
Eubuliminella tenuata as a new proxy for quantifying past bottom water oxygenation

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Abstract :

In response to modern global warming and climate emergency, large oxygen-depleted oceanic areas, known as Oxygen Minimum Zones (OMZs) have been expanding for the past decades, with negative ecological and economic consequences on food chains, marine ecosystems and resources, biodiversity, and fisheries. The future evolution of these areas and their expansion for the next decades and centuries remain uncertain, and information on their past behaviour during intervals of abrupt climate change (e.g. the last Glacial / Interglacial cycles) is needed to understand the biological and physical mechanisms involved.

In this study, a new approach to quantitatively reconstruct past bottom water oxygenation (BWO) was developed, based on the relative abundance of a single benthic foraminiferal species: *Eubuliminella exilis* (Cushman 1927). A taxonomic review as well as a systematic revision of this taxa, previously assigned to the genus *Buliminella* Cushman 1911, and synonymised with *Eubuliminella exilis* (Brady 1884), was also carried out.

The method was calibrated using 25 core tops recovered from the Western North Pacific (WNP), the Eastern North Pacific (ENP), the Eastern Equatorial Pacific (EEP), Eastern South Pacific (ESP) and the Arabian Sea (AS) OMZs. It was then applied to five cores from the WNP, and ENP OMZs. Data show a similar and consistent relationship with past [O₂] values estimated by using the assemblages method developed in previous studies. We thus propose that the relative abundance of *Eubuliminella tenuata* (Cushman 1927) could be used as a global proxy for estimating past dissolved oxygenation.

Highlights

► A new method for estimating past oxygenation was developed. ► This method was calibrated by using seven worldwide core tops of known [O₂]. ► This method estimations were compared to estimations from five Quaternary sedimentary records. ► This method is based on the relative abundance of a single benthic foraminiferal species. ► Taxonomy and synonymy of this species was reviewed.

Keywords : Micropalaeontology, Palaeoceanography, Benthic foraminifera, Oxygen minimum zone, Climate change, Oxygen reconstruction

1. Introduction

Oxygen Minimum Zones (OMZs) are large oceanic regions (usually from 200-500 to 1000-1500 mbsl) defined by a dissolved oxygen content of water lower than 0.5 mL.L^{-1} (corresponding to about $20 \mu\text{mol.kg}^{-1}$; Gilly et al., 2013). Their cores usually spread into the mesopelagic zone (Paulmier and Ruiz-Pino, 2009) which accounts for 70 % of the total respiration occurring under the photic zone (Arístegui et al., 2005). These areas thus play a key role in the oxygen and carbon cycles. The oxygen deficiency in OMZs is caused by the combination of several factors: 1) high oxygen-demand linked to biological remineralization of organic matter exported from the sea surface; 2) low physical $[\text{O}_2]$ -supply due to weak water masses ventilation (Wyrтки, 1962; Paulmier and Ruiz-Pino, 2009; Gilly et al., 2013; Praetorius et al., 2015).

Recent studies show that these areas are currently in expansion. However, the future evolution of OMZs is still debated in the context of global warming and a few studies have focussed on their recent expansion that is expected to further until the end of the century (Moss et al., 2008; Stramma et al., 2008, 2010; Gilly et al., 2013; Bopp et al., 2017). The understanding and quantification of their response to climate change is thus fundamental as these areas contribute significantly to the structuring of ecosystems, biodiversity, and fisheries, and can be achieved through an investigation of their past variability. To assess and quantify the future evolution of these areas, as well as their impacts on ecosystems integrity and services, quantitative data of past bottom water oxygenation (BWO) from OMZs are needed (Gilbert, 2017; Levin, 2018).

During the last decades, several authors highlighted the benthic foraminiferal interest for reconstructing past OMZs variability as they are sensitive tracers of bottom water and pore water oxygenation (Bernhard and Reimers, 1991; Kaiho, 1994; Cannariato and Kennett, 1999; Glock et al., 2011). New studies recently investigated species assemblages (Tetard et al., 2017a; Erdem et al.,

31 2020), test porosity (Tetard et al., 2017b), morphometry (Tetard et al., 2021),
32 and geochemistry (e.g. Hoogakker et al., 2015, 2018) to produce quantitative
33 past oxygen reconstructions for the Quaternary period. Most of previous
34 studies rely on qualitative reconstructions (e.g. den Dulk et al., 1998; Can-
35 nariato and Kennett, 1999; Cannariato et al., 1999; Bubenshchikova et al.,
36 2010; Mallon, 2012; Ohkushi et al., 2013; McKay et al., 2014, 2015; Moffitt et
37 al., 2014; Bubenshchikova et al., 2015; Cardich et al., 2015; Kim et al., 2017;
38 Ovsepyan et al., 2017; Cardich et al., 2019; Erdem et al., 2020). However, as
39 these quantitative methods request at least a substantial taxonomic knowl-
40 edge, or a stereoscopic and / or a transmitted light microscope equipped with
41 a camera, we aimed at developing an approach that is easy to use, and based
42 on the specific ecological preferences of a single species regarding dissolved
43 oxygenation.

44 The choice of the *Buliminella tenuata* / *Eubuliminella exilis* species group
45 was motivated by several reasons:

- 46 1) the species or group of species has to be widespread,
- 47 2) it has to be commonly found in most of the OMZs, and be a main
48 component of the benthic foraminiferal assemblage,
- 49 3) it must depend on dissolved oxygenation upon a relatively large gra-
50 dient,
- 51 4) it has to be easily recognisable.

