



# *Tegula atra* (Lesson, 1830) (Mollusca, Gastropoda) in the marine Quaternary of Patagonia (Argentina, SW Atlantic): Biostratigraphical tool and palaeoclimate-palaeoceanographical signal



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## ABSTRACT

Results of the systematic review and regional palaeobiogeographical context of *Tegula atra*, including morphometric, multivariate and cladistic analyses, show that it is a keystone species in the marine Quaternary of Argentina that can be used as Pleistocene biostratigraphical tool and paleoclimate-palaeoceanographical signal. While it was absent in warmer than present high sea-level episodes during the Miocene ("Entrerriense" transgression, ca. 10 Ma) and Pleistocene (MIS11), it exhibits an excellent and abundant fossil record within dominantly cool coastal settings exclusively during the Late Pleistocene (MIS9, 7 and 5) between Río Negro and southern Santa Cruz provinces (Patagonia). It first appeared in the SEP during the late Pliocene (cooling trend), dispersed during the Late Pleistocene into the SWA presumably by rafting on macroalgae along the Cabo de Hornos and Malvinas (Falkland) currents, but became extinct in the Mar Argentino (Magellan Malacological province) during the Holocene (amelioration trend). Its absence at present represents a climate change-driven range shift and independent evidence of palaeoceanographical changes after the LGM and at the Pleistocene/Holocene transition: changes in SST (ca. 2 °C higher), wind velocities (less), light (less), nutrient availability (less), extension and intensity of cold (less) and warm (increased) shallow water currents altering water masses and biogeographical boundaries. Altogether, these changes and the Holocene scenario were disadvantageous, causing direct effects on its physiology and survival, in turn preventing the occurrence of the associated macroalgae (*Durvillaea antarctica*) and its successful dispersal in the SWA or retraction to the cold Humboldt System waters. This study reinforces the importance of dispersalist models to explain the origin of key taxa, adding for a better understanding of molluscan taxonomic differences along the SWA and SEP margins of South America, with implications for future coastal scenarios. The distribution of *T. atra* across time is a new example of the strong linkage between earth history-climatic cycles-atmospheric and oceanic circulation and the late Quaternary biotic responses, showing a possible consequence of future climate change on nearshore communities.

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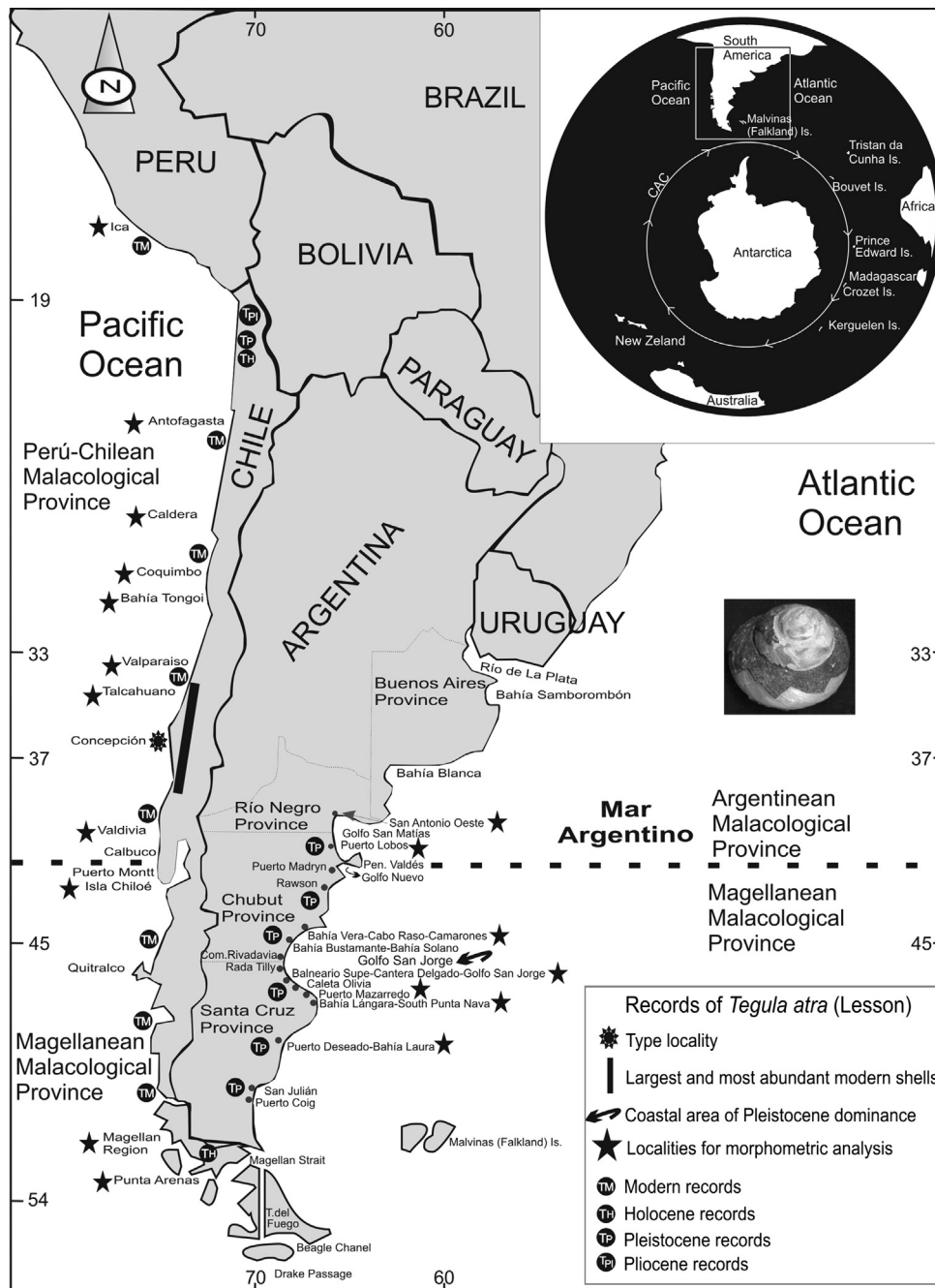
## 1. Introduction

