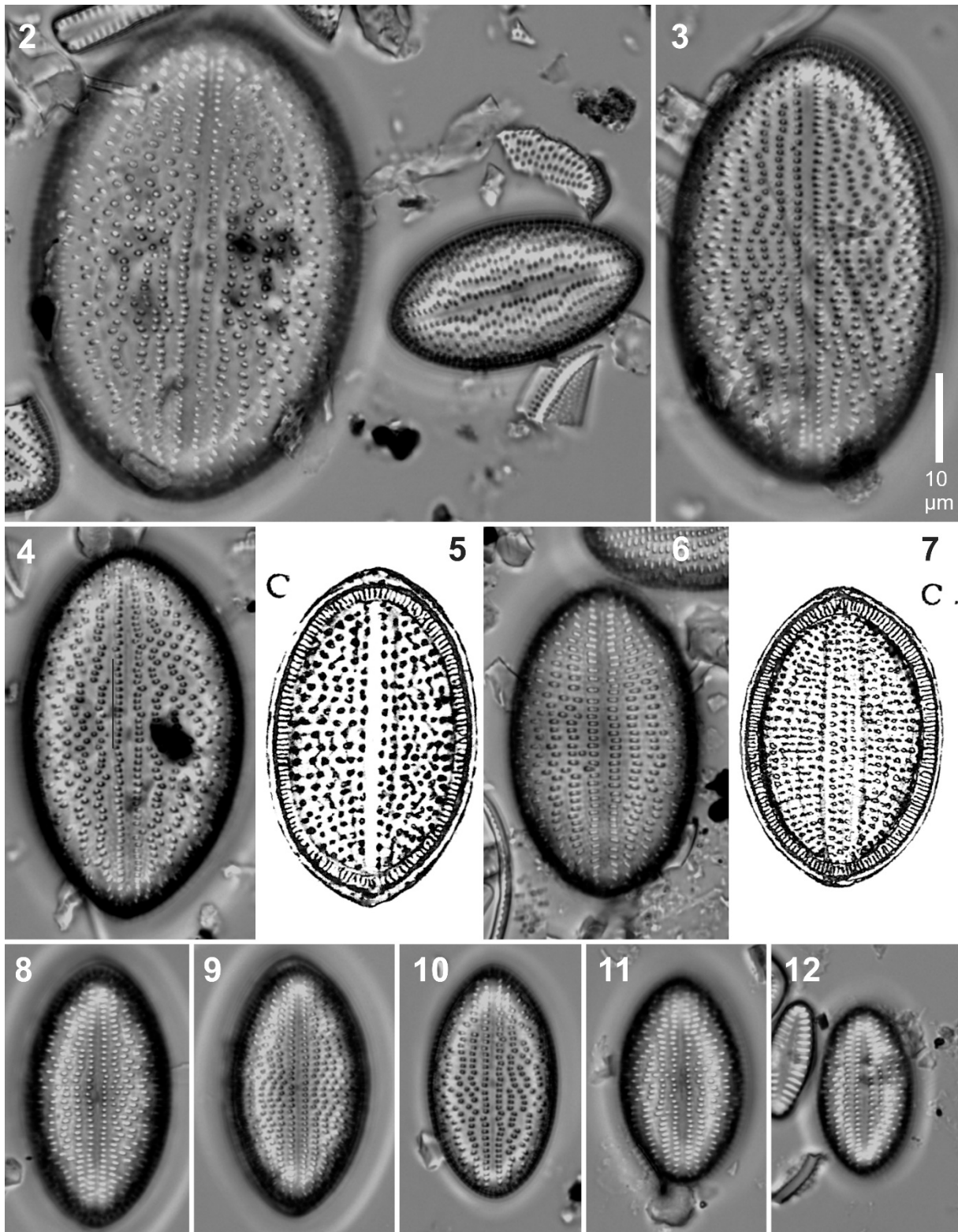
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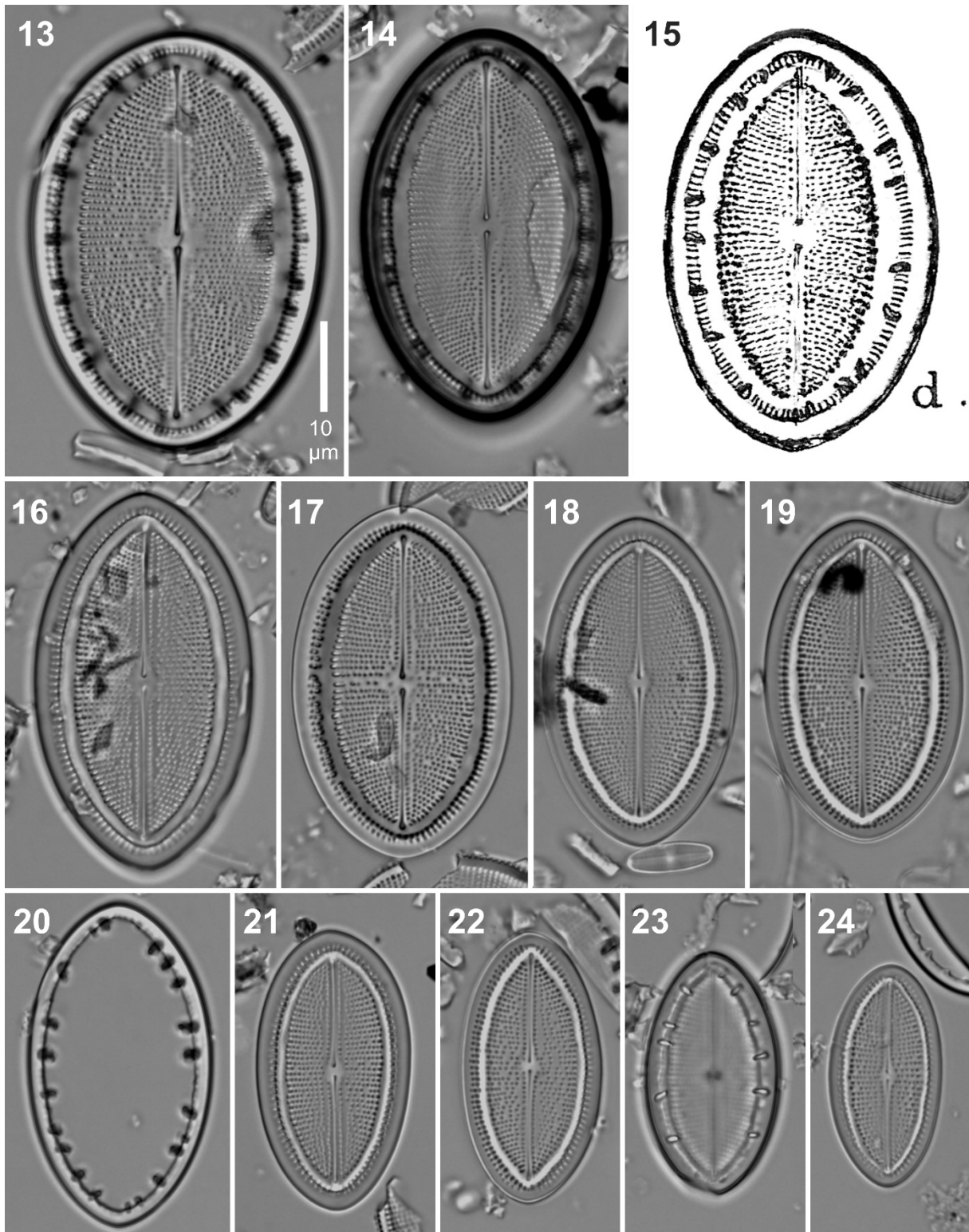
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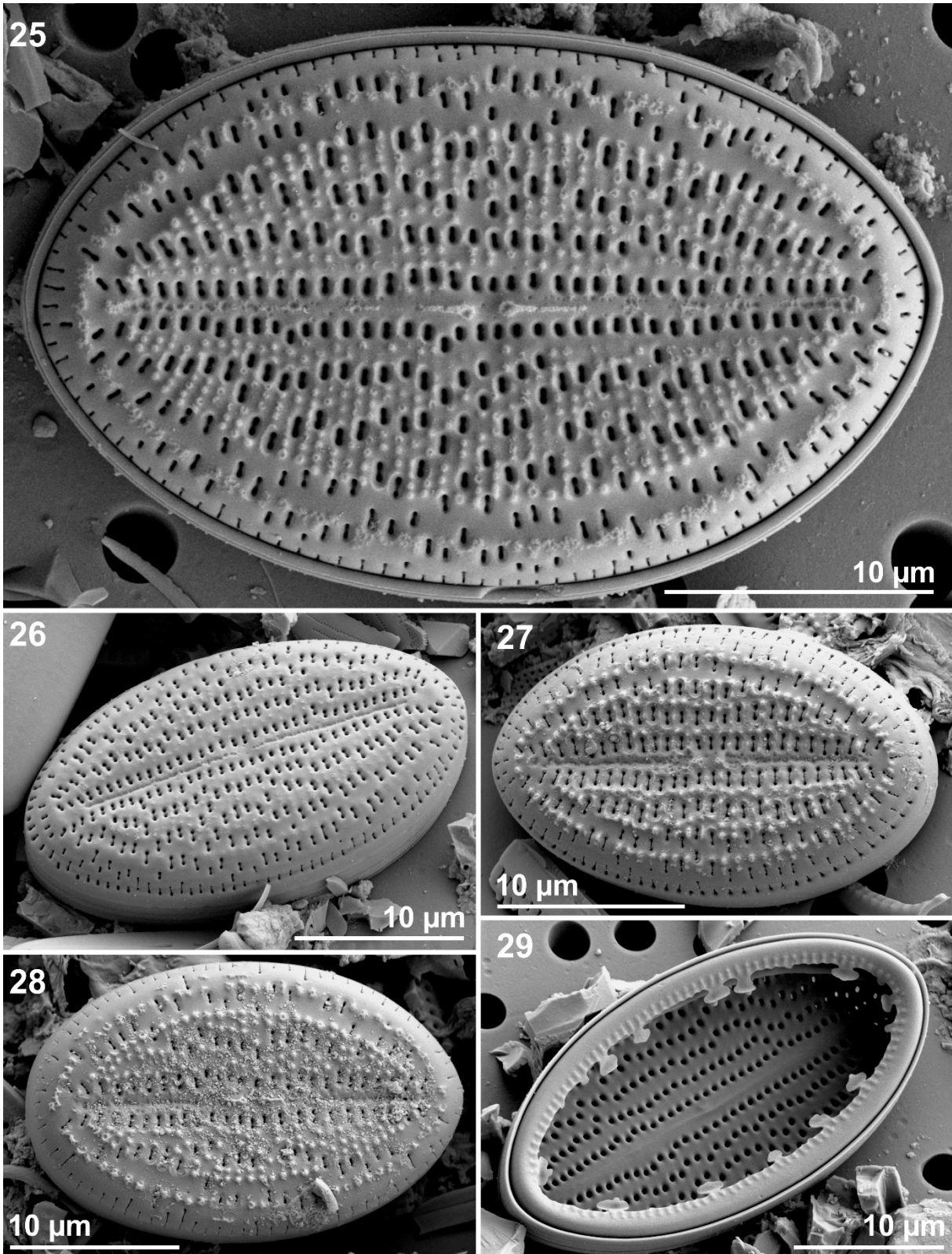
429 **Fig. 1.** Location of the Bernadette water source. a: France; b: location of the Auvergne region; c: four main
430 Departments showing the small creek at the Bernadette spring (d), that runs into the Allier river.
431



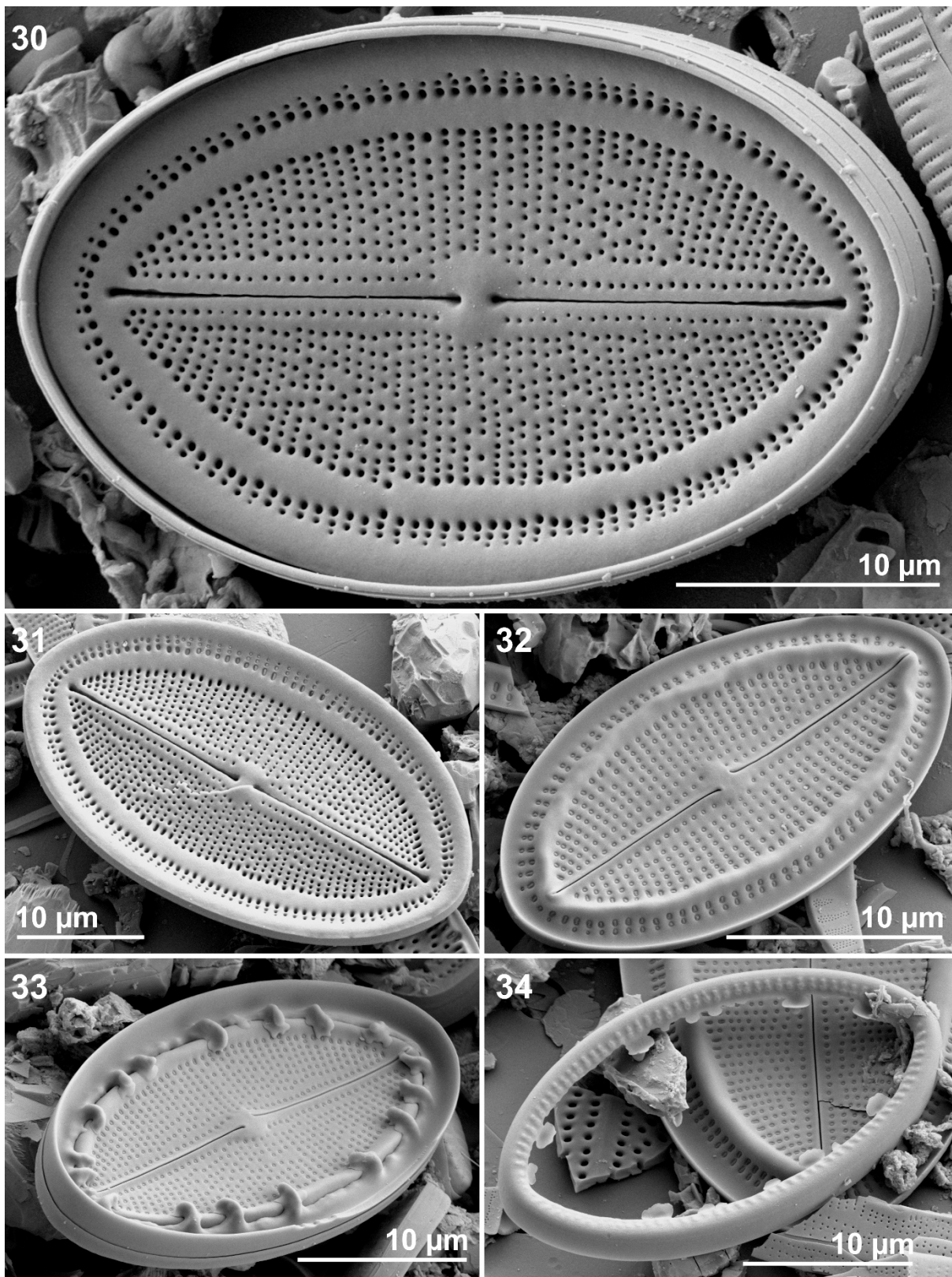
432
 433 **Figs 2–12. *Cocconeis rouxi*, SV.** Figs 2-4. Elliptical valve showing the largest specimens on the sample. Figs 5
