

1 **A Givetian tintinnid-like palynomorph from Libya**

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19
20 **Keywords**

21
22 Givetian, tintinnid, Libya, ciliate, protozoan

23
24 **Abstract**

25

26 Bulk maceration of Givetian palynological samples from A1-69 borehole drilled through the
27 Ghadamis Basin, western Libya yielded intriguing very large acid-resistant palynomorphs that
28 are described here. The palynomorphs come from an horizon containing also abundant large
29 megaspores and the enigmatic ‘mega-acritarchs’ *Vanguetainidium cucurbitulum* Steemans et
30 al. 2009. These palynomorphs are vase shaped; they include an open mesh structure; their size
31 is about 1 mm in length. Their shape and general appearance are tentatively compared with
32 those of tintinnids, extant ciliate protozoans characterised by an organic lorica. There is a
33 paucity of literature describing and detailing fossilised tintinnids. Nonetheless, the oldest
34 organic lorica which may be related to tintinnids have been extracted from the Jurassic and
35 Cretaceous pelagic limestone. However, vase-shaped organisms covered by agglutinate
36 mineral remains are described from Neoproterozoic sequences.

37

38 **1. Introduction**

39

40 Tintinnids are ciliate protozoans, an important component of the extant zooplankton (Dolan et
41 al., 2013). They are characterised by a vase-shaped organic covering (lorica) and are acid-
42 resistant like other palynomorphs (e.g. acritarchs, chitinozoans or miospores). The lorica may
43 be covered by attached mineral remains of other microorganisms such as foraminifera,
44 diatoms, coccolithes, etc. Tintinnids constitute an important link in the oceanic food chain:
45 they are primary consumers feeding on phytoplankton and in turn used as food by larger
46 zooplankton, mainly copepods, and fishes. They may be neritic or pelagic plankton living in
47 the upper part of the ocean. Additionally, several neritic species live in brackish environments
48 and rare extant species are present in fresh water lakes. Tintinnids are known under all
49 latitudes.

50

51 The lorica may have various shape, cup, vase, bottle, tube, horn, etc. They are generally
52 longitudinally symmetrical. The base of the lorica is closed and its top open, allowing the
53 protozoan to extrude. The oral diameter is related to the food items ingested. The size of the
54 prey ranges from 25% to 50% of the oral diameter. Extant tintinnids range in length from 10
55 μm to about 1 mm. Most of them range from 100 to 300 μm . Pre-Mesozoic tintinnid-like are
56 smaller than 300 μm in length, and with a lorica on which fragments of mineralised
57 microfossils are agglutinated. The lorica surface may be smooth or ornamented by
58 perforations, honey-like structures, ribs, fluting, shelves etc. For sexual reproduction, two (or
59 rarely more) specimens fuse together. Fossilised paired loricae have also been observed in
60 Upper Jurassic sediments of Greece (Bosak et al., 2011a). Spherical cysts have been observed
61 within the lorica of few extant species. The cyst is closed by an operculum. The cysts are thin-
62 walled or hyaline and acid-resistant. They may be smooth-walled, or ornamented or within an
63 outer very thin membrane. Their role in the tintinnid life cycle is not well understood. Cysts
64 may be developed in response to stress conditions (reduced salinity and high temperatures).
65 To our knowledge, there is only one occurrence of a vase-shaped microfossil containing a
66 spheroidal structure inside the test, which has been reported from the Neoproterozoic
67 Visingsö Group, Sweden (Mus and Moczydlowska, 2000).

68

69 Here we report very well preserved palynomorphs suggestive of organic lorica of putative
70 tintinnids observed in the organic residues of Givetian sediments from Libya. While selecting
71 megaspores under a dissecting microscope, two kinds of enigmatic large palynomorphs have
72 been observed. The first one has been identified as a very large acritarch: *Vanguetainidium*
73 *cucurbitulum* Steemans et al. 2009. The second kind, a vase-shaped palynomorph, is
74 described here.

75

2. Material and methods

Samples have been collected from cores of the A1-69 borehole drilled by SHELL in 1959 through the Ghadamis Basin (see Text-Figure 1 in Steemans et al. 2009) and provided during the eighties to the palynological laboratory of the Liège University thanks to the courtesy of D. Massa. Previous palynological results on this borehole have been published (Loboziak et al., 1992; Loboziak and Streel, 1989; Steemans et al., 2009; Streel et al., 1990). Some new levels have been investigated for a PhD research work on miospores (PB) and for a master degree on megaspores (FDVDG). All samples contain miospores and, in addition, nine samples contain megaspores (Steemans et al., 2011) . The level containing enigmatic palynomorphs, “acritarch-like” *V. cucurbitulum* and tintinnid-like palynomorphs is situated at 1293 ft of depth. This level is Givetian in age as demonstrated by miospore analysis (Breuer, 2007; Breuer and Steemans, In-press; Loboziak et al., 1992; Loboziak and Streel, 1989; Streel et al., 1990).