52 Of all the species that we have commonly encountered in the different
53 OMZs through our previous studies (e.g. *Bolivina argentea*, *B. pacifica*, *B.*
54 *seminuda*, *B. spissa*, *B. subadvena*, *Brizalina alata*, *Chilostomella oolina*,
55 *C. ovoidea*, *Globobulimina affinis*, *Takayanagia delicata*), the *Buliminella*
56 *tenuata* / *Eubuliminella exilis* species group is the best candidate as it meets
57 all the criteria. It is commonly found in OMZ areas from all over the world,
58 has a distinct relationship with dissolved oxygen (shallow infaunal species
59 that tolerates dysoxia), and is easy to distinguish (Revets, 1993; Bernhard et
60 al., 1997; Jannink et al., 1998; Cannariato and Kennett, 1999; Cannariato et
61 al., 1999; Schumacher et al., 2007; Caille et al., 2014; Cardich et al., 2015;
62 Erdem and Schonfeld, 2017; Tetard et al., 2017a; Erdem et al., 2020; Tetard
63 et al., 2021).

64 The other above-mentioned species are usually either not found in every
65 cores or limited to a specific OMZ (e.g. *Bolivina seminuda*, *B. subadvena*,
66 *Chilostomella oolina*, *C. ovoidea*, *Globobulimina affinis*), not characteristic of
67 dysoxic, but suboxic conditions and thus exhibit a complex relationship with
68 oxygen (relative abundance decreases in both dysoxic and oxic conditions;

69 e.g. *Bolivina argentea*, *B. pacifica*, *B. spissa*, *Brizalina alata*), or do not show
70 a consistent relationship with dissolved oxygen between every investigated
71 cores (e.g. *Takayanagia delicata*).

72 2. Material and methods

73 Several marine archives recovered from OMZs located in the Pacific Ocean
74 and the Indian Ocean were used for investigating the relative abundance of
75 *B. tenuata* / *E. exilis* regarding past oxygenation (see core cores location in
76 (Tetard et al., 2021, their Fig. 1). Overall, all core tops used in Tetard et al.
77 (2021) containing *Buliminella tenuata* or *Eubuliminella exilis* were used.

78 The Western North Pacific (WNP) cores SO201-2-77KL, SO201-2-85KL,
79 SO201-2-127KL, as well as minicore SO201-2-79MUC taken by a multicorer,
80 were collected from the Shirshov Ridge during R/V Sonne cruise Leg 201-2
81 in 2009 (Dullo et al., 2009). Age model of cores SO201-2-85KL and SO201-
82 2-77KL are well established and published in previous studies (Max et al.,
83 2012; Riethdorf et al., 2013; Ovsepyan et al., 2017). Regarding Core SO201-
84 2-127KL and minicore SO201-2-79MUC, only the core top samples (0-1 cm)
85 are investigated in this study.

86 Concerning the Eastern North Pacific (ENP) OMZ, cores MD02-2507,
87 MD02-2508, MD02-2519, MD02-2521C2, MD02-2525C2, and MD02-2529 were
88 retrieved during the R/V *Marion-Dufresne* MD126 MONA (IMAGES VII)
89 campaign in 2002 (Blanchet et al., 2007). Age model of these cores were re-
90 spectively published in Cartapanis et al. (2014), Arellano-Torres et al. (2015),
91 and Leduc et al. (2007, 2010).

92 Concerning the Eastern Equatorial Pacific (EEP) OMZ, cores JPC 9,
93 KAMA 8, KAMA 12 and KAMA 14 were retrieved during the research ex-
94 peditions AMADEUS, ME0005A, KNR 176-2, Y71-3, Y69-71, and PLDSII
95 (Patarroyo and Martinez, 2021).

96 Several Eastern South Pacific (ESP) samples were retrieved along the
97 Callao and Pisco transects using a mini multi-corer during R/V *SNP 2* and
98 R/V *Jos Olaya Balandra* CRIO and MiniOx cruises in 2009, 2010, and 2011.
99 They are associated with dissolved oxygen measurements using a CTDO. All
100 these ESP data were recovered from Cardich et al. (2015). From this study,
101 C1 and C2 station were not used as they are located in the inner shelf and
102 associated with sulfidic waters, a limiting condition for *B. tenuata* / *E. exilis*.

103 Regarding the Arabian Sea (AS) OMZ, Core MD04-2876 was retrieved
104 during the R/V *Marion-Dufresne* MD143 CHAMAK cruise in October 2004

105 (Pichevin et al., 2007; Boning and Bard, 2009). Age model was established
 106 in Pichevin et al. (2007) and reviewed in Bard et al. (2013).

Table 1: Core station location, depth, modern dissolved oxygen level, and relative abundance of *E. tenuata* for each investigated core top sample.

