

# First record of a brackish radiolarian (Polycystina): *Lophophaena rioplatensis* n. sp. in the Río de la Plata estuary

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*Vertically stratified bottle plankton samples collected in the Río de La Plata estuary (Atlantic coast of South America at ~35°S) and in coastal waters off Mar del Plata (~38°S) in December 1999 and November 2001 yielded up to 394 live cells l<sup>-1</sup> of a single new nassellarian species: Lophophaena rioplatensis n. sp. (family Plagoniidae). In estuarine waters, the species was recorded at salinities as low as 15.4 p.s.u.; densities in excess of 100 cells l<sup>-1</sup> were found at salinities ranging from 16.9 p.s.u. These extremely high concentrations (the highest ever reported in the literature), as well as the fact that >90% of the individuals recorded contain cytoplasm, indicate that these are self-sustaining populations which thrive in the estuary (and in nearshore coastal waters), probably due to plentiful dissolved silica and an abundant food supply. Lophophaena rioplatensis is the first polycystine brackish-water species described. This finding shows that radiolarian fossils are not unequivocally associated with open-ocean conditions, but may also be useful indicators of coastal and brackish estuarine paleoenvironments.*

## INTRODUCTION

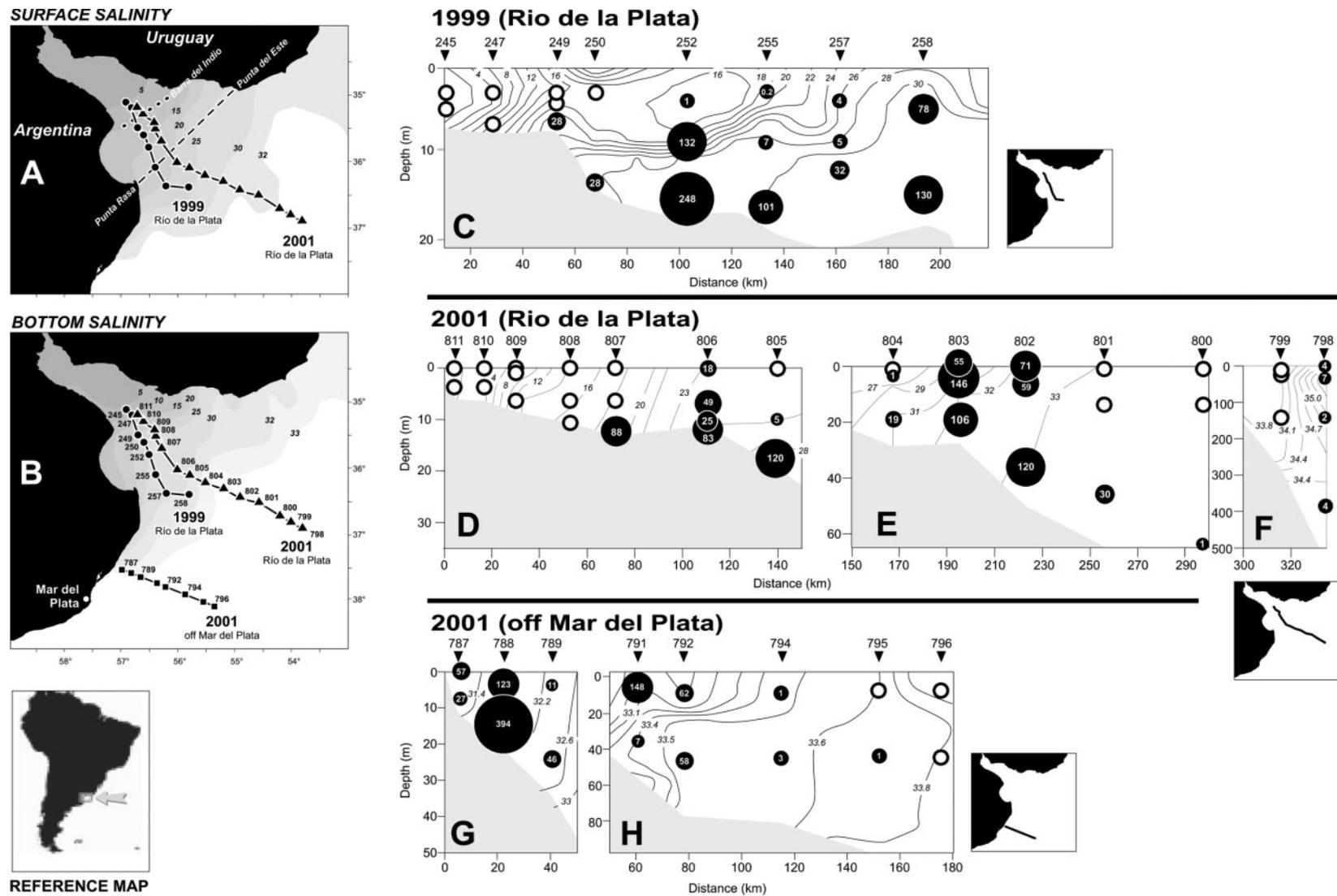
Polycystine radiolarians—marine planktonic protists with a siliceous skeleton—are typically pelagic organisms, very scarce or absent altogether in coastal waters, especially where salinity falls below normal open-ocean values (Kling, 1978; Anderson, 1983; Caron and Swanberg, 1990; Anderson *et al.*, 2002). Close to the coast, they may occur in sizable numbers in locations where the continental shelf is very narrow and oceanic waters impinge on the shore (Beers and Stewart, 1969), or in very special settings, like some Norwegian fjords (Swanberg and Bjørklund, 1986, 1987), yet invariably at salinities >30 p.s.u. Polycystines have not been found either in land-locked seas (Black and Caspian Seas) or in marginal seas with low salinity, such as the White and the Baltic Seas (Kruglikova, 1995).