In order to prevent the destruction of the large palynomorphs, samples have been submitted to a specific laboratory treatment, “softer” than the usual technique used for miospores. The technical process of the sample has been described by Steemans et al.(2009). The specimens observed here are exceptionally well preserved.

3. Tintinnid-like palynomorph description

Nassacysta gen. nov.

Type: *Nassacysta reticulata* gen. and sp. nov.

101 Derivation name: compounded name from the Latin word “*nassa*” meaning bow-net, referring
102 to the general aspect of the palynomorphs, and from the English word “cyst”, meaning “small
103 capsule-like sac enclosing an organism in a dormant stage”.

104

105 Diagnosis: Organic-walled palynomorph ranging from 564 μm to 1617 μm in length,
106 composed by two main structures: (i) an outer sheath looking like a fish trap open at its
107 narrowest tip, (ii) an inner rounded body enclosed in a thin membrane.

108

109 *Nassacysta reticulata* sp. nov.

110

111 Pl. 1, figs 1-11

112

113 Derivation name: From the Latin “*reticulata*”, meaning reticulated, referring to the general
114 structure of the palynomorph.

115

116 Holotype and type locality: Pl. 1 fig. 1 from 394.4 m in the A1-69 borehole, Ghadamis Basin.

117 Slide Number 63065 in the collections of the PPP Laboratory, Liège, Belgium. Specimen A.

118

119 Paratype: Pl. 1, fig. 6 from 394.4 m in the A1-69 borehole, Ghadamis Basin. Slide Number

120 63072 in the collections of the PPP Laboratory, Liège, Belgium. Specimen D.

121

122 Diagnosis: Outer sheath around 1.03 mm long and 550 μm wide at its largest extremity.

123 Opposite extremity open and 270 μm in width. Mesh of the outer sheath polygonal, with a

124 diameter size ranging from 50 to 90 μm ; “threads” of the mesh about 10 μm wide. Short

125 sticks visible on the “threads”. Central body 343 μm in diameter, enclosed in a thin indistinct
126 membrane.

127

128 Description: 14 specimens have been discovered. The palynomorphs are composed of two
129 well distinct parts: an inner body (Pl. 1, fig. 1A) is enclosed in an outer reticulate sheath (Pl.
130 1, fig. 1B). The central body is brown to dark brown in colour, spherical or ovoid, with a
131 diameter size ranging from 260 to 450 μm . It is covered by an outer membrane looking like a
132 network of interweaved fibres (Pl. 1, figs 1C, 7A). Under light microscope, the aspect is
133 fleecy, looking like a silk ball. The external reticulate sheath has a vase/bottle shape and looks
134 like a net closed at its largest part (Pl. 1, fig. 2A) and open at its narrowest extremity (Pl. 1,
135 figs 1B, 6B). The general aspect is that of a fish trap. The meshes are polygonal to subcircular
136 at the largest extremity and strongly elongated close to the opening. The mesh diameter size
137 ranges from around 40 μm to 60 μm at the base and from around 16x90 μm to 20x160 μm at
138 the top. The “threads” of the mesh are around 10 μm in width. Some specimens have sticks
139 (Pl. 1, fig. 4A) on the “threads” of the mesh, 20 to 50 μm long and 10 μm large at their base.
140 The sticks are enlarged at their extremity and flat. A very thin membrane, 5 to 20 μm thick,
141 runs all along the “threads” on the centre part of their surface (Pl. 1, figs 8A, 9A) and, more
142 rarely visible, along their internal edge (Pl. 1, fig. 10A). At some places, the meshes are
143 completely closed by the thin membrane (Pl. 1, fig. 10B). This suggests that the mesh
144 structure was closed by a membrane which has been destroyed during taphonomic processes.
145 When spines are present, they subtend the membrane. In one case, two palynomorphs are
146 attached to one another, one above the other (Pl. 1, fig. 3).

147

148 Dimensions: Length: 564-(940)-1617 μm (the lowest dimensions are underestimated as
149 several specimens are broken). Base width: 401-(500)-603 μm . Top width: 186-(260)-341
150 μm .