Core top station	OMZ	Site location (latitude)	Site location (longitude)	Water depth (mbsl)	[O ₂] measurement method	Modern [O ₂] mL.L ⁻¹	<i>E. tenuata</i> relative abundance (%)	Author (name, year)
MD02-2507	ENP	25°08.00'N	112°42.09'W	495	WOA2013	0.25	24.00	This study
MD02-2508	ENP	23°27.91'N	111°35.74'W	606	WOA2013	0.13	11.33	This study
MD02-2519	ENP	22°30.89'N	106°39.00'W	955	WOA2013	0.21	10.06	This study
MD02-2521C2	ENP	15°40.25'N	95°18.00'W	718	WOA2013	0.09	37.80	This study
MD02-2525C2	ENP	12°00.47'N	87°54.44'W	877	WOA2013	0.28	00.91	This study
SO201-2-79MUC	WNP	56°42.99'N	170°29.78'E	1161	WOA2013	0.83	01.25	This study
SO201-2-127KL	WNP	54°23.66'N	162°13.34'E	1440	WOA2013	1.14	01.61	This study
JPC 9	EEP	56°19.90'N	170°41.97'E	2163	WOA2009	1.65	00.33	Patarroyo and Martinez (2021)
KAMA 8	EEP	56°42.99'N	170°29.78'E	1161	WOA2009	0.83	00.32	Patarroyo and Martinez (2021)
KAMA 12	EEP	57°30.30'N	170°24.79'E	968	WOA2009	0.34	00.36	Patarroyo and Martinez (2021)
KAMA 14	EEP	54°23.66'N	162°13.34'E	1440	WOA2009	1.14	01.57	Patarroyo and Martinez (2021)
0904 C3	ESP	12°02.34'S	77°22.53'S	117	CTDO	0.11	41.10	Cardich et al. (2015)
0904 C4	ESP	12°02.93'S	77°29.01'S	143	CTDO	0.19	09.20	Cardich et al. (2015)
0904 C5	ESP	12°02.22'S	77°39.07'S	175	CTDO	0.13	37.30	Cardich et al. (2015)
0908 C4	ESP	12°02.93'S	77°29.01'S	143	CTDO	0.22	07.50	Cardich et al. (2015)
0908 C5	ESP	12°02.22'S	77°39.07'S	175	CTDO	0.19	18.00	Cardich et al. (2015)
1004 C3	ESP	12°02.34'S	77°22.53'S	117	CTDO	0.12	62.10	Cardich et al. (2015)
1004 C4	ESP	12°02.93'S	77°29.01'S	143	CTDO	0.09	21.60	Cardich et al. (2015)
1004 C5	ESP	12°02.22'S	77°39.07'S	175	CTDO	0.18	37.80	Cardich et al. (2015)
1004 P1	ESP	14°01.20'S	76°18.78'S	120	CTDO	0.07	10.90	Cardich et al. (2015)
1004 P2	ESP	14°04.32'S	76°25.20'S	180	CTDO	0.04	44.80	Cardich et al. (2015)
1004 P3	ESP	14°07.50'S	76°30.54'S	300	CTDO	0.04	14.40	Cardich et al. (2015)
1104 C5	ESP	12°02.22'S	77°39.07'S	175	CTDO	0.09	19.70	Cardich et al. (2015)
1104 P2	ESP	14°04.32'S	76°25.20'S	180	CTDO	0.04	17.20	Cardich et al. (2015)
MD04-2876	AS	24°50'57N	064°00'49E	828	WOA2013	0.17	09.12	This study

107 For each core, the core site location (latitude and longitude), water depth,
 108 and mean annual modern [O₂] according to the World Ocean Atlas 2009 and
 109 2013 datasets (Garcia et al., 2014, <http://www.nodc.noaa.gov/OC5/woa13/>)
 110 and CTDO measurements for the ESP samples, are detailed in Table 1. Core
 111 top samples of the previously-listed cores were used for calibration purposes.
 112 The benthic foraminiferal census data downcore used in this study for com-
 113 parison with other past oxygenation estimation methods originate from the
 114 manual picking of Tetard et al. (2017a, MD02-2508), Ovsepyan and Ivanova
 115 (2009, MD02-2529), Ovsepyan et al. (2017, SO201-2-85KL) Ovsepyan et al.
 116 (2021, SO201-2-77KL), and the virtual picking and automated identification
 117 of Core MD02-2519 using convolutional neural networks trained to recognised
 118 ENP OMZ benthic foraminifera in Marchant et al. (2020).

119 3. Systematic palaeontology

120 3.1. State of the art

121 A clear and unambiguous taxonomy is necessary for paleoenvironmental
 122 reconstructions based on a single species. This section will review the orig-

123 inal description of *Buliminella tenuata* and *Eubuliminella exilis* that were
124 synonymised by Revets (1993).

125 **Infrakingdom** Rhizaria Cavalier-Smith, 2002, sensu Cavalier-Smith, 2003

126 **Phylum** Foraminifera (d'Orbigny, 1826)

127 **Class** Globothalamea (Pawłowski et al., 2013)

128 **Order** Rotaliida Delage and Hérouard, 1896

129 **Family** Buliminellidae Hofker, 1951

130 **Genus** *Buliminella* Cushman, 1911

131 **Type species** *Buliminella elegantissima* (d'Orbigny, 1839)

132 Original genus description: Test composed of chambers triserially ar-
133 ranged, but in later development becoming involute and spirally coiled, the
134 aperture being in the umbilicus thus formed; wall calcareous, perforate; aper-
135 ture in the species but little twisted spirally, long and narrow, nearly vertical,
136 in the closely spiral species becoming rounded in the middle of the concave
137 umbilical area.

138 *Buliminella tenuata* Cushman, 1927

139 **Synonymies** *Bulimina exilis* var. *tenuata* (Cushman, 1927)

140 *Bulimina tenuata* (Cushman, 1927)

141 *Buliminella subfusiformis* var. *tenuata* Cushman, 1927

142 Original species description: Test more elongate and slender than the
143 type (*Buliminella subfusiformis* Cushman, 1925), chambers somewhat more
144 elongate, the apertural end pointed.

145 Original type (*Buliminella subfusiformis* Cushman, 1925) description:
146 Test spiral, much elongate, subcylindrical, early portion tapering, sides for
147 most of the test nearly parallel, periphery lobulate; chambers numerous, in-
148 flated, distinct, 3 or 4 making up a coil; sutures distinct, depressed, wall
149 smooth, very finely punctate; aperture narrow, elongate.