As far as we are now concerned, based on field work and molluscan records of many years from the marine Quaternary of Argentina between the Río de la Plata margin and southern Patagonia (Southwestern Atlantic, SWA; Fig. 1), *Tegula atra* (Lesson)

(Gastropoda, Trochidae) is the only example of an endemic species documented by huge quantities of shells, of all dimensions and ontogenetic stages, excellently preserved and frequently exhibiting perfectly maintained original colour and luster, occurring over a large geographical area (more than 1000 km along Río Negro, Chubut and Santa Cruz provinces, Patagonia) where it is characteristic of beach ridges and marine terraces at ~8–35 m above present m.s.l. Overall, this pattern suggests that it represents an autochthonous element of the original nearshore molluscan associations from Patagonia during the last Quaternary high sea-

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**Fig. 1.** Study area along Patagonia (Argentina, South Western Atlantic margin) and position of the localities with fossil and modern records of *Tegula atra* (Lesson, 1830) in South America. Modern biogeographic regions (Argentinean and Magellan = Magellanean Malacological provinces in the SW Atlantic and Magellan and Peru-Chilean in the Southeastern Pacific). Symbols show different aspects concerning the spatial and temporal/through time distribution of *Tegula atra*.

level episodes. This benthic intertidal species is very abundant today in the Magellan and Peruvian Malacological Provinces along the southeastern Pacific (SEP), between southern-central Peru and the Magellan (also called Magellanean) region in southern Chile (e.g., Carcelles, 1945; Osorio, 1979; Guzman et al., 2000; Véliz and Vásquez, 2000; Aldea and Valdovinos, 2005), a littoral area controlled by the cold Humboldt system (Thiel et al., 2007).

Curiously, its dominance in the Patagonian marine Quaternary landforms contrasts with its scarcity/absence today in the Magellanean Province along the SWA where, although living records have traditionally been mentioned in local catalogues (e.g., Castellanos, 1967; Castellanos and Landoni, 1988–1993; Nuñez Cortés and Narosky, 1997), pioneer authors including Feruglio (1933, 1950)

and Carcelles (1945) and more recently Pastorino (1994) and Aguirre et al. (2008, 2009, 2011) suggested it is not currently present. Whatever the records or authors are considered reliable, its distribution in space and time in the Mar Argentino is as yet not well documented, its occurrence during the last high sea-level episodes in Patagonia not constrained (Pleistocene and Holocene?, exclusively Pleistocene?) and the reason/s for its eventual absence (extinction?) in the SWA still need to be deciphered.

Determining the stratigraphical range of *T. atra* and its potential value as a biostratigraphical tool is of primary importance for interdisciplinary studies dealing with the Patagonian marine Quaternary. Patagonia exhibits the most abundant and best preserved marine Quaternary coastal deposits (beach ridges, marine terraces)

chronological distinction within the Pleistocene or between late Pleistocene and Holocene landforms. Deposits at the same height relative to the present mean sea level have yielded ages which correlate with different MIS, while others at different altitudes and distances relative to the present coast correlate with the same MIS. Moreover, in many coastal sectors, nothing other than height differences between littoral ridges and terraces are apparent, as geomorphological and sedimentological features can be very similar or identical, precluding a clear age differentiation.

Main coastal areas from Argentina with rich Quaternary molluscan assemblages containing *Tegula atra* in Patagonia. Source of information on stratigraphy, age control, and geomorphology of the deposits from Argentina and other areas of Atlantic South America available in [Supplementary material Appendix 1](#).

