NEW INSIGHTS ON THE SYSTEMATIC CLASSIFICATION OF CERTAIN PALYNOLOGICAL TAXA (TINTINNOMORPHS) FROM HOLOCENE DEPOSITS OF THE COASTAL PLAIN OF SOUTHERN BRAZIL

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ABSTRACT – Tintinnomorphs is a term used for the grouping of palynomorphs resembling organic remains of tintinnids, which are not always identifiable as true lorica, cysts or pouch, being able to correspond to other protozoans and may even represent others structures of distinct organisms, such as rotifers and turbellarians. This paper presents tintinnomorphs recorded in Holocene sediments of the well PSC-03, drilled in the Coastal Plain of Santa Catarina, southern Brazil. A total of six tintinnomorphs types is described and illustrated (SPHERO-1, ELELNO-14, ESABNO-6, HEXANO-2, RECTNO-1, AROBNO-3), some of which are compared with specimens previously reported from Quaternary deposits of southern Brazil, southern South America and other regions of the world. Although tintinnomorphs are associated to marine palynomorphs, they cannot be used as a conclusive paleoenvironmental evidence due to uncertainties about their biological affinity.

Key words: tintinnomorphs, tintinnids, Holocene, Coastal Plain of Santa Catarina.

RESUMO – Tintinomorfos é um termo usado no agrupamento de palinomorfos assemelhados a restos orgânicos de tintínídeos, os quais nem sempre são passíveis de serem identificados como verdadeiras lóricas, cistos ou bolsas, podendo corresponder a outros protozoários e até representar outras estruturas de organismos distintos, como rotíferos e turbelários. Este trabalho apresenta tintinomorfos registrados em sedimentos do Holoceno do poço PSC-03, perfurado na Planície Costeira de Santa Catarina, sul do Brasil. Um total de seis tipos de tintinomorfos é descrito e ilustrado (SPHERO-1, ELELNO-14, ESABNO-6, HEXANO-2, RECTNO-1, AROBNO-3), alguns dos quais comparados a espécimes previamente registrados em depósitos quaternários do sul do Brasil, sul da América do Sul e outras regiões do mundo. Embora estejam associados a palinomorfos marinhos, tintinomorfos não podem ser utilizados como indicadores paleoambientais conclusivos devido às incertezas sobre sua afinidade biológica.

Palavras-chaves: tintinomorfos, tintínídeos, Holoceno, Planície Costeira de Santa Catarina.

INTRODUCTION

Tintinnids are unicellular, planktonic, heterotrophic, protist organisms of reduced size (20–200 μm), belonging to the phylum Ciliophora. The cell is always surrounded by a test named lorica, which is secreted by the organism, organic or agglutinated with biogenic and abiogenic particles attached to the wall (Barnes, 1990; Adamonis *et al.*, 2007; Agatha & Strüder-Kypke, 2013). The lorica presents distinct shapes at the intraspecific level, depending on the environmental conditions (e.g. temperature, salinity and particle availability) during its construction, thus influencing its size, shape and structure (Agatha & Strüder-Kypke, 2013).

Due to the chemical composition (proteins and polysaccharides) and the agglutinating property of the lorica, tintinnomorphs are a unique suborder of the Ciliophora likely to remain as fossil record (Canudo, 2004; Adamonis *et al.*, 2007; Lipps *et al.*, 2013) as only two features make them assignable to the tintinnids: the shape and the composition (Lipps *et al.*, 2013).

Different approaches to the chemical composition (chitin, pseudochitin, cellulose, proteins and polysaccharides) and to the texture (delicate, gelatinous, membranous and firm) of the constitution of organic lorica are verified in the literature (Tappan & Loeblich, 1968; Van Waveren, 1994; Canudo, 2004; Lipps *et al.*, 2013). Recent studies have shown that

many of these unicellular organisms are able to construct several types of lorica, which can lead to classifications into divergent tintinnids families (Agatha & Strüder-Kypke, 2013).