150 Remarks: According to Matoba and Yamaguchi (1982): "this species
151 varies greatly in the diameter of its test", and indeed, a gradation is largely
152 visible among all the samples from the same core (e.g. Core MD02-2508,
153 Core SO201-2-85KL). No groups can be formed based on the size variability
154 of this taxa. Due to the images resolution, the presence or absence of a
155 crista and toothplate cannot be determined in Uchio (1960) and Matoba and

156 Yamaguchi (1982) specimens, but a crista is well visible in Heinz et al. (2005)
157 and in our specimens. The specimens presented in these and in our studies
158 never exhibit a basal spine.

159 **Family** Turritinidae Cushman, 1927

160 **Genus** *Eubuliminella* Revets, 1993

161 **Type species** *Eubuliminella exilis* (Brady, 1884)

162 Original genus description: Test free, a high trochospiral, usually 4 to
163 5 chambers per whorl, may reduce to triserial; chambers spherical to ovate,
164 inflated; sutures marked, sometimes to a considerable extent due to the con-
165 trast with the densely perforated chamber walls and the pore-free sutural
166 bands; apertural face commonly depressed, aperture at axial side, delimited
167 at peripheral side by a crista and at axial side by the previous chamber,
168 number of teeth on crista increasing during ontogeny; toothplate present,
169 descending into lumen while the two edges curve towards each other, finally
170 butting into the foramen between crista and wall of prepenultimate chamber,
171 at which point the edges have fused, ending blindly; wall calcareous, hyaline,
172 finely and commonly densely perforate.

173 Remarks: According to Revets (1993): " *Eubuliminella* differs from *Bu-*
174 *liminella* in possessing a toothplate, having rounded chambers, in being tetra-
175 or pentaserial, and in possessing a distinct crista which surrounds the aper-
176 ture only partially." *Buliminella* species usually possess an almost spirally
177 arranged succession of chambers (well visible in its type species *Buliminella*
178 *elegantissima*) while *Eubuliminella* shows a serial arrangement.

179 *Eubuliminella exilis* (Brady, 1884)

180 **Synonymies** *Bulimina elegans* var. *exilis* Brady, 1884

181 *Bulimina exilis* Brady, 1884

182 *Buliminella elegans* var. *exilis* (Brady, 1884)

183 *Stainforthia exilis* (Brady, 1884)

184 Original species description: Test forms a medium-sized, elongate, high
185 trochospire in the earlier part (four chambers per whorl) reducing to a tris-
186 erial, very slender (about five times as long as broad) tapered form in the
187 later portion. The test is subcircular in cross section, with a subacute initial
188 portion bearing a spine and a subacute or subrounded apertural end. The
189 inflated, ovate chambers are arranged in a straight or slightly oblique series,

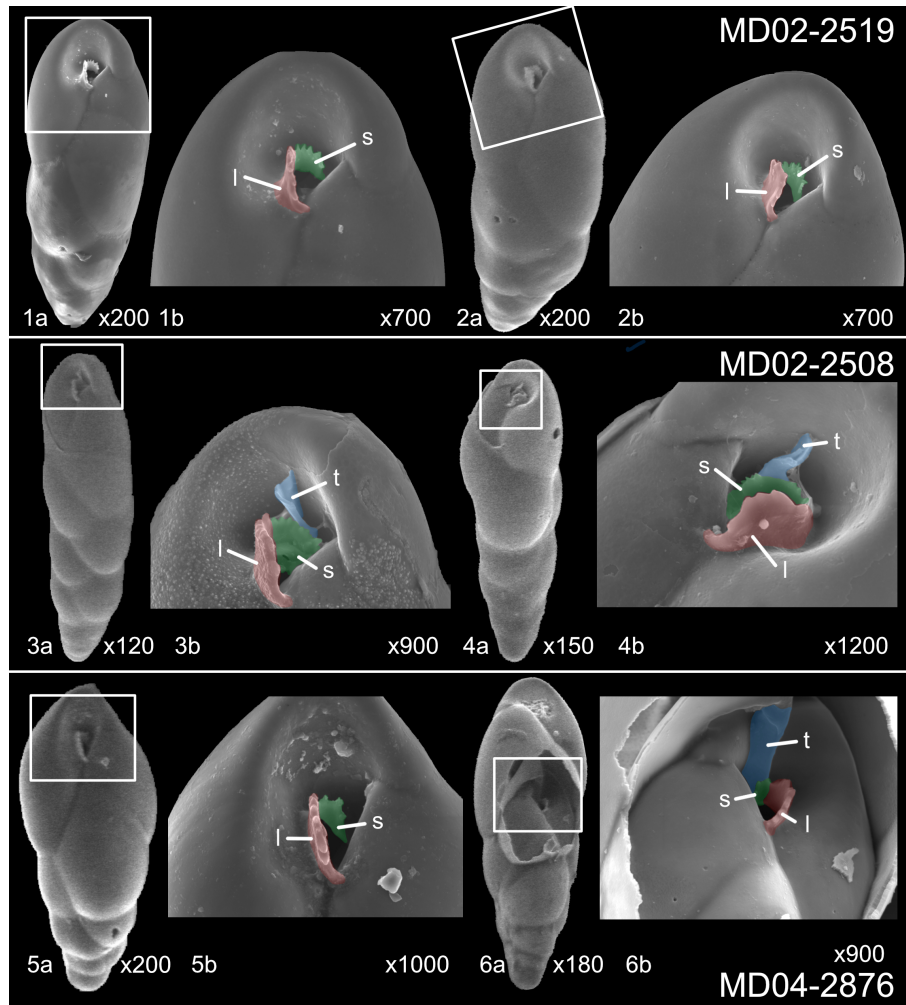


Figure 1: **1a.b. - 2a.b.** *Buliminella tenuata* Cushman, 1927 specimens from Core MD02-2519. **3a.b. - 4a.b.** *B. tenuata* Cushman, 1927 specimens from Core MD02-2508. **5a.b. - 6a.b.** *Ebuliminella exilis* (Brady, 1884) specimens from Core MD04-2876. All these specimens are now recognised as *E. tenuata* (Cushman, 1927). l = lip, s = crista or comb, t = toothplate.