151

152

153 **4. Discussion**

154

155 **4.1. Fourier transformed infrared (FTIR) micro-spectroscopy**

156

157 In order to chemically establish the biological affinity of the enigmatic specimens studied
158 here, we undertook FTIR microspectroscopic analysis on one specimen of *N. reticulata* (for
159 technical aspect see in Steemans et al., 2009). Unfortunately, no more palynological material
160 from the Lybian sample is available, and additional analyses are impossible.

161

162 The spectrum shown in Fig. 1 contains absorption bands centred at: a strong broad absorption
163 at 3362 cm^{-1} assigned to alcoholic OH, phenolic OH, and/or carboxylic OH; medium broad
164 aliphatic absorptions between 2700 and 3000 cm^{-1} with a noticeable shoulder at 2960 cm^{-1}
165 and maxima centered at 2920 and 2850 cm^{-1} assigned to anti-symmetric stretching vibrations
166 from CH_2 and symmetric stretching vibrations from CH_2 methylene groups, respectively; a
167 slight absorption centered at 1710 cm^{-1} assigned to the vibration of carbonyl $\text{C}=\text{O}$; a strong
168 absorption of aromatic $\text{C}=\text{C}$ centered at 1600 cm^{-1} ; weak deformation vibrations from CH_2
169 methylene groups; medium absorption of deformation bending of terminal methyl CH_3 groups
170 centered at 1345 cm^{-1} ; and a weak absorption centered at 740 cm^{-1} assigned to $\text{C}=\text{C}-\text{H}$
171 aromatic out-of-plane vibration. A slight shoulder appears at 2960 cm^{-1} (anti-symmetrical C-
172 H_3 stretch of methyl groups). The shoulder at 2960 cm^{-1} and in addition the broad aliphatic

173 stretching region is indicative of branched polymethylenic chains. In general, FTIR spectra
174 obtained from the putative tintinnids specimens is characteristic of a biopolymer with a
175 macromolecular structure of aromatic rings bridged by short branched aliphatic chains.

176

177 From the same residues, the FTIR spectra acquired from the acritarch *Vanguetainidium*
178 *cucurbitulum* reveals a palynomorph wall composed of a macromolecular material consistent
179 with algaenan (Stemans et al., 2009). The comparison

180

181 of both spectra shows strong differences: (i) by the intensity of absorbance bands (e.g. the
182 stronger absorbance of the 2920 and 2850 cm^{-1} bands compared to the others in the case of *V.*
183 *cucurbitulum*); (ii) and by the presence/absence of absorbance bands (e.g. the 1700 cm^{-1} band
184 in the spectra of *V. cucurbitulum* is represented by a light shoulder in the spectra of *N.*
185 *reticulata*; there is no absorbance band at 720 cm^{-1} in the spectra of *N. reticulata*). Clearly
186 both palynomorphs do not have the same biopolymer composition and hence their biological
187 affinity is different.

188 However, caution should be exercised when comparing FTIR spectra of fossilised
189 palynomorphs from the literature as biopolymers may be modified by diagenesis and thermal
190 alteration. More work is needed to distinguish between source of biopolymers and importantly
191 taphonomic effects during burial.

192

193 **4.2 Morphological comparison with other palynomorphs/organisms**

194

195 Foreword - We confidently exclude contamination of our palynological preparations by
196 modern palynomorphs: (i) before being processed, samples have been carefully washed with
197 distilled water; (ii) the enigmatic palynomorphs here observed are strongly flattened as are all

198 the others discovered from the same palynological sample; (iii) framboidal pyrite has been
199 observed inside of the palynomorphs; (iv) the colour of the enigmatic palynomorph walls is
200 similar to all the others present in the maceration residues.

201

202 The following hypotheses on the biological affinities of *N. reticulata* have been considered.

203 - (i) Dinoflagellates are much smaller (20-250 μm). The cysts are composed of a
204 complex paratabulation and many show a bilateral symmetry. Others display a uniform cyst
205 ornamented by various ornaments. They usually have an archeopyle and an operculum. They
206 have a cingulum and a sulcus. The widespread first occurrence of dinoflagellates is Late
207 Triassic.

208

209 - (ii) There is no acritarch displaying an organization such as that described here. They
210 are usually more or less spherical with various degrees of ornamentation. The giant acritarch
211 *V. cucurbitulum* observed in the same sample excepted, they are always much smaller (20-250
212 μm).