 434 & 7. Original drawings from Héribaud (1893, pl 1, fig. 3c). Note the straight wide axial area and the irregular
 435 round areolae on the valve face. Fig. 6. Elliptical valve with a rather regular spaced areola. Figs 8-12: Smaller
 436 specimens showing slightly cuneate apices.



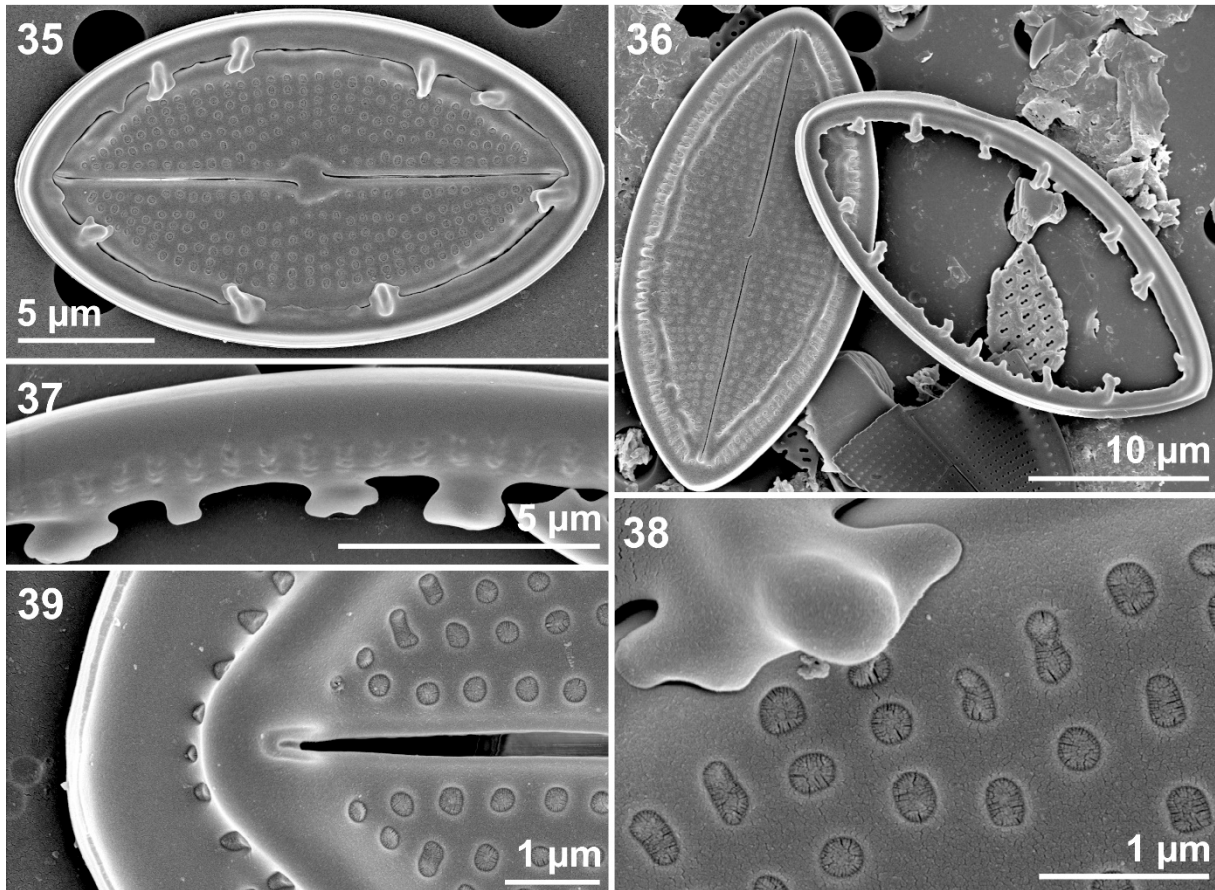
437
 438 **Figs 13-24. *Cocconeis rouxii*, RSV.** Figs 13-14. Large valves that correspond to the drawings (Fig. 15) provided
 439 by Héribaud (1893, pl. 1, fig. 3d) showing the valvocopulae with irregular fimbriae and a wide space between
 440 the hyaline area and the valve border. Figs 16-24: Valve diminution series showing the size variability and shape