190 increasing rapidly in height (last whorl represents one third of test length),
191 and are separated by distinct, curved, depressed sutures. Chamber walls are
192 calcareous, finely perforate, and smooth. The primary aperture is almost in
193 the coiling axis, with prominent crista and a short toothplate attached to
194 the lateral chamber wall.

195 Remarks: Revets (1993) reveals that "the specimens conforming to Cush-
196 man's *tenuata* species are indistinguishable from the macrospheric generation
197 of this species". Matoba and Yamaguchi (1982) had considered the eventual
198 synonymy between these two species, but deemed the evidence insufficient.
199 According to them, the specimens they studied were perfect intermediaries
200 between the spined *exilis* and the spineless *tenuata*. According to den Dulk
201 et al. (2000), it is, like *B. tenuata*, a deep infaunal taxon, characteristic of
202 oxygen-depleted sediments from oxygen minimum zones. Schumacher et al.
203 (2007) and den Dulk et al. (1998) observed this species with a distinct lip and
204 crista, but only the latter possesses a basal spine. McKay et al. (2014, 2015)
205 show SEM images of typical *Eubuliminella exilis* specimens (synonymized
206 with *Bulimina exilis*) which exhibit a lip and a crista, but are also very
207 slender and show a distinct basal spine which is, in this way, conform to
208 the original species description and clearly differ from all the *B. tenuata* we
209 observed and its original diagnosis.

210 3.2. Taxonomic revision of *B. tenuata* and *E. exilis*

211 After the careful examination of the original diagnosis of the *Buliminella*
212 and *Eubuliminella* genera, as well as the *B. tenuata* and *E. exilis* species,
213 and considering the morphological features of the specimens recovered from
214 the Arabian Sea and Eastern North Pacific OMZs, originally assigned to one
215 or other of these two taxa, it appears that:

216 1) The specimens observed in the current and previous studies (Tetard
217 et al., 2017a) and assigned to either *B. tenuata* or *E. exilis* show similar
218 morphological features and cannot be distinguished based on the literature
219 diagnosis, they should thus be considered as a single species, or morphogroup.

220 2) Both taxa fit to the original diagnosis of the *Eubuliminella* genus by
221 Revets (1993), especially with regard to the multi-serial arrangement of their
222 chambers, the densely and finely perforated chambers with pore free areas
223 along sutures, to the peripheral side of the aperture showing a distinct crista
224 (or comb) and a toothplate descending into the aperture. However, both taxa
225 differs from *Buliminella* in possessing a toothplate and a distinct crista (or

226 comb) partially surrounding the aperture (Revets, 1993) and in not exhibiting
227 a spiral arrangement of chambers. They should thus be assigned to the
228 *Eubuliminella* genus.

229 3) Both taxa however differ from the original *E. exilis* description (Revets,
230 1993) as they lack (among the ~ 7.300 cumulated specimens considered in
231 this study) the typical very elongated body commonly exhibiting a basal
232 spine that may correspond to very fine and delicate elongated first cham-
233 bers (as visible in Revets, 1993; den Dulk et al., 1998; Holbourn et al.,
234 2013; McKay et al., 2014, 2015). They should not be considered as *E. exilis*
235 which should remain a separated species. On the contrary, every specimen
236 is characterised by a large and subspherical proloculus, typical of the *tenuata*
237 species as visible in Bandy (1961); Heinz et al. (2005); Tetard et al. (2017a).
238 Other features such as elongated test are also in agreement with the origi-
239 nal description of the *tenuata* species. In the Eastern South Pacific OMZ,
240 reported specimens of *Bulimina exilis* (e.g. Erdem et al., 2020) is likely to
241 correspond to *Eubuliminella tenuata* (e.g. Cardich et al., 2015) as we man-
242 aged to observe them alive during the 2015 CRIO campaign and again, never
243 observed a basal spine.

244 We thus do not agree with the synonymy of *Buliminella tenuata* and *Eu-*
245 *buliminella exilis* by Revets (1993) and recently adopted by the WORMS
246 institute (revision proceeded on the 30th of May 2019). We propose that
247 both species should remain separated. *Eubuliminella exilis* is not emended
248 and its nomenclature is left untouched. We also propose to re-assign the
249 *tenuata* species to the *Eubuliminella* genus, as it fits the original *Eubulim-*
250 *inella* diagnosis and rare available SEM close-up images of the aperture show
251 characteristic feature of this genus (e.g. Heinz et al., 2005). We thus as-
252 signed what was originally described in Tetard et al. (2017a) to *Eubuliminella*
253 *tenuata* (Cushman, 1927) new combination.

254 A focus on molecular genetics using DNA sequencing would help to un-
255 derstand and settle the affiliation between both species. Since the first stud-
256 ies on DNA sequencing of foraminifera in 1993 (Langer et al., 1993; Wray
257 et al., 1993), and later well developed by Pawlowski (2000) and Pawlowski
258 and Holzmann (2002), investigation of their genomes were largely used for
259 improving taxonomic identification of species commonly used in paleoceanog-
260 raphic and geochemical studies (e.g. *Ammonia* spp., Cibicididae; Pawlowski
261 and Holzmann, 2008; Schweizer et al., 2009). These investigation of molecu-
262 lar genetics of some benthic foraminifera of interest have proven the existence
263 of cryptic species among individual species, while originally distinct taxa we

264 proven to belong to the same species. Even though the present study could
265 not rely on such techniques due to the lack of living material from the main
266 OMZs, a focus on both *E. tenuata* and *E. exilis* is more than welcome in
267 the future. However, even molecular investigation should be carefully inter-
268 preted as demonstrated by Grimm et al. (2007) who focused on *Chilostomella*
269 species and show that invasive sequences found in *Chilostomella* shells indi-
270 cates that their calcareous tests may have been inhabited and contaminated
271 by other non-calcareous taxa.