213

214 - (iii) Chitinozoans are usually smaller, but some specimens may exceed 1 mm. They
215 usually are bottle-shaped, but the body of the chitinozoans does not resemble to the reticulate
216 structure of *N. reticulata*. Some chitinozoans have complex carina looking like an
217 “embroidery” (e.g. *Sagenochitina*), but it never encloses the chitinozoan body.

218

219 - (iv) Thecamoebian are small testate protists known from Neoproterozoic sequences
220 onwards. They are generally sac-like or cap-like test. Most of them are smaller than 200 μm .
221 They never display a complexity such as that of *N. reticulata*.

222

223 - (v) Some spores like *Retispora lepidophyta* (Kedo) Playford 1976 are composed of
224 two layers, the outer layer being reticulate, but no spore have a bottle shape. They may have
225 only a round, oval or triangular shape. They usually show an opening structure such as a
226 monolete or trilete mark. It is extremely rare that spores are so large; most spores range in
227 between 20-150 μm .

228

229 - (vi) The pollen of gymnosperm show air sacs with an internal alveolate structure.
230 This cannot be confused with the reticulate mesh of the enigmatic palynomorphs here
231 described. In addition, pollen does not occur before Carboniferous times and are never so
232 large.

233

234 - (vii) The similitude between the palynomorphs studied here and extant orchid seeds
235 is striking. Several orchid seeds have been processed with acids, in order to compare their
236 aspect with that of our specimens. The treatment resulted in no modification of the structure
237 and colour of the orchid seeds, leading us to conclude that our specimens are not such modern
238 material.

239

240

241 Several morphological characteristics of *N. reticulata* suggest a tintinnid affinity:

242

243 - (i) The vase-shaped organic lorica displays a very similar aspect to that of extant
244 tintinnids characterised by a net structure. It is not possible to know if fragments of
245 mineralised microfossils were originally agglutinated on the organic lorica, because
246 they would have been dissolved during sample processing with strong acids such as
247 HF and HCl. However, the observation of specimens attached to one another casts

248 doubtful on the possibility that mineral fragments existed on the lorica; the dissolution
249 of the mineral particles would presumably have resulted in the breaking apart of the
250 two loricae. To our knowledge, there is a unique occurrence of putative tintinnids
251 enclosed within an organic lorica from strata older than the Mesozoic (Bosak et al.,
252 2011b). However, these authors could not demonstrate that there were no agglutinate
253 mineral fragments because they also used acids to process the samples.

254

255 - (ii) The lorica is longitudinally symmetrical. The base or largest extremity of the lorica
256 is closed and its top or narrowest extremity is open.

257

258 - (iii) The palaeoenvironmental conditions in which the tintinnid-like palynomorphs
259 were found have been previously described. (Stemans et al., 2011; Stemans et al.,
260 2009): “Such an assemblage, rich in continental palynomorphs and plant remains, and
261 low diversity acritarchs, represents a nearshore environment (Traverse, 2007). Large
262 megaspores, >1 mm in diameter (Ville de Goyet et al., 2007), are extremely well-
263 preserved, indicating reduced transport by water currents. This is confirmed by the
264 presence of other delicate cocoon-like enigmatic palynomorphs (Stemans, 2006). The
265 environment was probably a coastal swamp periodically inundated by the sea”. The
266 cocoon-like palynomorphs mentioned here before are the specimens that we interpret
267 now as putative tintinnids. Several neritic extant species live in brackish environments
268 that is similar to the one described in the Givetian of the Ghadamis Basin.

269

270 - (iv) Under stressing environment conditions, extant tintinnids are known to being able
271 to produce an internal acid resistant cyst, which may be enclosed in an envelope. The
272 palaeoenvironment as described here is typically a biotope in which physico-chemical

273 conditions, as the salinity or the abundance of preys may abruptly change. This could
274 explain why most of our specimens contain such cysts.

275

276 On the other hand, other morphological characteristics question the biological affinities of *N.*
277 *reticulata*:

278

279 - (i) Our specimens are up to more than 1.5 mm in length, which is larger than extant
280 tintinnids which are not longer than 1 mm.

281

282 - (ii) Extant tintinnids are characterised by a well differentiated oral aperture, while our
283 specimens are not. However, all the specimens show that the delicate open extremity
284 has been torn; therefore, the aperture may have been destroyed during fossilization
285 processes.