Areas	Ref.	Ridges/marine terraces/SC/ – MIS – (some examples of modern ages available)		Height (+m a m.s.l.)	Geographical location (most representative localities revisited)	Better examples of palaeontological samples <b>PA</b> .: material illustrated here
San Antonio Oeste 40°47'S–40°49'S (MIS1, 5, >5)	Feruglio, 1950 Angulo et al., 1978 Fidalgo et al., 1980 Rutter et al., 1990 Pastorino, 2000 Codignotto et al., 2003 Kokot et al., 2004	MIS 1 (H)		8–12	40°47'0.930"S–64°50' 57"W (P. Villarino)	PV1–PV2; PA06–27 (SAE)
		MIS 5 (PL)	20–40 ka <sup>14</sup> C 83–115 ka ESR	10–11	40°49'11.94"S–64°44' 06.51"W (Bal. SM)	PA6–24 (R.3 a costa espiga SAE)
		MIS 7/9 (PL)	>208–>230 ka ESR	10–11	40°47'13.48"S–65°03' 12.21"W (N LGr SPDeIlg) 40°42'15"S–64°55' 43.5"W (R.3) 40°42'36.76"S–65°00' 05.67"W (cruce) 40°47'52.05"S–64°43' 04.76"W (Int)	PD1–PD2; PA0620–21 (SAO)
Puerto Lobos 41°59'S–42°02'S (MIS1, 5, >5)	Feruglio, 1950 Bayarski and Codignotto, 1982 Codignotto, 1983 Aguirre et al., 2005	SC VI, V (H)	6–0.750 ka <sup>14</sup> C	2–4	41°59'9.6"S–65°04' 12.4"W (cañadón)	PA08–69
		SC IV, III (PL)	20.3–30.4 ka <sup>14</sup> C	8–10	42°01'55"S–65°03' 38"W (cantera ext e int))	PA04Q4, PA04Q5, PA4Q6– <b>PA08–71</b> , PA04Q3
		SC II, I (PL)	32–40 ka <sup>14</sup> C	>10–16	42°02'S–65°03'54"W (interior)	PA04Q1, PA04Q2, PA04Q3 PA02Hol5, PA02Hol6
Bahía Vera–Cabo Raso 44°16'S (MIS1, 5–11?)	Feruglio, 1950 Codignotto, 1983 Schellmann and Radtke, 2000 Aguirre et al., 2006 Schellmann and Radtke, 2007 Schellmann and Radtke, 2010 Ribolini et al., 2011	MIS 1 (H)	3.6–1.2 ca. 0.631 ka <sup>14</sup> C (B. Vera) 3.6–2.6; 2.1; 1.2 ka <sup>14</sup> C (NPLo) 5.5–1.4 ka <sup>14</sup> C (SPLo) 4.5–6.5 ka <sup>14</sup> C (C. Raso)	4, 5, 7, 10	44°14'45.17"S–65°18' 06.19"W (NPLo)	
		MIS 5–11 (PL) at least 4–5 ridge series	No dating	14, 16, 18, 20, 22, 26, 37, >40, >47	44°15'39.21"S–65°18' 10.91"W (B. Vera) 44°15'47.8"S–65°18' 02.4"W (B. Vera) 44°15'53"S–65°18' 18.5"W (B. Vera) 44°15'50"S–65°18'10"W (S B. Vera) 44°16'41"S–65°16' 58"W (SPPesc) 44°19'42.49"S–65°16' 52.82"W (SPPesc) 44°19'49"S–65°16' 8.6"W (C. Raso) 44°19'47"S–65°17' 07"W (C. Raso)	PA02Q10; PA02Q11 <b>PA08–12</b>
Camarones North 6 South 44°47'S (MIS1, 5.7, 9, >9)	Feruglio, 1950 Codignotto, 1983 Schellmann and Radtke, 2000 Aguirre et al., 2006 Schellmann and Radtke, 2007 Schellmann and Radtke, 2010	MIS 1 (H)	3.380–7.250 ka <sup>14</sup> C (Co) ca. 1.4–6.7 ka <sup>14</sup> C; ca. 7 ka (Th/U) > <b>6.2 ka <sup>14</sup>C</b> , 6.7 – ca. 0.487–500 ka <sup>14</sup> C	4.5–5.6; 8.5–9.5 10–12	44°39'27.12"S–65°37'13.30"W (PF, Camarones) 44°47'37.11"S–65°42'11.96"W (N Camarones) 44°49'35.85"S–65°43'48.69"W (S Camarones)	PA02Hol7
		MIS 5–11 (PL)	ca. 112–117 ka (Th/U) ca. 110–114 ka (ESR) ca. 92–115; 117–135 ka (Th/U) ca. 178,180,196,200 (Th/U, ESR) ca. 342,372,378,380/	2–6; 12–13 15–17 ca. 16–18 ca. 16–19 +22, 22–26 28–40 40–>40	44°41'36.3"S–65°40'23.8"W (N Camarones)  44°20'28"S–65°14'43"W (N Camarones) 44°16'41"S–65°16'58"W (N Camarones) 45°03'49.8"S–66°34'13.8"W (S Camarones)	<b>PA08–33</b> ( ~ =Pa47 S & R, 2000) MIS5c, MIS5e PA02Q13 PA02Q14, <b>PA02Q15</b> <b>PA08–63</b> PA08–40

(continued on next page)



Table 1 (continued)