Nevertheless, many loricae and cysts are recovered by palynological processing (Reid & John, 1978; Meckler *et al.*, 2008; Mudie *et al.*, 2010, 2011; Pienkowski *et al.*, 2011, 2013), being classified within the palynomorphs as zoomorphs (Traverse, 1994). In modern marine sediments, a large quantity and variety of tintinnid cysts and loricae is known (Reid, 1975; Reid & John, 1978; Van Waveren, 1994; Van Waveren & Visscher, 1994; Kawamura, 2004; Hardy & Wrenn, 2009; Lipps *et al.*, 2013; Pienkowski *et al.*, 2011, 2013; Matsuoka *et al.*, 2017).

Fossil tintinnids are almost exclusively marine, comprising few described taxa. During the fossilization, diagenetic processes can change the morphological characters of the ciliates specimens, limiting an accurate description. As a result, there are misconceptions in the descriptions and taxonomic assignments of several specimens attributed to the group, and molecular analysis is not adequate for taxonomic assignment of fossil taxa (Lipps *et al.*, 2013).

According to Canudo (2004), the ciliate fossil record is composed almost exclusively by loricae analogue to the tintinnids loricae, some of which belong to other groups. Due to the great difficulty in observing and interpreting the tintinnids fossils, Canudo (2004) defends the creation of a comprehensive term (*e.g.* tintinnoids or tintinnomorphs) to encompass the true tintinnid loricae and similar forms, thus minimizing the mistaken designations.

However, morphological studies on the organic remains attributed to tintinnids are needed. Van Waveren (1994) proposed an informal morphological system, with description and illustration of the cysts, loricae and the pouches in which the cysts were originally encapsulated, as well as considering their ontogenetic stages. As a result, 76 morphological types were presented, grouped under the term “tintinnomorphs”. This term is used to link organic remains found in palynological preparations resembling tintinnids, which are not always identifiable as true lorica, cysts or pouches, being able to correspond to other protozoans and may even represent structures of other distinct organisms, such as rotifers and turbellarians.

Certain specimens resembling tintinnomorphs were recorded from Quaternary deposits of the Brazilian Coastal Plain, especially from Rio Grande do Sul (CPRS) and Santa Catarina (CPSC), described as flatworm eggs (Neves & Bauermann, 2003; Cancelli *et al.*, 2012; Roth & Lorcheistter, 2016). Many of them are comparable to some morphological types proposed by Van Waveren (1994).

The palynological analysis of a core sample taken from the Coastal Plain of Santa Catarina revealed the presence of tintinnomorphs at several levels. These were found associated with dinoflagellate cysts, foraminiferal linings, along with terrestrial nature taxa (spores, pollen grains, fungi and freshwater algae). The main goals of this paper are to describe, Brazilian Holocene tintinnomorphs using the Van Waveren (1994) descriptive system; compare them with specimens previously reported for the Quaternary of southern Brazil,

southern South America, and similar forms from other regions of the world; and discuss their environmental significance.

ECOLOGICAL AND STRATIGRAPHIC CONSIDERATION OF TINTINNIDS

Ecology

Tintinnids are one of the most important and abundant components of microzooplankton (Tappan & Loeblich, 1968; Tenenbaum & Gomes, 2006). Currently 1,200 species are known, allocated in 75 genera, most of them distributed in marine and brackish environments (Tappan & Loeblich, 1968; Tenenbaum & Gomes, 2006; Adamonis *et al.*, 2007; Lipps *et al.*, 2013). Among them, about 10 species are recorded from freshwater environments (Tappan & Loeblich, 1968; Lipps *et al.*, 2013).

In terms of biogeographical distribution, Dolan & Pierce (2013) compartmentalized them into five biotas: (i) cosmopolitan; (ii) neritic; (iii) warm-water; (iv) boreal; and (v) austral, each biota involving species with distinct morphologies. Although they have a wide geographical distribution, tintinnids are subject to ecological restrictions, which control their abundance and diversity. In cold waters, assemblages are low in diversity and high in abundance, while in tropical waters diversity is higher but cells are smaller and less numerous.

In modern oceans, blooms of tintinnids seem to be strongly seasonally influenced (Armstrong & Brasier, 2005; Dolan & Pierce, 2013). Tintinnids with agglutinated and organic lorica are common in open sea and neritic environments (Lipps *et al.*, 2013). Ecological studies have shown that many species of tintinnids are tolerant to large variations in salinity and water depth. Tintinnid species with agglutinated lorica preferentially inhabit the proximal environments and can serve as a good environmental indicator, suggesting brackish waters or, at least, a proximity to sites of freshwater discharge (Echols & Fowler, 1973).