286

287 - (iii) When modern tintinnids are agglutinated, they are associated by joining their oral
288 pole one to the other, while our specimens are laterally associated. However, the
289 tintinnid life cycle is not well known (Tappan, 1993). Lateral fusion has been observed
290 among other ciliate like dinoflagellates during sexual reproduction or because of
291 unfavourable conditions.

292

293 - (iv) It has not been possible to verify the presence or absence of an opening structure
294 in the cyst.

295

296 - (v) No tintinnids including an exclusively organic lorica are known older than the
297 Mesozoic (Lipps et al., 2013; Tappan, 1993). In addition, according to Lipps et al.

298 (2013) no published palynomorphs from layers older than Jurassic are tintinnids.
299 However, the authors conclude that “The first organic tintinnid from the Jurassic
300 appears to be a fully developed form, thus indicating a previous undiscovered history.”
301

302 **Conclusions**

303

304 Despite several uncertainties, the morphology of the palynomorphs described here may be
305 interpreted as being in accordance with a tintinnid affinity. Tintinnids belong to the
306 zooplankton: this could explain the absence of algaenan polymer in the composition of the
307 palynomorph wall. If our specimens are correctly identified, it is the first time that such
308 palynomorphs are observed in Palaeozoic sequences. The presence of a cyst inside of the
309 lorica is interpreted as being due to a stressing environment which is consistent with the
310 sedimentary and palynological data. Biologically, the environment in which the Givetian
311 sediments are deposited and the types of palynomorphs present are intriguing as this
312 exceptionally well preserved residue contains the largest megaspores of the Devonian
313 (Steemans et al., 2011), giant acritarchs (Steemans et al., 2009) and now tintinnid-like
314 palynomorphs.

315

316 **Fig caption**

317 Fig. 1: Micro-FTIR spectra from a specimen of *Nassacysta reticulata* sp. nov. Band

318 Assignments:

319 $\nu(\text{OH})$: alcoholic OH, phenolic OH, and/or carboxylic OH

320 $\#(\text{CH})$: aromatic C-H stretching

321 $+ \nu_{\text{as}}(\text{CH}_3)$: Antisymmetric methyl CH_3 stretch

322 $\nu_{\text{as}}(\text{CH}_2)$: Antisymmetric methylene CH_2 stretch

- 323 $\nu_s(\text{CH}_2)$: Symmetric methylene CH_2 stretch
324 $\nu(\text{C}=\text{C})$: aromatic ring stretch
325 $\delta(\text{CH}_2)$: Methylene CH_2 bend
326 * $\delta(\text{CH}_3)$: Terminal methyl deformation
327 $\delta(=\text{C}-\text{H})$: aromatic C-H out-of-plane bending modes.

328

329 **Plate 1**

330 *Nassacysta reticulata* sp. nov. All specimens are from 394.4 m in the A1-69 borehole,

331 Ghadamis Basin, Libya. Scale bars: 10 μm . All slides are housed in the collections of the

332 PPP laboratory, University of Liège, Belgium.

333 Fig. 1 Holotype, Specimen A, Slide number 63065. 1A: Inner body; 1B: outer reticulate

334 sheath, open mesh extremity; 1C: outer membrane enclosing the inner body.

335 Fig. 2 Specimen B. Slide number 63065. 2A: outer reticulate sheath, closed mesh extremity.

336 Fig. 3 Specimens C. Slide number 63072. Two specimens associated laterally.

337 Fig. 4 Specimen B. Slide number 63072. 4A: sticks on the “threads” of the mesh.

338 Fig. 5 Badly preserved specimen D. Slide number 63065.

339 Fig. 6 Paratype, Specimen D, Slide number 63072. 6B: outer reticulate sheath, open mesh

340 extremity

341 Fig. 7 Enlargment of the specimen Fig. 1. 7A: outer membrane enclosing the inner body and

342 looking like a network of interweaved fibres. 7B: Pyrite

343 Fig. 8 Enlargment of the specimen Fig. 6. 8A: detail of the very thin membrane running all

344 along the “threads” on the centre part of their surface

345 Fig. 9 Enlargment of the specimen Fig. 6. 9A: detail of the very thin membrane running all

346 along the “threads” on the centre part of their surface.

347 Fig. 10 Enlargement of the specimen Fig. 4. 10A: detail of the very thin membrane running all
348 along the internal border of the “threads”. 10B: Detail of a completely closed by the thin
349 membrane.

350 Fig. 11 Enlargement of the specimen Fig. 1. Detail of the “threads” and of the outer membrane
351 enclosing the inner body and looking like a network of interweaved fibres

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353

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356

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