This paper reports the discovery of very dense monospecific populations of a new nassellarian species in the estuary of the Río de la Plata at salinities as low as 15.4 p.s.u., and in coastal marine waters off Mar del Plata,

Argentina, at salinities <31.4 p.s.u. This finding casts doubts on the traditional view that all radiolarians are typically pelagic organisms, opening interesting questions on the use of their fossils as indicators of coastal, brackish conditions.

## METHOD

Samples used for this work were obtained in the Río de la Plata estuary during INIDEP cruises CC-1799 (December 12–14, 1999) and EH-0901-II (November, 22–26 2001), and off Mar del Plata on INIDEP cruise EH-0901-II (November 20–21, 2001) (Figure 1). Plankton were collected by means of 5 l Niskin bottles. Four liters of water were concentrated by reverse filtration through a 20- $\mu$ m-mesh gauze and preserved with Bouin's solution. Counts of the microzooplanktonic organisms were carried out under the inverted microscope in 10 or 25 ml settling chambers. Temperature and salinity profiles were measured using a SeaBird 9plus conductivity–temperature–depth



**Fig. 1.** Geographic location of the transects performed superimposed on the typical summer salinity field for the surface (**A**) and for the bottom waters (**B**), as indicated by long-term, historical data [from Guerrero *et al.* (Guerrero *et al.*, 1997)], and vertical profiles of salinity (p.s.u.) and radiolarian concentrations (ind. l<sup>-1</sup>, open circles are zero values) in the Río de la Plata in 1999 (**C**) and in 2001 (**D–F**, note changes in depth scale), and off Mar del Plata in 2001 (**G** and **H**, note change in depth scale). The broken line between Punta del Este and Punta Rasa indicates the conventional outer limit of the estuary.

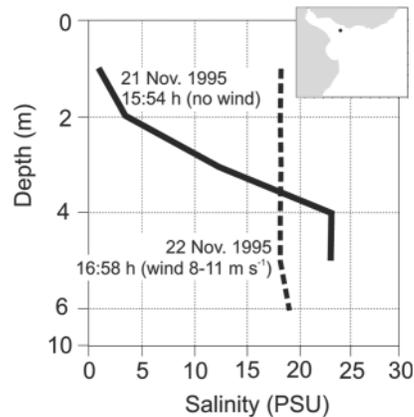
(CTD) profiler. Data were standardized to 0.5 m bins, with a precision of  $\pm 0.03^\circ\text{C}$  for temperature and  $\pm 0.01$  p.s.u. for salinity.