Stratigraphy

The stratigraphic record and phylogeny of this group still holds uncertainties and controversies. Possible occurrences of tintinnids in Proterozoic (Li *et al.*, 2009) and Paleozoic (Cuviller & Sacal, 1963) strata have been reported, but as these records were based on fragile evidence, they are questionable (Tappan & Loeblich, 1968; Lipps *et al.*, 2013). Remane (1971) proposed a phylogenetic relationship between tintinnids and calpionellids, due to the morphological similarity between the lorica of these two groups; but this hypothesis cannot be confirmed because no modern species of tintinnid is known to have a carbonate lorica (Lipps *et al.*, 2013). On the other hand, Reid & John (1981) suggested a relationship between tintinnids and chitinozoans, an *incertae sedis* organic microfossil recorded from the Ordovician to the Devonian. Adamonis *et al.* (2007) contested this relationship.

The oldest stratigraphic occurrence of tintinnids is dated to the Jurassic (Rüst, 1885), and based on the recognition and description of agglutinated loricae. According to Lipps

et al. (2013), agglutinated loricae are abundant in the shallow, neritic waters of the Cretaceous mid-continental seaway that flooded a central corridor through the center of North America, from the Gulf of Mexico to the Arctic Ocean. There is a gap in the geological record of agglutinated loricae, after the Cretaceous, having been found again in the Upper Pleistocene (Echols & Fowler, 1973; Lipps *et al.*, 2013).

Records of organic walled remains of tintinnids in Pre-Quaternary deposits are scarce. The earliest known occurrences are from the Lower Triassic of Ireland and Israel (Van Waveren, 1994) and the Lower Cretaceous of France (Gorin & Steffen, 1991). Although there are several gaps in the fossil record of this group, tintinnid organic remains are frequent only from Holocene marine deposits (Reid, 1975; Reid & John, 1978; Grill *et al.*, 2002; Roncaglia, 2004; Borromei & Quattrocchio, 2001, 2007; Meckler *et al.*, 2008; Mudie *et al.*, 2010; Pienkowski *et al.*, 2011, 2013), and may aid in understanding recent environmental changes (Grill *et al.*, 2002; Roncaglia, 2004; Borromei & Quattrocchio, 2001, 2007; Meckler *et al.*, 2008; Mudie *et al.*, 2010).

STUDY AREA

This study was developed from samples collected from a core (PSC-03) carried out along of the BR 101 highway (km 243 – South, Lat. 27°53'22"S; Long. 48°39'04"W), in the Municipality of Palhoça, the State of Santa Catarina (SC), in southern Brazil. This core is located approximately 6 km from the modern coastline (Figure 1). The Municipality of Palhoça is inserted in the Central Sector of the CPSC, which is characterized by a Quaternary lagoon complex, comprising colluvial, alluvial, beach, paludal and eolian deposits (Horn Filho, 2003), mainly of Holocene age. In this sector, the coast presents South-North orientation (Figure 1). The CPSC comprises a series of geomorphological features and depositional facies represented by various sedimentary facies, under marine, transitional and continental influences. These controls are directly related to transgressive and regressive Quaternary sea-level cycles.

Figure 1. A–B, geographic localization of the studied core, in Santa Catarina, southern of Brazil. C, satellite image locating the core sample (PSC-03) site on the Coastal Plain of Santa Catarina (adapted from: Google Earth, 2017).

MATERIAL AND METHODS

The 300 cm long of PSC-03 core consists of fine sand layers, intercalated with silt layers, bearing high organic content (Figure 2). Sixty palynological samples (3 cm³ each) were selected along the core, spaced 5 cm apart, which were processed at the Marleni Marques Toigo Palynology Laboratory, Department of Paleontology and Stratigraphy, Geosciences Institute, Universidade Federal do Rio Grande do Sul (LPMMT/IG/UFRGS). Laboratorial procedures are according to conventional method described by Wood *et al.* (1996) and following the Dale (1976) proposal, where each sample is treated with cold acids (HCl, HF), without oxidation and acetolysis are applied in order to prevent the loss of more fragile protoperidiniacean cysts. One tablet of *Lycopodium clavatum* was added in each sample to allow calculation of palynomorphs concentration (Stockmarr, 1971). Final residues were obtained by sieving. Slides were mounted using the fraction between 10 and 250 µm. Slides are stored in the LPMMT/IG/UFRGS collection under code "MP-P" (Figure 2).