Areas	Ref.	Ridges/marine terraces/SC/ – MIS – (some examples of modern ages available)		Height (+m a m.s.l.)	Geographical location (most representative localities revisited)	Better examples of palaeontological samples <b>PA..</b> : material illustrated here
Puerto Deseado– B. Laura 47°45'S–48°20'S	Feruglio, 1950 Codignotto, 1988 Rutter et al., 1990 Rostami et al., 2000 Aguirre et al., 2009 Schellmann and Radtke, 2010	MIS 1 (H)	1.8; 2.9; 4.8 ka <sup>14</sup> C	8–10	(P. Mazarredo) 47°03'04"S–66°26'50"W (SPNava) 47°45'04.66"S–65°51'58.12"W (N P. Deseado) 47°02'12"S–66°42'15"W (B. Laura) 48°03'11.9"S–66°58'10.4"W (E. Ferrer)	PA010 PA0611 PA06-12-13; PA011-12-17
		MIS 5 (PL) >?	Min 43 ka <sup>14</sup> C ca. ≥242 ka (ESR) ca. 450 ka (ESR)	20–25; 28–30; 38–45	47°02'12"S–66°42'15"W (P. Deseado) 47°45'01"S–65°52.4'W (N P. Deseado) 47°45'10"S–65°53'33.13"W (P. Deseado)	PA010-1,2 PA010-3
San Julián 49°20'S (MIS1, 5.7, 9, >9)	Feruglio, 1950 Codignotto, 1988 Rostami et al., 2000 Schellmann and Radtke, 2007 Schellmann and Radtke, 2010	MIS 1 (H)	0.6–1.7, 6.2–6.4 ka <sup>14</sup> C	3–6	49°16'08.25"S–67°42'31.20"W (N S. Julián) 49°13'43.65"S–67°38'39.18"W (Co. Curioso)	PA06-1, PA06-2 PA06-7
		MIS 5>?	Min 43 ka <sup>14</sup> C ca. 99 ka (ESR) ca. 115, 128, 134, 240 ((Th/U) ≥242 ka (ESR)–>355, ca. 400 (Th/U)	8–11	49°15'57.42"S–67°42'02.53"W (N S. Julián) 49°17'50.25"S–67°44'56.69"W (S. Julián)	PA06-5 PA06-6 PA06-7, PA06-8 PA06-9

References for geomorphology, sedimentology and modern dating available for different coastal sectors along Patagonia can be obtained from previous work performed in the area: Feruglio (1950), Codignotto (1983, 1987) and Codignotto et al. (1988, 1992 among others); Rutter et al. (1989, 1990), Schellmann and Radtke (2000, 2007, 2010 among others); Rostami et al. (2000), Kokot et al. (2004) and Ribolini et al. (2011). General location of the main areas is approximate (i.e., Schellmann and Radtke, 2010). Complete palaeontological sources in Feruglio (1933, 1950), Aguirre et al. (1998), Pastorino (2000), Aguirre (2003) and Aguirre et al. (2005, 2006, 2009, 2011 among others). Other references therein.

Pleistocene samples assigned to Marine Isotope Stages (MIS) are as follows and based on modern dating performed by previous authors. MIS5: PA0624, PA04Q4, PA04Q5, PA04Q6, PA2Q12, PA02Q15, PA02Q7, PA2Q8, PA02Q9, PA4, PA6, PA7, PA04Q12, PA04Q13, PA04Q14; MIS7: PA04Q1, PA04Q2, PA04Q3, PA2Q10, PA02Q11, PA02Q13, PA02Q14, PA02Q4, PA02Q5, PA02Q6, PA3; MIS9 and/or older: PA04A7, PA02Q16, PA02Q16', PA010-24, 25, 26, 27. Note that not all the locations are transformed into sexagesimal grades.

Assuming that shifts in geographical range limits together with adaptations to new conditions are one possible biotic response of marine molluscs to climate change (Hellberg et al., 2001; Roy et al., 2009; Drinkwater et al., 2010; Jones et al., 2010; Beu, 2012; Vermeij, 2012), the study of the (palaeo) biogeographical pattern of *T. atra* and a search for its explanatory mechanisms offer an opportunity to assess whether: 1) it has simply been missed in the Mar Argentino, but certainly occurs, although scarcely, in the modern littoral; or alternatively 2) its absence represents a biotic response to climate change (e.g., changes of abiotic controlling factors, such as sea surface temperature (SST), salinity, substrate nature, currents and winds; changes of intrinsic factors, such as larval feeding requirements, dispersion mechanisms and abilities); if so, 3) whether it can be useful as a palaeoenvironmental signal, altogether bringing light on palaeoclimatic/palaeoceanographical conditions different from the present. Providing an independent (biotic) source of evidence can contribute to filling a gap for a target area in the Southern Hemisphere (SH) linked to the Southern Ocean (SO) which controls the global oceanic circulation pattern.

The biogeography of recently extinct species and range shifts compared with modern patterns is a fascinating subject that has caught the attention of naturalists, geologists, palaeontologists, biologists, biogeographers, oceanographers and even researchers from geophysical and meteorological backgrounds since the mid-19th century. However, these approaches have used many standpoints and case studies mostly from Northern Hemisphere (NH) areas and taxa, with far fewer studies referring to the Southern Hemisphere (SH). In South America and in the SO, there is still only evidence of local Quaternary climate change-driven range shifts/extinctions. Specifically for the SWA, there is a lack of evidence

based on endemic taxa from nearshore environments which can be linked to Pleistocene climatic reversals, changes following the Last Glacial Maximum (LGM; 25 ka B.P., Rabassa et al., 2011) or at the Late Pleistocene–Holocene transition leading to the increased trend in sea surface temperature (SST) and sea-level.