### Environmental setting

The Río de la Plata is a funnel-shaped estuary 320 km long and 230 km wide at the mouth. Its depth varies between  $<5$  and  $\sim 15$  m. The discharge of the Paraná and Uruguay rivers into the estuary moves oceanwards within a relatively shallow (1–4 m) buoyant plume overlaying a saltwater wedge originating offshore. The oceanward extension of this plume, its spatial and seasonal distribution, and the vertical salinity gradient are controlled by wind stress, river discharge and the Coriolis force. During the spring–summer, freshwater run-off occurs chiefly along the south-western (Argentine) coast; the freshwater plume extends as far as  $>300$  km into the ocean from the outer limit of the estuary [the line from Punta Rasa, Argentina, to Punta del Este, Uruguay, see Figure 1A; (Guerrero *et al.*, 1997)]. In calm weather (wind below  $\sim 10$  m  $\text{s}^{-1}$ ), the water column is characterized by a strong vertical salinity gradient with maximum values up to 15 p.s.u.  $\text{m}^{-1}$  (at a bottom depth of 6 m), especially in the central and southern sections of the estuary (Framiñan *et al.*, 1999). Beyond the Barra del Indio shoal (Figure 1A), the estuary discharges waters chiefly along the two coasts; strong stratification may occur in both or in only one of these coastal channels. Farther offshore, a partially stratified regime is characterized by an increase in thickness (7–8 m) of the upper layer. The boundary between the partially stratified regime and the open ocean defines the surface salinity front (Mianzan *et al.*, 2001). In the inner portion of the estuary, the saltwater wedge is restricted to periods of calm weather, at wind speeds  $>11$  m  $\text{s}^{-1}$  the halocline disappears completely (Figure 2). Nevertheless, some degree of stratification seems to be the norm in the estuary, rather than the exception: synoptic data indicate that mean annual surface to bottom salinity gradients are around 5 p.s.u. [(Guerrero *et al.*, 1997); see Figure 1A and B]. Temperature in the estuary is around  $10^\circ\text{C}$  in June–August and  $21$ – $25^\circ\text{C}$  in December–February at all depths.

The tidal regime is mixed, mostly semidiurnal. Maximum tidal current speeds for a rising tide are slightly over  $0.4$  m  $\text{s}^{-1}$ , whereas for an ebb tide they are around  $0.5$  m  $\text{s}^{-1}$ . Somewhat stronger currents lasting longer periods of time (usually 1–3 days) may occur during storm surges due to strong and persistent north-westward winds (Framiñan *et al.*, 1999).

Waters off Mar del Plata can be divided into three more or less clearly defined longshore bands (Fernández Aráoz *et al.*, 1991; Carreto *et al.*, 1995): (i) slope waters (at bottom depths  $>150$ – $180$  m) dominated by the



**Fig. 2.** Short-term changes in the stratification of the Río de la Plata as indicated by vertical distributions of salinity on two consecutive days in 1995 [modified from Framiñan *et al.* (Framiñan *et al.*, 1999)].

subantarctic Malvinas (= Falkland) Current; (ii) Subantarctic Shelf Waters, separated from the former by a shelf-break front; and (iii) the Inner Coastal System area (to  $\sim 30$  km offshore), where wind- and tide-induced mixing yield a homogeneous water column year round. Waters between the coastline and the Malvinas Current are periodically influenced by Río de la Plata freshwater run-off (Carreto *et al.*, 1995; Piola and Rivas, 1997; Lucas *et al.*, 1999). These intrusions typically occur in the spring–summer, and are indicated by low salinities and by the presence of subtropical planktonic flora and fauna advected from the Río de la Plata plume area (Lange, 1985; Negri *et al.*, 1992; Lucas *et al.*, 1999).