The material was studied and photomicrographs were taken under an Olympus BX61 optical light microscope. For each sample, percentages of the palynomorphs composition (spores, pollen grains, fungi, freshwater algae, dinoflagellate cysts, foraminiferal linings and tintinnomorphs) were calculated from the raw total counts (Table 1). Radiocarbon dating was obtained along the core, which was performed at the CAIS Laboratory (University of Georgia, USA), using Accelerator Mass Spectrometry (AMS). The program CALIB (Radiocarbon Calibration 7.1, Stuiver *et al.*, 2016) was used for the calibration of these datings, considering the SHCal13 radiocarbon calibration curve (Southern Hemisphere, Hoog *et al.*, 2013) (Table 2).

RESULTS

Most specimens recorded from the PSC-03 core were well preserved, allowing for the use of the descriptive system proposed by Van Waveren (1994). Tintinnomorphs occur in the majority of samples between 275 cm to 175 cm of depth, in varying amounts (1 to 5 %), always subordinated to the other palynological groups (spores-pollen, fungi, freshwater algae, foraminiferal linings, dinoflagellate cysts), except at 245 cm of depth, where they reached 14% of the total palynomorphs (Table 1). Six tintinnomorphs types were recorded; only one or two distinct types are represented per stratigraphic level (where they occur). ESABONO-6 and HEXANO-2 are the most frequent types.

Analysis of the descriptive system of tintinnomorphs types

The three main morphological structures of tintinnids are: (i) a lorica; (ii) a pouch attached to the aboral (basal) side of the lorica; (iii) a cyst encapsulated in the pouch (Van Waveren, 1994) (Figure 3A). Ideally, the cyst is encapsulated in the pouch, which in turn is inserted in the aboral portion of the lorica. However, the remains recovered from the palynological slides are dissociated, and are often misinterpreted, generically designated as lorica or cyst.

Figure 2. Stratigraphic column of the PSC-03 core, Holocene of the Coastal Plain of Santa Catarina, showing the position of palynological sampling, radiocarbon ages and list of palynological slides and their codification (the abbreviation MP-P concerns the slide collection of the LPMMT/IG/UFRGS).

Table 1. Quantification of the palynomorphs recorded in the PCS-3 core (highlighted the levels where tintinnomorphs were found).
Abbreviations: a, counts; %, relative frequencies.