This study considered several standpoints and methods. Firstly, systematic aspects of *T. atra* in Argentina and South America were determined, including a morphometric analysis of fossil and modern shells. Secondly, *T. atra* was investigated from a regional biogeographical perspective, applying multivariate and cladistic techniques to a large database of gastropod records from Pleistocene, fossil Holocene and modern sites from Argentina and other areas of Atlantic South America: a search for patterns between localities through time, the role of *T. atra* in this context, and whether fossil vs. modern biogeographical patterns could be linked to the effects in the SWA and surrounding SO of the last climatic cycles on abiotic and intrinsic parameters (Hodell et al., 2002; Poulin et al., 2002; Behrenfeld et al., 2006, 2009; Otto-Bliesner et al., 2006; Filippelli and Flores, 2009; Escutia et al., 2012).

## 2. Geographical, geological and palaeontological setting

### 2.1. Marine Quaternary deposits

In Argentina, extensive coastal sectors along Patagonia and northwards along the Bonaerensian area exhibit marine Quaternary littoral deposits rich in molluscan concentrations in shell ridges, marine terraces and marginal marine deposits (Fig. 2). They extend almost continuously from the modern supratidal zone to a few kilometers inland, reaching 20–30 km inland in some regions



(Bonaerensian coastal area, southern Bahía Samborombón) but generally ca. 5–10 km (Camarones, Bahía Bustamante area in Patagonia). Most of the fossiliferous deposits were accumulated during the Holocene (MIS1) and Mid-Late Pleistocene (MIS11, 9, 7, 5) of which the most continuous and richest belong to MIS1, 5 and 7 (Table 1; Supplementary Appendix 1). Earlier highstands (pre-MIS 11) may have been preserved further inland, but the molluscan content, at least superficially, is either scarce and highly abraded or completely unpreserved.

The Pleistocene deposits are in general restricted, preserved with a patchy distribution, except for Patagonia where they are more extensive and better preserved, with altitudes between 10 and 74 m above m.s.l. The fossiliferous Patagonian coastal deposits containing *T. atra* belong to the so called Marine Terraces (MT, “Terrazas Marinas” sensu Feruglio, 1950; namely MTIV, MTV) later assigned, according to modern geochronological dating (D/L racemization ratios, ESR and U/Th) to several highstands since at least the MIS11 Interglacial (Table 1; Supplementary Appendix 1). In the Río Negro province, Pleistocene littoral ridges and Holocene terraces were studied in San Antonio Oeste and surroundings in the Golfo San Matías. The molluscan samples come from Pleistocene deposits assigned to Baliza San Matías Fm. and Holocene deposits of San Antonio Fm. and to MIS1–9. In Chubut province, the best preserved deposits are located at: Puerto Lobos, Bahía Vera—Cabo Raso, Camarones, Bahía Bustamante—Caleta Malaspina, Solano and Comodoro Rivadavia. The Pleistocene samples belong to Caleta Malaspina Fm., MTV and equivalents, and the Holocene to the Zanjón El Pinter Fm. MTVI and equivalents and to MIS1–11. In Santa Cruz province, the localities selected are located in Golfo San Jorge (north and south of Caleta Olivia, Puerto Mazarredo, Bahía Sanguineto), Puerto Deseado—Bahía Laura, Ensenada Ferrer, Rincón del Buque—Puerto Coig surroundings and belong to MIS1–9. The height and age of the Pleistocene deposits, as well as the number of high sea-level episodes preserved, are not yet fully understood. These approaches still need to be augmented by geomorphological revisions. Complete information available for morphostratigraphy, sedimentology and geological aspects of the deposits sampled can be obtained from previous studies (among others, Feruglio, 1950; Bayarski and Codignotto, 1982; Codignotto, 1983–1992; Cionchi, 1988; Rostami et al., 2000; Schellmann and Radtke, 2000, 2003; Schellmann, 2007; Ribolini et al., 2011).

The deposits sampled correlate with approximately synchronous shelly accumulations preserved in nearby coastal areas of Atlantic South America (Surinam, southern Brazil and Uruguay). Specific information on molluscan systematics, palaeoecology and distribution was published previously, including detailed information on complete species composition and illustrations (Aguirre et al., 2008, 2011; and references therein).

## 2.2. Molluscan assemblages

The molluscan shells form in general parautochthonous assemblages (sensu Kidwell, 1986) (Fig. 2) which due to their young age, high preservation grade and similarity (taxonomic fidelity) regarding the present-day nearshore associations, allow objective palaeoenvironmental and palaeobiogeographical analyses. Also, because they are time-averaged, the assemblages can record long-term conditions of the depositional littoral environments. Gastropod shells show, in general, more abraded surfaces with greater loss of their original colour and luster, except for *T. atra* (Lesson) in Patagonia.