 441 outline. Note the lack of areolae in the central portion of the valves as well as the small central area present.
 442 Large terminal and proximal raphe end with large drop-like aperture. Fig. 20. Closed fimbriate valvocopulae.



443
 444 **Figs 25-29. *Cocconeis rouxii*, SV.** Fig. 25. External view showing irregularly distributed areolae. Note the
 445 hyaline surrounding depression near the valve margins, commonly observed in this species. Fig. 26. Tilted view
 446 showing the groove in the axial area and slightly elongated and constricted areolae. Note the higher density of
 447 areolae near the valve mantle. Fig. 27. Valve with areolae slightly constricted. Note the variability of the areolae
 448 near the valve mantle, now showing drop-like shaped. Fig. 28. Specimen with strongly irregular spaced areolae
 449 and highly silicified valve surface. Fig. 29. Internal view showing small rounded foramina. Note the closed
 450 fimbriate valvocopulae still attached to the SV.



451
 452 **Figs 30-34. *Cocconeis rouxii*, RSV.** Figs 30-31. External view showing strongly silicified valves. Wide hyaline
 453 area interrupting the hymenate areolae. Number of areolae near the margins varying from 2 to 3. Terminal and
 454 proximal raphe ends drop-like shaped. Fig. 32. Internal view showing the helictoglossae and the proximal raphe
 455 ends deflected to opposite sides. Fig. 33. Internal view showing surface with attached valvocopula with and
 456 irregular and thickened fimbriae. Note the expanded central area. Fig. 34. Upside-down view of the closed
 457 valvocopula showing the negative mold of the mantle areolae, which are highlighted in Héribaud's drawings.
 458
 459



460
 461 **Figs 35-39. *Cocconeis rouxii*, RSV and valvocopulae.** Figs 35-36. Internal view of RSV and valvocopulae. Fig.
 462 37. Fimbriate valvocopula. Fig. 38. Internal view showing small rounded foramina. Note the strongly silicified
 463 fimbriae still attached to the RSV. Fig. 39. Internal view showing the helictoglossae.