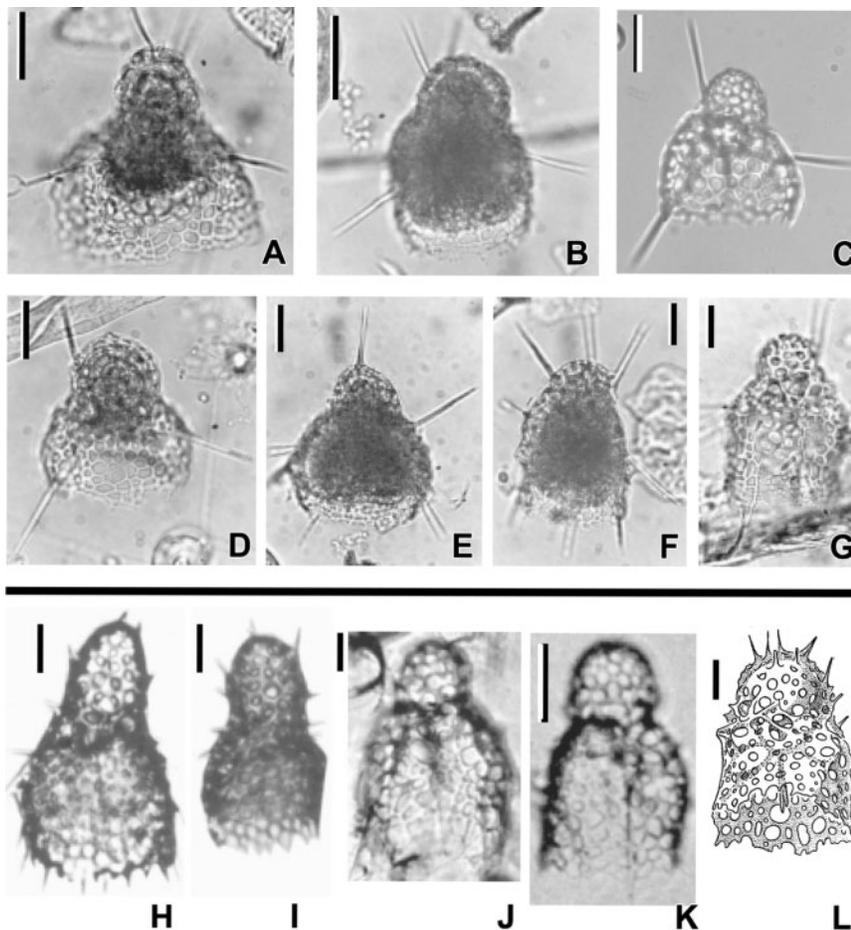
## RESULTS

Figure 1A and B illustrate the distribution of the sampling stations occupied superimposed on the typical summer salinity field for the surface (Figure 1A), and for the bottom waters (Figure 1B). Figure 1C–H are vertical profiles of the transects investigated, illustrating the distribution of salinity at the time of sampling and the radiolarian concentrations recorded.

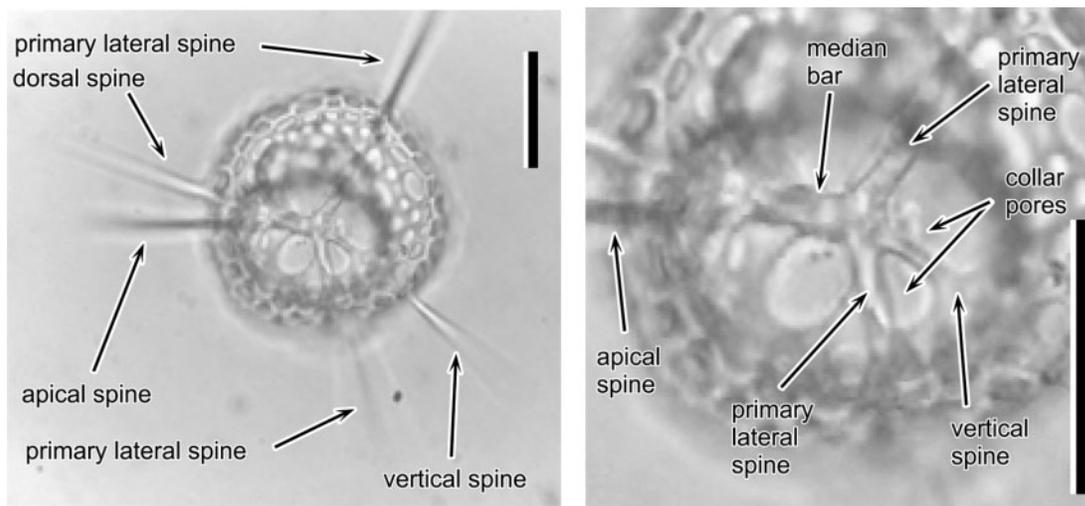
During 1999, in the estuary the water column was strongly stratified (Figure 1C); highest numbers of radiolarians were observed in the bottom layers and in the middle and outer sections of the estuary, in association with the highest salinity values. In 2001, on the other hand, vertical stratification was weak; radiolarian densities were evenly distributed from surface to bottom, and maximum concentrations occurred  $\sim 100$  km away from the oceanward end of the transect (Figure 1D–F).