Studies dealing with large scale Quaternary molluscan palaeobiogeography or focused on dominant target molluscan taxa are scarce. In most cases, geographical displacements were based on records of relatively few specimens of certain taxa and on taxa occurring in a restricted area only (Pastorino, 1991; Aguirre, 1993a,

1993b, 2003; Aguirre and Whatley, 1995; Aguirre et al., 2009). Most systematic work has emphasized bivalves, primarily due to their better preservation and higher palaeoecological value. In contrast, gastropods have been less studied and characterized. In addition, very few gastropod taxa of the fossil assemblages can be considered autochthonous elements of the original littoral communities (e.g., intertidal Trochidae, supralittoral to shallow infralittoral Patellidae, Siphonariidae, Fissurellidae), with the exception of *T. atra* in Patagonia.

Regarding the modern Patagonian molluscs, most contributions have emphasized on taxonomic similarities along both sides of the so-called Magellan Malacological province (SWA and SEP), a biogeographical unit characterized by cold waters along central-southern Chile, Argentina, Malvinas (Falkland) and around Antarctica: in the SWA between Golfo Nuevo (43°S, Chubut province) and Tierra del Fuego (55°S) and in the SEP between the Drake Passage and Concepción (Chile, 37°S) (Fig. 1). It has been acknowledged since the XIX century based on various taxonomic groups (Brattström and Johanssen, 1983; Valdovinos, 1999; Fernández et al., 2000; Lee et al., 2008; review in Balech and Ehrlich, 2008 and other references therein) but the biological knowledge about this zone is still scarce or incomplete (Boltovskoy, 2007).

## 2.3. Modern littoral

### 2.3.1. Argentine coast

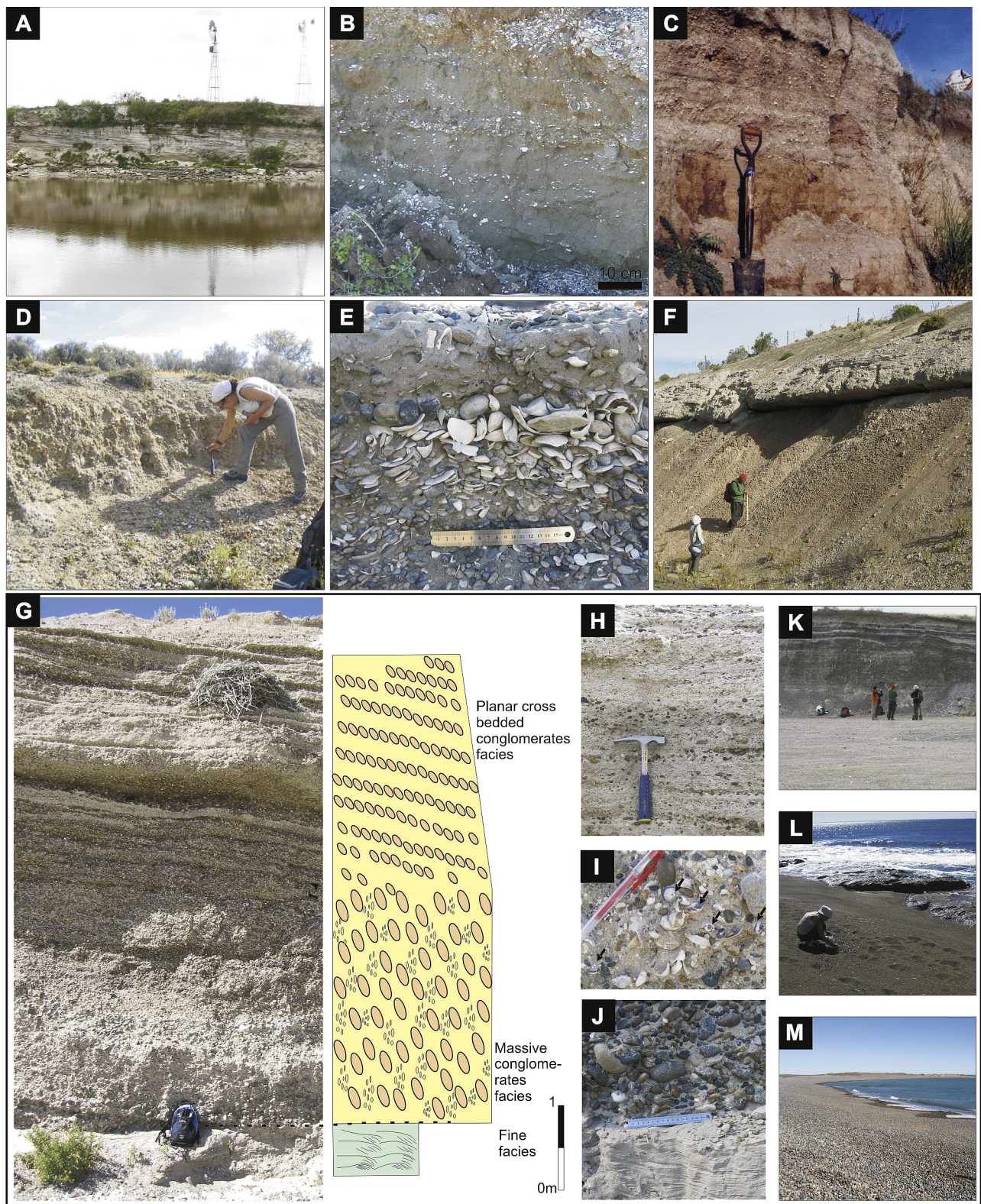
The main physical features of the Argentine continental shelf have been gathered through studies from different standpoints (e.g., Podestá, 1997; Hoffmann et al., 1997; Acha et al., 2004, 2008; Palma et al., 2004, 2008; Bogazzi et al., 2005; Lucas et al., 2005; Boltovskoy, 2007; Balech and Ehrlich, 2008; Piola et al., 2008, 2010; Paparazzo et al., 2010; and previous references therein) Four zones of the SWA are most relevant to this study: 1, the Temperate estuarine zone; 2, the Patagonian tidal zone; 3, Argentine shelf-break zone; 4, Patagonian cold estuarine zone, in the tip of South America (on the Atlantic and Pacific sides). Three thermal fronts and four salinity fronts have been recognized in the SWA margin (Fig. 3A–C).