272 *Ebuliminella tenuata* (Cushman, 1927) new combination

273 **Synonymies** *Buliminella tenuata* Cushman, 1927

274 *Bulimina exilis* var. *tenuata* (Cushman, 1927)

275 *Bulimina tenuata* (Cushman, 1927)

276 *Buliminella subfusiformis* var. *tenuata* Cushman, 1927

277 Description: Chamber arrangement forms a medium-sized, elongated and
278 slender triserial test, about four to five times as long as broad for adult forms.
279 The basal part of the test is rounded (for microspheric and macrospheric
280 forms) and do not bear a spine. The apertural part of the test is subacute or
281 subrounded, and the aperture clearly exhibit a distinct lip and crista coiling
282 into the test. A toothplate is joining the crista to the chamber wall in the
283 pre-ultimate chambers (see intact and broken specimens in Fig. 1). The
284 chambers are usually poorly inflated, and the slightly curved suture only
285 create a small depression. Ovate chambers increase rapidly in height (up to
286 the third or fourth whorl). Chamber walls are calcareous, smooth, and the
287 alternance of clear pore-free areas along sutures and very finely perforated
288 white areas in the unattached and visible part of the chamber wall, creates
289 a distinct pattern.

290 Remarks: This species was originally assigned to *Buliminella* Cushman,
291 1911 due to its affinities with *Buliminella subfusiformis* Cushman, 1925 and
292 was later on (Revets, 1993) synonymised with *Ebuliminella exilis* (Brady,
293 1884). It however differs from the latter by never exhibiting a basal spine,
294 showing a less slender and elongated test, chambers are less inflated, and the
295 test pattern formed by the alternance of clear pore-free areas along chamber
296 sutures and white porous areas is clearly visible.

312 used to reconstruct past dissolved oxygenation in oxygen-deficient areas from
313 different OMZs based on the relative abundance of *E. tenuata*, following
314 Equation 1:

$$[O_2]_{(E. \textit{tenuata} \textit{ method})} = 0.72 \times \textit{relative abundance of } E. \textit{tenuata}^{-0.60} \quad (1)$$

315 In order to assess a measurement error for this new method, we decided to
316 use the same approach as the one used in Tetard et al. (2021). We computed
317 the standard deviation of the percentage corresponding to the differences
318 between the measured and the estimated $[O_2]$ values for the 25 core tops
319 used for the calibration. The error for each estimated $[O_2]$ value is then
320 assessed to be about + and - 40 % of this value.

321 4.2. Applicability of the new *E. tenuata* method

322 This relationship was then applied on five marine archives (533 samples)
323 recovered from oxygen-deficient areas from the WNP and ENP OMZs from
324 which census data counts were available downcore (Fig. 3). Using census
325 data, a comparison between $[O_2]$ estimations based on the new *E. tenuata*
326 method and the assemblages method developed in Tetard et al. (2017a) and
327 calibrated in Tetard et al. (2021) was carried out.

328 Regarding the ENP OMZ, Core MD02-2508 ($R^2 = 0.63$, covering the last
329 80 kyr), Core MD02-2519 ($R^2 = 0.34$, covering the last 130 kyr), Core MD02-
330 2529 ($R^2 = 0.24$, covering the last 260 kyr) exhibit a consistent relationship
331 (Fig. 3a) between both approaches. This relation is also consistent in the
332 WNP OMZ as the studied upper part of Core SO201-2-77KL ($R^2 = 0.52$,
333 covering the last 19 kyr) and Core SO201-2-85KL ($R^2 = 0.80$, covering the
334 last 10 to 21 kyr) show a significant relationship between both methods (Fig.
335 3a).

336 When regrouped for both the ENP ($R^2 = 0.79$) and the WNP OMZs (R^2
337 $= 0.69$), the fit curves show very similar trends and slopes, with only a slight
338 shift between both. These results lead us to regroup the ENP and WNP
339 data to test the relationship between both methods at the Pacific scale (Fig.
340 3c). A significant correlation ($R^2 = 0.74$) between both past oxygenation
341 reconstructed by the new *E. tenuata* and the assemblages approaches evi-
342 dencing the interest and reliability of this new method, which is very close
343 from the 1:1 line. By comparison with the assemblages-based approach, the
344 new method seems to be slightly under-estimating $[O_2]$ estimates when con-
345 ditions start to become more and more oxidic (e.g. Fig. 3c, the fit curve