Depth (cm)	Spores		Pollen grains		Fungi		Fresh algae		Dinoflagellate cysts		Foraminiferal linings		Tintinnomorphs		Total palynomorphs
	(a)	(%)	(a)	(%)	(a)	(%)	(a)	(%)	(a)	(%)	(a)	(%)	(a)	(%)	
5	153	58	67	25	44	17	1	0	0	0	0	0	0	0	265
10	144	53	92	34	34	13	0	0	0	0	0	0	0	0	270
15	153	52	108	37	32	11	0	0	0	0	0	0	0	0	293
20	116	32	157	43	74	20	20	5	0	0	0	0	0	0	367
25	103	33	50	16	136	44	23	7	0	0	0	0	0	0	312
30	69	24	22	8	183	63	17	6	0	0	0	0	0	0	291
35	68	22	99	31	133	42	15	5	0	0	0	0	0	0	315
40	40	12	199	61	78	24	8	2	0	0	0	0	0	0	325
45	39	11	246	66	80	22	6	2	0	0	0	0	0	0	371
50	79	21	173	46	118	31	5	1	0	0	0	0	0	0	375
55	81	25	129	39	114	35	5	2	0	0	0	0	0	0	329
60	116	41	96	34	40	14	29	10	0	0	0	0	0	0	281
65	99	41	57	23	41	17	47	19	0	0	0	0	0	0	244
70	103	45	45	19	39	17	44	19	0	0	0	0	0	0	231
75	77	35	51	23	65	30	26	12	0	0	0	0	0	0	219
80	42	14	34	12	208	71	7	2	0	0	0	0	0	0	291
85	82	26	16	5	170	54	44	14	0	0	0	0	0	0	312
90	32	12	10	4	188	69	41	15	0	0	0	0	0	0	271
95	36	25	21	15	58	40	29	20	0	0	0	0	0	0	144
100	26	21	24	19	41	33	34	27	0	0	0	0	0	0	125
105	73	32	34	15	78	34	45	20	0	0	0	0	0	0	230
110	45	29	17	11	64	42	28	18	0	0	0	0	0	0	154
115	24	20	6	5	57	47	34	28	0	0	0	0	0	0	121
120	31	21	14	9	60	41	43	29	0	0	0	0	0	0	148
125	24	16	14	10	39	27	69	47	0	0	0	0	0	0	146
130	30	13	14	6	77	34	107	47	0	0	0	0	0	0	228
135	54	28	32	17	47	25	57	30	0	0	0	0	0	0	190
140	44	27	26	16	63	38	33	20	0	0	0	0	0	0	166
145	69	42	13	8	83	50	0	0	0	0	0	0	0	0	165
150	38	44	15	17	32	37	0	0	1	1	1	1	0	0	87
155	43	59	5	7	19	26	1	1	4	5	1	1	0	0	73
160	46	62	1	1	4	5	0	0	21	28	2	3	0	0	74
165	21	36	5	8	22	37	1	2	8	14	2	3	0	0	59
170	44	54	16	20	5	6	0	0	15	18	2	2	0	0	82
175	55	51	5	5	13	12	2	2	26	24	2	2	5	5	108
180	41	71	3	5	7	12	0	0	3	5	2	3	2	3	58
185	38	40	10	11	5	5	5	5	22	23	10	11	4	4	94
190	19	46	2	5	3	7	0	0	16	39	1	2	0	0	41
195	31	45	5	7	10	14	3	4	15	22	5	7	0	0	69
200	24	44	4	7	11	20	0	0	11	20	2	4	3	5	55
205	96	48	17	8	76	38	1	0	5	2	3	1	3	1	201
210	51	51	14	14	12	12	0	0	16	16	2	2	5	5	100
215	31	52	3	5	5	8	0	0	14	23	6	10	1	2	60
220	24	28	18	21	20	23	1	1	20	23	3	3	0	0	86
225	31	48	8	12	14	22	0	0	5	8	5	8	2	3	65
230	31	58	4	8	8	15	0	0	4	8	4	8	2	4	53

Table 1. Cont.

Depth (cm)	Spores		Pollen grains		Fungi		Fresh algae		Dinoflagellate cysts		Foraminiferal linings		Tintinnomorphs		Total palynomorphs
	(a)	(%)	(a)	(%)	(a)	(%)	(a)	(%)	(a)	(%)	(a)	(%)	(a)	(%)	
235	27	47	2	4	10	18	0	0	14	25	3	5	1	2	57
240	13	52	1	4	4	16	0	0	4	16	3	12	0	0	25
245	17	39	7	16	4	9	0	0	6	14	4	9	6	14	44
250	30	61	7	14	3	6	0	0	3	6	5	10	1	2	49
255	25	44	10	18	7	12	0	0	5	9	10	18	0	0	57
260	17	26	18	27	10	15	1	2	14	21	3	5	3	5	66
265	35	40	21	24	18	20	2	2	4	5	6	7	2	2	88
270	24	32	19	25	9	12	1	1	17	22	5	7	1	1	76
275	15	56	3	11	5	19	0	0	0	0	3	11	1	4	27
280	15	27	12	22	2	4	0	0	23	42	3	5	0	0	55
285	21	36	10	17	11	19	0	0	14	24	2	3	0	0	58
290	11	48	5	22	3	13	0	0	2	9	2	9	0	0	23
295	19	36	7	13	11	21	0	0	14	26	2	4	0	0	53
300	12	32	14	38	10	27	0	0	1	3	0	0	0	0	37

Table 2. AMS ^{14}C and calibrated ages of selected samples (using CALIB 7.1; Stuiver *et al.*, 2016) from the PSC-03 core. *pMC is the percentage of modern carbon relative to the modern reference, is presented when the analyzed material has more ^{14}C than the modern reference, this sample is indicating a post bomb (Modern).