Along the SWA, winds and currents control the latitudinal distribution of shallow water masses, the Subtropical–Subantarctic Convergence Zone and the boundaries for marine provinces, the species range endpoints of several taxonomic groups including molluscs. In general terms, the Argentinian biogeographical province extends between 41°S–43°S northwards and 28°S–32°S (Río Grande do Sul, Brazil) from the coastline to ~82–95 m depth (but from the coast to 70 m depth between 35°S and 39°S). The Magellan = Magellanean province extends from north of Península de Valdés/Golfo Nuevo to the southernmost tip of Argentina (Cabo de Hornos, 55°S) (Fig. 1). The Magellan province is highly influenced by the Malvinas (Falkland) Current (MC). The Argentine province (an ecotonal region) is a transitional area influenced by the cool MC and the warm Brazilian Current (BC).

### 2.3.2. Chilean coast

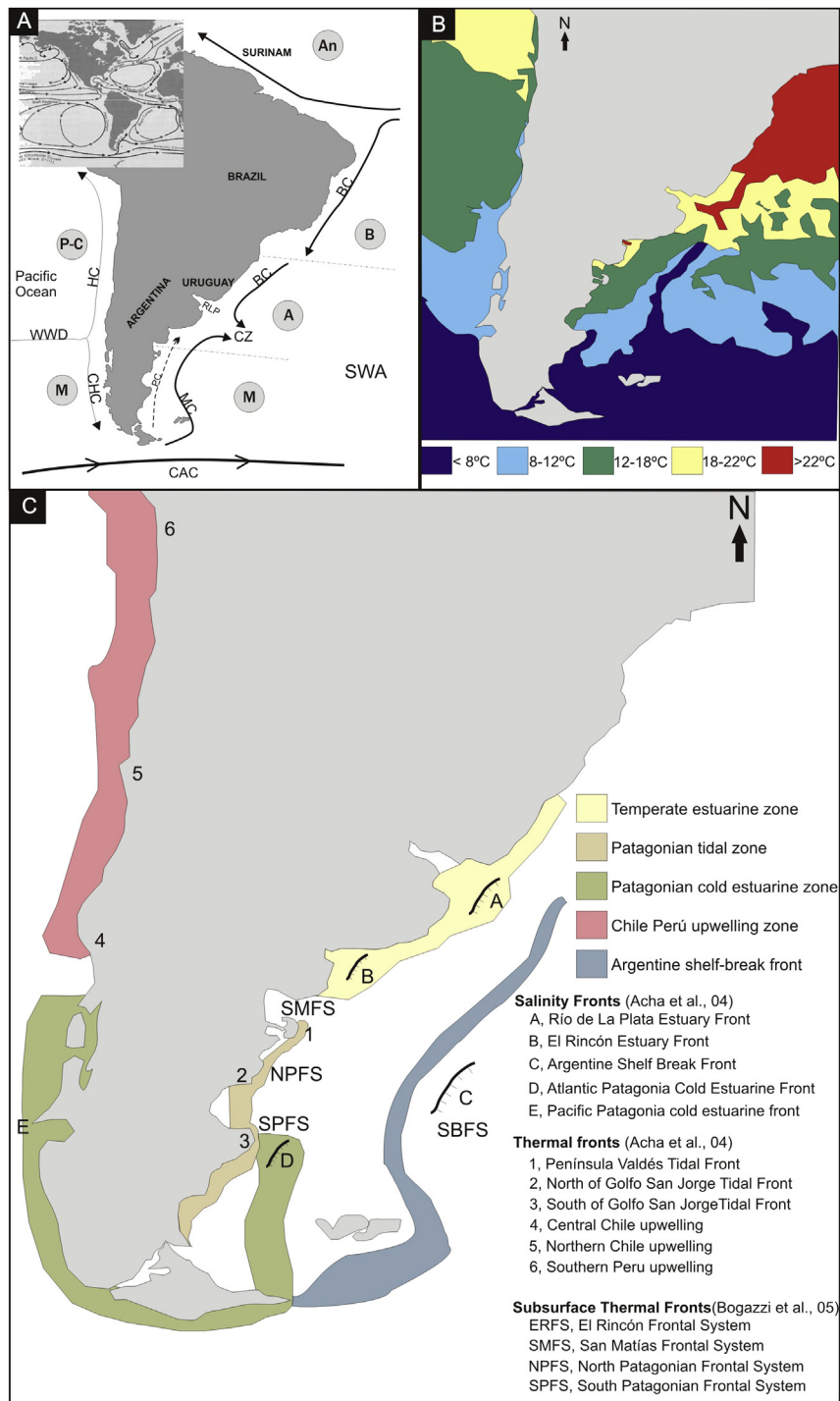
Along the SEP, two major zones are relevant to this study: the Patagonian cold estuarine zone and the Chile–Perú upwelling zone (high productivity), while three thermal fronts and one salinity front have been recognized (Fig. 3A–C). The Patagonian Cold Estuarine Zone extends south of 42°S (Chiloé Island) south to the Drake Passage, an area represented by the so-called “dismembered” Chilean coast, a product of the successive glaciations that affected this region since the Pliocene and during the Pleistocene from 37°S to Cabo de Hornos (Rabassa et al., 2011), resulting in extensive erosion caused by glacier ice cover and retreats. It exhibits numerous channels, fjords, islands, archipelagos, bays, and rocky features in a series of complex inshore zones of cold estuarine waters along a wide area, where depths are relatively low and an