Off Mar del Plata, highest concentrations occurred  $\sim 20$  km off the coast (up to  $394$  shells  $\text{l}^{-1}$ ; Figure 1G)





**Fig. 4.** *Lophophaena rioplatensis* n. sp. (C: holotype), general view of shells from the Río de la Plata (A–G) and illustrations of similar morphotypes from the literature (H–L). All specimens from the Río de la Plata contain cytoplasm, except for (C) and (G), which are empty skeletons. (H) and (I) *Lithomelissa* cf. *galeata* (Ehrenberg), according to Benson (Benson, 1966). (J) *Lithomelissa setosa* Joergensen, according to Boltovskoy and Riedel (Boltovskoy and Riedel, 1980). (K) *Trisulcus* sp. aff. *T. testudus* Petrushevskaya, according to Boltovskoy and Riedel (Boltovskoy and Riedel, 1987). (L) *Antarctissa* cf. *longa* (Popofsky), according to Petrushevskaya (Petrushevskaya, 1971). Scale bars represent 20 μm.



**Fig. 5.** *Lophophaena rioplatensis* n. sp.. Details of the internal skeleton. Scale bars represent 20 μm.

recorded, and none of them was retrieved from brackish waters. *Lophophaena* was not found in brackish waters before either, but the definition of the genus fits our organisms adequately [cf. (Petrushevskaya, 1981; De Wever *et al.*, 2001)]. In oceanic samples from this area, Boltovskoy and Riedel (Boltovskoy and Riedel, 1980) recorded specimens roughly similar to *L. rioplatensis*, but with a comparatively larger and rounder cephalis, and larger and more regular pores (Figure 4I). At any rate, given the widely different ecological settings involved, we contend that skeletal similarity between *L. rioplatensis* and any previously described polycystine species would indicate cryptic speciation, rather than synonymy.

### Ethymology

The name '*rioplatensis*' refers to the estuary where it was first recorded: the Río de la Plata.

### Type locality

35°50'45"S, 56°30'07"W (Río de la Plata), subsurface plankton.

### Holotype

Deposited in the Museo Argentino de Ciencias Naturales under number MACN-Fo 13619, England Finder coordinates O33.

## DISCUSSION

To our knowledge, this finding reports the highest polycystine densities ever recorded in the water column, as well as the lowest salinities where live radiolarians have been observed.

Radiolarian abundances in most open-ocean environments, including the Southwestern Atlantic, seldom exceed 1–2 individuals (ind.)  $l^{-1}$  (Boltovskoy, 1999). In coastal upwelling and other very productive nearshore areas, like Norwegian fjords, values as high as 70–80 ind.  $l^{-1}$  have been reported (Caron and Swanberg, 1990); this is still substantially lower than our maxima of 248 (in the Río de la Plata estuary) to 394 ind.  $l^{-1}$  (off Mar del Plata; Figure 1).

In her extensive monograph on the Nassellaria from the World Ocean, Petrushevskaya (Petrushevskaya, 1971) lists the salinity ranges of 145 polycystine species; the lowest value given is 32 p.s.u. (for *Amphimelissa setosa*). In the Norwegian fjords, where input of continental fresh water can be very substantial, radiolarian populations are restricted to depths below the permanent halocline, whereby only the uppermost 20–25 m host low-salinity waters (down to 10–12 p.s.u.), whereas the remainder of the water column has normal marine values (Swanberg and Bjørklund, 1987); in these fjords,

radiolarians have not been found at salinities <30 p.s.u. (K. Bjørklund, personal communication). In our materials, on the other hand, although highest polycystine densities are generally associated with salinities ~30 p.s.u., live radiolarians were present at salinities as low as 15.4 p.s.u. (Figure 3). Figure 1C suggests that in calm weather, when the water column in the estuary is strongly stratified, *L. rioplatensis* dwells preferably within the near-bottom saltwater wedge; however, since this halocline can be swiftly destroyed by wind action (see Figure 2), the near-bottom saline waters cannot represent a permanent refuge for this population. Thus, while the protists prefer a more saline milieu, they can withstand long periods (at least days, probably weeks) of salinity levels below 20 p.s.u.