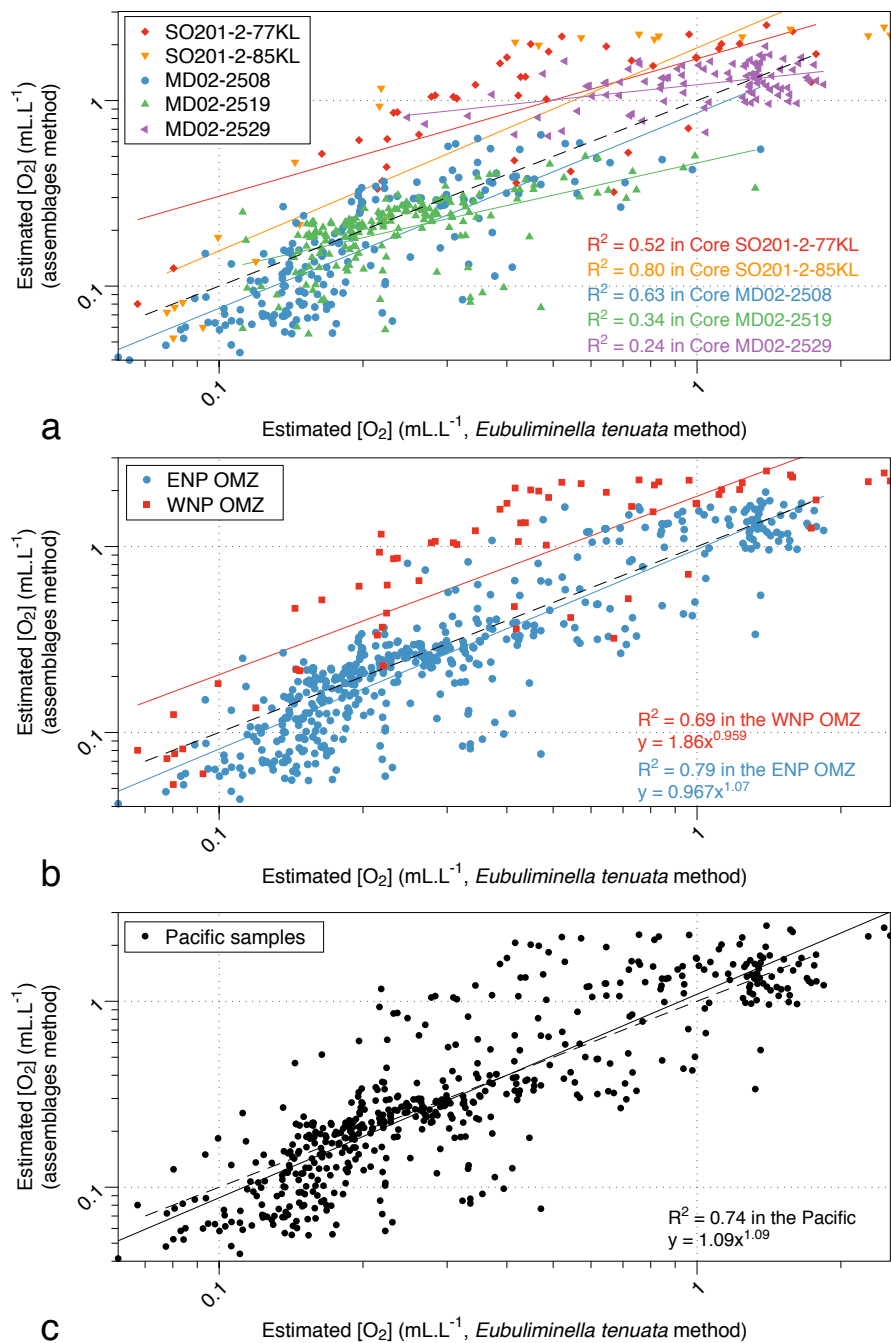


Figure 3: Relationship between the past [O₂] estimated by using the benthic foraminiferal assemblage method (Tetard et al., 2017a, 2021) and the past [O₂] estimated by using the relative abundance of *E. tenuata*. **a.** Blue dots = MD02-2508; Green triangles = MD02-2519; Purple sided triangles = MD02-2529; Red diamonds = SO201-2-77KL; Orange reversed triangles = SO201-2-85KL. **b.** Blue dots = ENP OMZ; Red squares = WNP OMZ. **c.** Black dots = Pacific signal. Dashed line correspond to the 1:1 line between both estimations.

346 shows that *E. tenuata*-based estimates of about 2 mL.L⁻¹ are associated with
 347 assemblages-based estimates of about 2.32 mL.L⁻¹). On the contrary, more
 348 dysoxic conditions are associated with an over-estimation of the *E. tenuata*-
 349 based method by comparison with the assemblages-based approach (e.g. Fig.
 350 3c, the fit curve shows that estimates of 0.06 mL.L⁻¹ based on the *E. tenuata*
 351 method are associated with estimates of about 0.05 mL.L⁻¹ based on the as-
 352 semblages method). This slightly more restricted [O₂] estimation range could
 353 be easily explained by the single species-based nature of the new *E. tenuata*
 354 method, as a single species is likely to respond and be present in a narrower
 355 [O₂] gradient than the whole benthic foraminiferal assemblages which covers
 356 a relatively larger oxygen gradient, from about 0.03 to 2.88 mL.L⁻¹ (Tetard
 357 et al., 2017a, 2021).