Laboratory reference	Depth (cm)	^{14}C age BP	Age (cal yr BP 2σ)	Mean calibrated age (cal yr. BP)	Material
UGAMS # 25848	10	100.85 $\pm$ 0.30 *pMC	Modern	----	sediment
UGAMS # 26518	90	2520 $\pm$ 25	2426 – 2721	2579	wood
UGAMS # 26983	120	2660 $\pm$ 20	2723 – 2777	2751	sediment
UGAMS # 26517	265	3340 $\pm$ 25	3598 – 3607	3522	sediment
UGAMS # 26982	280	5490 $\pm$ 25	6195 – 6299	6246	sediment
UGAMS # 22214	300	6960 $\pm$ 30	7676 – 7832	7744	sediment

The descriptive key proposed by Van Waveren (1994) is based on the morphological characterization of tintinnid organs, but the proposed types are designated as tintinnomorphs. Moreover, these features are named with different terms from those used for tintinnids, in order to avoid a direct attribution to the latter. In this way, the six main features are: (i) a corolla enclosing a chamber; (ii) an opening (sometimes with operculum); (iii) a calyx (a hollow appendix); (iv) a stem (a massive appendix); (v) a horn (calyx plus stem) and (vi) a collar (Figure 3B). Variations in shape, surface structure (ornamentation), presence, number and type of stems, opening position, shape and ornamentation of collar are the parameters used in the classification criteria (Figures 3C–K).

Because the thickness of the wall may reflect the organism's life cycle (Van Waveren, 1994), this characteristic was not used as a classification criterion. Size and color were not used as a classification criterion for tintinnomorphs either. A total of eleven main types of tintinnomorphs can be recognized by means of this description: (1) spherical ("SPHER"); (2) elliptical ("ELLIP"); (3) elongated elliptical

("ELEL"); (4) egg-shape, aborally blunt ("ESAB"); (5) egg-shape, orally blunt ("ESOB"); (6) hexagonal ("HEXA"); (7) rectangular ("RECT"); (8) asymmetrically rhombic, aborally blunt ("ARAB"); (9) asymmetrically rhombic, orally blunt ("AROB"); (10) triangular ("TRIA"); (11) tetragonal ("TETRA").

At the end of each coding, an indication for the presence (O) or the absence (NO) of ornamentation is given, as well as, a final number (1, 2, n...) identifying differences within the morphotypes.

SYSTEMATIC AND DESCRIPTION OF TINTINNOMORPHS TYPES

Six tintinnomorphs types were described according to their morphological features. The recognized types are SPHERO-1, ELELNO-14, ESABNO-6, HEXANO-2, RECTNO-1 and AROBNO-3 (Figure 4). Although the size of the tintinnomorphs is not a classification criterion, it is worth mentioning that these specimens presented average measurements of 170 μm in length per 100 μm wide.

Figure 3. General framework of classification criteria: **A**, three different categories of organic remains assignable to tintinnids: a lorica, a pouch attached to the aboral (basal) side of the lorica, a cyst encapsulated in the pouch; **B**, main features of tintinnomorphs: a corolla enclosing a chamber, an opening (sometimes with operculum), a calyx (a hollow appendix), a stem (a massive appendix), a collar; **C**, shapes of the corolla of tintinnomorphs; **D**, surface structures of tintinnomorphs; **E**, shapes of the calyx of tintinnomorphs; **F**, presence and number of stems of tintinnomorphs; **G**, types of stems of tintinnomorphs; **H**, distinct positions of the opening in tintinnomorphs; **I**, collar elongation of tintinnomorphs defined by the ratio between its height and its diameter (h/d); **J**, collar shapes of tintinnomorphs; **K**, collar ornamentation of tintinnomorphs. All the figures have been modified from Van Waveren (1994).

SPHERO-1
(Figure 4A)

Description. One specimen: tintinnomorph of spherical shape ornamented, without calyx, without stem, opening large (equatorial), no collar.

Occurrence. Depth of 265 cm.

Comment. Specimens of tintinnomorph type SPHERO were recorded from modern surface sediments of the Banda Sea, Indonesia (Van Waveren, 1994).

ELELNO-14
(Figure 4B)

Description. One specimen: tintinnomorph elongated with triangular calyx, not ornamented, tailed stem, no collar, opening inferior to equatorial.