The fact that the radiolarians recorded represent an actively growing *in situ* population, rather than expatriated specimens, is suggested by the presence of cytoplasm in almost all the shells observed. Admittedly, the presence of cytoplasm alone does not unequivocally prove that these were living cells at the time of collection (Boltovskoy and Lena, 1970; Bernhard, 1988), but the fact that the radiolarians recorded are not the relict of an earlier saltwater intrusion in the form of advected dead cells is suggested by the protist's extremely high densities and by the fact that all specimens belong to a single morphotype. Indeed, a random, physically driven advection process would not be expected to bring into the estuary very large numbers of a single morphotype, but only a few representatives of the >100 species that inhabit the offshore waters (Boltovskoy and Riedel, 1980; Boltovskoy, 1999).

The presence of extremely high densities of a single species points to the fact that although the estuarine milieu is strongly adverse to the polycystines in general, it is beneficial to the only species that managed to overcome the limiting conditions. This association between low diversity and high standing stock has been noticed before in radiolarians, both in the open ocean (Boltovskoy *et al.*, 1993) and in coastal areas (Swanberg and Bjørklund, 1986, 1987). A few authors also suggested that neritic radiolarian assemblages are less diverse than their pelagic counterparts, but reports of radiolarian specific composition indicative of nearshore environments are sketchy and contradictory (McMillen, 1979; Palmer, 1986; Kruglikova, 1989; Nishimura *et al.*, 1997).

Because salinity plays a major role in the distribution of most marine organisms, we contend that this may be one of the major limiting factors for the radiolarians as well. On the other hand, abundant food resources and skeleton-building material, as well as low grazing pressures, may be responsible for the unusually high

standing stocks of the only species present. Typical chlorophyll *a* concentrations in the Río de la Plata ( $\sim 3 \text{ mg m}^{-3}$ ) are 2–6 times higher than in nearby oceanic waters [ $0.5\text{--}1.5 \text{ mg m}^{-3}$ ; (Armstrong *et al.*, 2004)]. Furthermore, particulate organic carbon, a more realistic indicator of food availability, is 15–20 times more abundant in the Río de la Plata than in marine offshore waters (Bonetto and Lancelle, 1981; Depetris and Kempe, 1993; Boltovskoy *et al.*, 2000). In addition, estuarine waters are normally >30 times richer in dissolved silica, a key nutrient for the growth of siliceous polycystine skeletons, than the nearby ocean (Carreto *et al.*, 1986; Piola and García, 1993). During the 1999 cruise, silica concentrations in the Río de la Plata fell from  $124 \mu\text{M}$  in the estuary (station 245) to  $11 \mu\text{M}$  at its mouth (station 257; see Figure 1B).

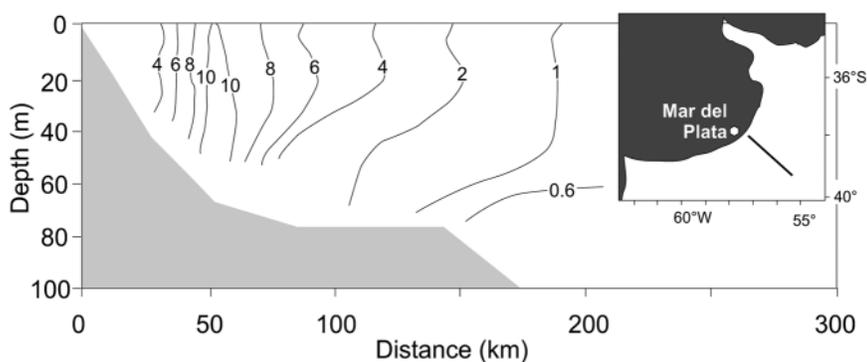
Up to  $\sim 30\text{--}32$  p.s.u., recorded densities of *L. rioplatensis* in the Río de la Plata increase with increasing salinity (Figure 3), but maximum concentrations do not occur in the outermost section of the estuary, where salinity values are highest, but 100–200 km from the innermost station occupied, about midway between the fresh waters and the open ocean. Also off Mar del Plata, densities peak where salinities are <32 p.s.u., falling to near zero values in offshore waters with normal marine salinity values (Figure 1G and H). This pattern may support the above interpretation of the influence of food availability on the unusually high radiolarian abundances found: in the estuary, highest concentrations of particulate organic matter, including phytoplankton, are permanently located in this middle section (Boschi, 1988). Off Mar del Plata, the area of highest chlorophyll concentrations is more variable, but peak values in the coastal front are common in the spring and in the fall [(Carreto *et al.*, 1995); see Figure 6].