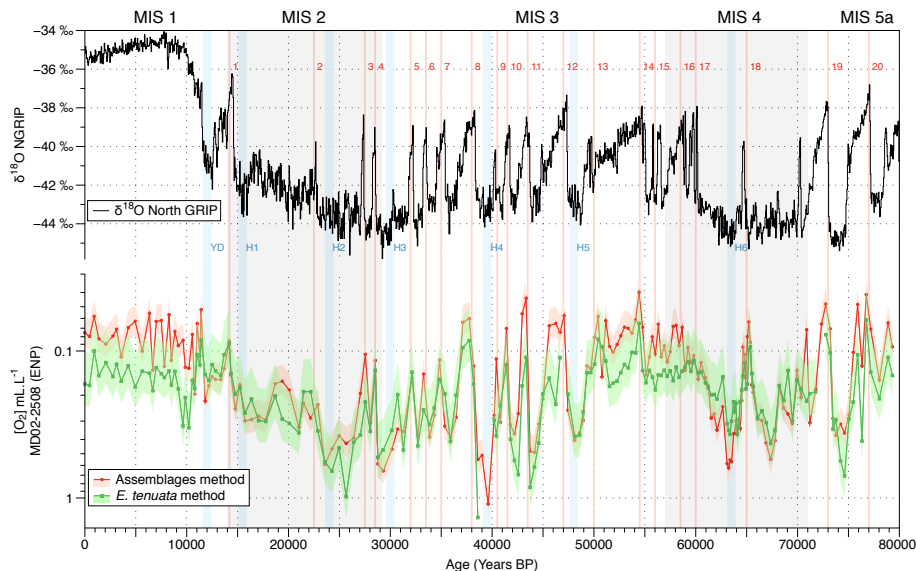


Figure 4: Comparison between the isotopic composition ($\delta^{18}\text{O}$ record) of the NGRIP ice core from Johnsen et al. (2001) and bottom water [O₂] variations estimated using the calibrated assemblages (red circles), and the *E. tenuata* (green squares) methods. The pink and light green shades represent the 23 and 40 % uncertainty on the assemblages (Tetard et al., 2021) and *E. tenuata* approaches, respectively.

358 This more restricted [O₂] gradient is also visible on the comparison be-
 359 tween the oxygen reconstructions based on the *E. tenuata* and the assem-
 360 blages methods applied on Core MD02-2508 (Fig.4), where oxygen is slightly
 361 higher during the MIS1, 2, and 3 with the *E. tenuata* approach than with the

362 assemblages method, for example. Both approaches exhibit past $[O_2]$ values
363 that are nevertheless comprised within each others margin of error.

364 5. Discussion

365 *E. tenuata* is usually reported to be associated with *B. seminuda* (Cardich
366 et al., 2015; Tetard et al., 2017a) which are considered as potential extremely
367 low bottom-water dissolved oxygen indicator in the fossil record (Shibahara
368 et al., 2007; Erdem et al., 2020). Indeed, *E. tenuata* is considered to be in-
369 dicative of dysoxic (<0.3 mL.L) conditions (Kaiho, 1994; den Dulk et al., 1998;
370 Jannink et al., 1998; Cannariato et al., 1999; Cauille et al., 2014; Praetorius et
371 al., 2015; Tetard et al., 2017a), and found in all major OMZs (Bernhard and
372 Sen Gupta, 1999). According to Cardich et al. (2015, 2019), both species
373 are generally found together and abundant under very low $[O_2]$, and the
374 dominance of one over the other might depend on the quality of the organic
375 matter and the presence of sulfidic waters. *E. tenuata* would be more abun-
376 dant when organic matter is more labile, and sulfidic water would be acting
377 as a limiting factor. Moreover, *E. exilis* is also considered as an indicator
378 of fresh organic input under low oxygen conditions (Caralp, 1989; Filipsson
379 et al., 2011; McKay et al., 2016). Geochemical studies by Praetorius et al.
380 (2015) and Belanger et al. (2020) reported that the relative abundance of *B.*
381 *exilis*, *B. seminuda* and other typical species usually found in OMZs such as
382 *T. delicata* and *Suggrunda eckisi* show a correlation with authigenic redox-
383 sensitive trace metals ratio such as Mo/Al and U/Al, and considered to be
384 indicators of low oxygen conditions.

385 We are aware that the absence of this species in given samples does not
386 necessarily imply that the bottom water conditions were too oxygenated,
387 as its presence / absence might also be influenced by other factors such
388 as other environmental and ecological parameters (e.g. food availability as
389 discussed above), or patchiness (uneven spatial distribution in the sediment).
390 Thus, while the presence of *E. tenuata* could indicate fresh input of labile
391 organic matter, and why this species is dominating instead of *B. seminuda*
392 for example, it has to be considered nevertheless as a low-oxygen tolerant
393 species, and we remain confident that the relative abundance of *E. tenuata*
394 is primarily and intimately linked with dissolved oxygen.

395 As the calibration is based on core tops recovered from the biggest OMZs
396 worldwide, this approach is likely to be used to estimate past oxygenation
397 from oxygen deficient areas (about less than 2 mL.L⁻¹, according to Murray

398 (2001) from at least the Pacific Ocean, and possibly from all over the world,
399 whenever this species is present and recorded downcore).

400 6. Conclusions

401 We conclude that the species formerly identified and described as *Bu-*
402 *liminella tenuata* should be emended and now combined with the *Eubulim-*
403 *inella* genus. Due to morphological differences (e.g. the presence or not of
404 a basal spine) without visible gradation between *E. tenuata* and *E. exilis*,
405 both species should not be synonymised and should remain distinct taxa.
406 However, only genetic sequencing might confirm or reject this hypothesis.
407 Nevertheless, both taxa are considered as infaunal species characteristic of
408 dysoxic conditions and can be used together as past oxygenation proxies with
409 similar affinities.

410 The relative abundance of this taxa show a consistent and negative re-
411 lationship with past oxygenation (an increase in the relative abundance of
412 this taxa is linked with a decrease in dissolved oxygen) in numerous marine
413 archives recovered from different oxygen deficient areas, such as the ENP,
414 the AS, and the WNP OMZs. The relation between the *E. tenuata* method
415 and an already published and used $[O_2]$ estimation approach based on the
416 complete benthic foraminiferal assemblage of each sample was tested for com-
417 parison and reliability testing of the new method. Results show a consistent
418 relationship between both methods and similar estimated $[O_2]$ values for five
419 cores located in the Pacific. As a consequence, we proposed that *E. tenuata*
420 can be used in these low oxygen environments, whenever this biomarker is
421 available, for reconstructing past oxygenation.

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