Occurrence. Depth of 250 cm.

Comment. Specimens of tintinnomorph type ELELNO were recorded from modern surface sediments of the Banda Sea, Indonesia (Van Waveren, 1994). Oliveira (2003) reported specimens similar to tintinnomorph type ELELNO, identified as worm eggs, from Pleistocene marine environment of Campos Basin (Brazil). Matsuoka *et al.* (2017) reported specimens assigned to the type ELELNO-13 (*sensu* Van Waveren, 1994) from modern marine deposits in Asia.

ESABNO-6
(Figures 4C–E)

Description. Six specimens: tintinnomorph egg-shaped, aborally blunt type, not ornamented, without calyx, without stem, rooted stem, opening medium (between 30°–75°).

Occurrence. Depth of 260, 255, 250, 200, 185 and 175 cm.

Comment. Specimens of tintinnomorph type ESABNO were recorded from modern surface sediments of the Banda Sea, Indonesia (Van Waveren, 1994). Stancliffe & Matsuoka (1991) reported a specimen similar to tintinnomorph type ESABNO. This specimen was identified as ? *Domasiella* sp. (acritarch), from Holocene marine sediments, off coast of northwestern Kyushu (Japan). Sparica *et al.* (2005) reported specimens similar to tintinnomorph type ESABNO, identified as tintinnid chitinous loricae, from Holocene shallow-marine environment of northern Dalmatia (Croatia).

RECTNO-1
(Figure 4F)

Description. Two specimens: tintinnomorph rectangular type, not ornamented, without calyx, without stem, opening equatorial and no collar.

Occurrence. Depth of 225 and 185 cm.

Comment. Specimens of tintinnomorph type RECTNO were recorded from modern surface sediments of the Banda Sea, Indonesia (Van Waveren, 1994).

HEXANO-2
(Figures 4G–H)

Description. Six specimens: tintinnomorph hexagonal type, not ornamented, with small calyx, without stem, opening large, no collar.

Occurrence. Depth of 275, 235, 215, 210 and 205 cm.

Comment. Similar specimens to tintinnomorphs included in type HEXA have been recorded from middle to late Holocene sediments with marine influence of CPRS in Capão do Leão (Neves & Bauermann, 2001, 2003); from Upper Pleistocene to Holocene sediments of Piratuba and Faxinal (Roth & Lorscheister, 2016); from Holocene brackish swamp deposits sediments of CPSC, in São João do Sul (Cancelli *et al.*, 2012), identified as remains of flatworm eggs. Holocene marine sediments from Lapatia Bay (Beagle Channel, Argentina), Borromei & Quatrocchio (2001) found a specimen similar to the tintinnomorph HEXANO-3 (*sensu* Van Waveren, 1994), identified as tintinnid lorica. Mudie *et al.* (2011) recorded specimens related to the tintinnomorph HEXANO-2 from Holocene marine deposits of the Marmara Sea (Turkey), identified as tintinnid lorica or Turbellaria Class worm egg capsule.

AROBNO-3
(Figure 4I)

Description. One specimen: tintinnomorph asymmetrically rhombic, orally blunt, not ornamented, without calyx, without stem, with more than three tail-like stems, opening medium, middle to long diverging collar, no collar ornamentation.

Occurrence. Depth of 265 cm.

Comment. Similar specimens to tintinnomorphs, included in type AROB, were recorded from marine fine-grained carbonates deposit of the Early Cretaceous (Berriasian) of France (Gorin & Steffen, 1991), identified as tintinnids (*sensu* Reid & John, 1981) or single chamber foraminiferal linings (*sensu* Stancliffe, 1989).

TINTINNOMORPHS: ENVIRONMENTAL SIGNATURE

In modern marine sediments, tintinnomorphs always are subordinated to others marine palynomorphs (dinoflagellate cysts, acritarchs, foraminifera linings and copepod eggs) (Kawamura, 2004; Hardy & Wrenn, 2009; Matsuoka *et al.*, 2017). Kawamura (2004) suggests that the concentration of the tintinnomorphs in sediments is inversely correlated to the depth of the water column.