The fact that all the other  $\sim 500$  living polycystine species are strictly oceanic leaves little doubt that the original seeding area for *L. rioplatensis* is the marine waters off the Río de la Plata. As a matter of fact, it is

widely acknowledged that estuaries are a major doorway for the immigration of marine species into continental waters (Pennack, 1989), and although the comparatively strong environmental variability of fresh waters in general makes this doorway a difficult one to pass (Pearse, 1950), there are examples of species that adapted to the fresh-water environment in historical times (Miller, 1958).

The above considerations suggest that the Río de la Plata population of *L. rioplatensis* is presently a self-sustaining one, whose connections with other populations of the species are restricted by the surrounding open ocean. On the other hand, the origin and fate of the population detected in marine coastal waters off Mar del Plata are less clear. The distribution pattern illustrated in Figure 1G and H strongly suggests that this species is either absent or very rare offshore, where it has not been recorded in pelagic waters (Boltovskoy, 1999). This, and the fact that the area of the innermost stations of our transect off Mar del Plata, the ones with highest concentrations of *L. rioplatensis*, is periodically influenced by Río de la Plata waters (see above), associated with the low salinities in this area, suggests that this southern population is connected with, and probably fed by, the Río de la Plata pool.

It seems interesting to point out that two-segmented plagoniids generally similar to the one recorded in the Río de la Plata were found to dominate widely different environments which share one major trait: their very high loads of particulate organic carbon. In the California Current, a highly productive western boundary current area, small, two-segmented plagoniids comprise up to 70% of the polycystines present year around in the upper 100 m (Boltovskoy and Riedel, 1987). In the highly productive coastal upwelling system off Cap Blanc (eastern tropical Atlantic), plagoniids represent 42% of all polycystines (Boltovskoy *et al.*, 1996). On the other hand, in open-ocean plankton and sediment samples, these morphotypes usually account for <5% of overall polycystines (Boltovskoy and Riedel, 1980;



**Fig. 6.** Distribution of chlorophyll *a* ( $\text{mg m}^{-3}$ ) in September 1987 off Mar del Plata [from Carreto *et al.* (Carreto *et al.*, 1995)].

Boltovskoy, 1991, 1992). Although high plagoniid abundances are not circumscribed to eastern boundary current and upwelling areas [plagoniids are dominant components of Arctic, Subarctic and North Atlantic radiolarian assemblages; (Kruglikova, 1988; Swanberg and Eide, 1992)], in transitional to tropical areas upwelling conditions seem to favor their development selectively. Thus, our present results reinforce the assumption that plagoniids might be useful paleoindicators of high productivity and/or high particulate organic carbon conditions.

This finding has implications for paleoceanographic interpretations. The close association of polycystine radiolarians with open-ocean areas has traditionally been used in microfossil-based paleoenvironmental work as an indicator of pelagic paleosettings. Because practically all of the known radiolarian assemblages are oceanic, fossil facies containing radiolarian remains are assumed to have been engendered in normal salinity, marine settings. Our finding shows that abundant radiolarian remains can also be associated with brackish, estuarine waters. Furthermore, it provides useful data for the interpretation of the paleoenvironmental signal conveyed by very low diversity or monospecific radiolarian assemblages.

## ACKNOWLEDGEMENTS

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