Tintinnomorphs were found as an accessory element of the zooplankton component of palynomorph association from the outer shelf to lower continental slope of the Sunda Shelf, South China Sea. The tintinnomorphs were recorded in all sites of transect, but presented better concentrations from the inner shelf and slope palynological assemblage (Kawamura, 2004). The occurrences of tintinnomorphs in slope assemblages suggest a mixed signal of estuary high productivity species and oceanic low productivity species. This mixed signal is resulting by transport processes of the circulation of seafloor bottoms (Kawamura, 2004).

Figure 4. Photomicrographs of tintinnomorphs recorded from the PSC-03 core. **A**, SPHERO-1 (slide MPP: 11262, England Finder: K35); **B**, EELNO-14 (11258, T46); **C–E**, ESABNO-6 (11245, G45-4), (11244, C57-4), (11249, W31-4); **F**, RECTNO-1 (11246, B52); **G–H**, HEXANO-2 (11251, D35-2); **I**, AROBNO-3 (11262, E37-2). Scale bars = 50 μ m.

Preservation of tintinnomorphs in sediments may be related to the combined effect of high productivity and high sedimentation rates in the depositional site (Van Waveren, 1994; Van Waveren & Visscher, 1994). Hardy & Wrenn (2009) studying the palynomorph distribution in modern deltaic and shelf sediments of the Mahakam delta (Borneo), recorded a low quantity and variety of tintinnomorphs, however this low concentration was also verified in dinoflagellate cysts.

In palynological assemblages in South America, where they were reported, paleoenvironmental interpretations are implying marginal marine conditions with high input

of continental organic matter (Grill *et al.*, 2002; Borromei & Quattrocchio, 2001, 2007). According to Roncaglia (2004), the increase of tintinnid loricae, dinoflagellate cysts concentration, planktonic crustacean eggs as well as structured brown phytoclasts, plant tissue and sporomorphs from Holocene sediments of the Skálafjörð (Faroe Islands) were related to the increase of primary productivity in the waters of the fjord. For Mudie *et al.* (2010, 2011), in restricted marine basins, such as Black and Caspian Sea, the literature on living equivalents of the tintinnids suggests that nutrients are probably more important than salinity for the blooms.

During a combined optical and biomarker analysis of Holocene sediments of the Gulf of Mexico, Meckler *et al.* (2008) identified tintinnid loricae in excellent state of preservation, associated with chitinous crustacean remains and dinoflagellate cysts. In this case, the alternation of levels with marine palynomorphs (tintinnid loricae, crustacean remains and dinoflagellate cysts) with those ones of terrestrial palynomorphs (pollen grains and spores) was resulting from the interference of climatic and ecological oscillations.

FINAL REMARKS

The tintinnomorphs recorded in the PSC-03 core are associated with terrestrial (spores, pollen grains, fungi and freshwater algae) and marine (dinoflagellate cyst, foraminifera linings) palynomorphs. They become absent from levels where marine palynomorphs show a tendency of scarcity or are absent (Table 1).

Samples from the PSC-03 core where tintinnomorphs occur also bear dinoflagellate cysts of the genera *Brigantedinium*, *Lejeunecysta*, *Operculodinium*, *Spiniferites*, *Selenopemphix* besides foraminifera linings. All these taxa are reliable indicators of marine conditions, suggesting that the depositional site area was influenced by marine water.

The inference of marine incursion over Coastal Plains is supported by other studies on the coastal plain of Santa Catarina (Behling & Negrelli, 2001; Amaral *et al.*, 2012; Angulo *et al.*, 2006; Kuhn *et al.*, 2017), as well as in Coastal Plain of Rio Grande do Sul (Lorscheitter & Dillenburg, 1998; Meyer *et al.*, 2005; Medeanic *et al.*, 2009). Similarly, the Coastal Plain of the South Atlantic margin of South America offers further environmental proxies (Martínez & Rojas, 2013; Mourelle *et al.*, 2015; Candel & Borromei, 2016).

The scarcity of systematic studies on tintinnomorphs as well as the uncertainties on their biological affinity impairs the use of this organic-walled microfossil for paleoenvironmental interpretations; the analysis considering the total fossil association can elucidate this issue. The morphological system proposed by Van Waveren (1994) has proved to be effective in the initial characterization of these fossil organic structures, since it allows their characterization in an artificial grouping. This bars the controversial classification of palynomorphs as lorica, cyst or pouch that has been observed in previous studies.

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