**Fig. 2.** Field observations on Mid-Late Pleistocene and Holocene molluscan assemblages including the modern littoral along the coastal area of Argentina. Buenos Aires Province: **A:** Holocene beach ridge at Bahía Samborombón; **B:** Pleistocene beach ridge at Bahía Samborombón; **C:** Pleistocene beach ridges at Bahía Blanca; Patagonia: **D:** Pleistocene marine terrace at Zanjón El Pinter area (Bahía Bustamante); **E:** Pleistocene marine terrace between Arroyo Marea and Estancia La Ibérica area (Bahía Bustamante); **F:** Pleistocene marine terrace outside Camarones town; **G, H, J:** shell quarry in Pleistocene marine terrace at Bahía Bustamante; **I:** Pleistocene marine terrace at Cabo Raso with arrows showing details of *Tegula atra* shells; **K:** shell quarry in Pleistocene marine terrace at Camarones town; **L:** modern littoral at Cabo Raso; **M:** modern littoral at Camarones.





**Fig. 3.** Modern littoral along southern South America: oceanic circulation, biogeographical provinces, sea surface temperature (SST), salinity, coastal zones, thermal and salinity fronts. Partially modified from Aguirre et al. (2011). Complete source of references in Acha et al. (2004), Bogazzi et al. (2005), Lucas et al., 2005, Boltovskoy (2007) and Piola et al. (2008, 2010). **A:** Synthesis of shallow oceanic currents within the worldwide context and along Pacific and Atlantic South America; biogeographic provinces along the SW Atlantic (An: Antillean; **B:** Brazilian; **A:** Argentinean; **M:** Magellanean) and Southwestern Pacific (**M:** Magellanean; **P-C:** Perú-Chilean). **BC:** Brazil Current; **MC:** Malvinas (Falkland) Current; **PC:** Patagonian Current; **CZ:** Subtropical-SubAntarctic Convergence Zone; **CHC:** Cabo de Hornos Current; **HC:** Humboldt Current; **WWD:** West Wind Drift (branch of the CAC); **CAC:** Circumpolar Antarctic Current (modified among others from Acha et al., 2004; Boltovskoy, 2007; Balech and Ehrlich, 2008); **B:** Sea Surface temperature; **C:** Salinity and thermal fronts. Synthesized and modified from Acha et al. (2004), Bogazzi et al. (2005), Piola et al. (2008, 2010) and other references therein.

interplay of various water masses (Antarctic, Subantarctic, and Circumpolar Antarctic) takes place. As the main source of nutrients is from Subantarctic waters, these estuarine waters are relatively poor in nutrients. Chiloé represents the approximate northernmost latitude reached by glacial ice during the Pleistocene LGM (42–43°S) and influenced by postglacial melting affecting the salinity

of coastal waters. North of Chiloé, in general terms the coast offers a pattern with higher salinity in more open conditions and varied substrates. However, several hydrographic discontinuities characterized by minimum salinity and oxygen levels can be found (24, 30, 33 and 38°S) and the archipelago conditions are partially continued in several areas northwards (Camus, 2001).



The Chile–Perú Upwelling Zones (Central-Northern Chile and Southern Perú Upwelling Zones, Fig. 3), extends between 40°S and 4°S, characterized by very high primary productivity, with high nutrient concentration but low phytoplankton mass. Upwelling is greater in summer and less intense in winter, and cold waters originated by upwelling can be established at ca. 23°S (Acha et al., 2004). The area is influenced by the Peru/Humboldt current system (extending from ca. 42°S to Ecuador), which is one of the most productive marine ecosystems worldwide, with surface Subantarctic waters flowing northwards and strong upwelling of cool-nutrient-rich subsurface waters of Equatorial origin, characterized by localized upwelling along northern and central Chile, with a seasonal (continuous) occurrence in northern Chile and more seasonal in central-southern Chile (Thiel et al., 2007).

At the latitude of Chiloé (ca. 42–43°S), two cold branches of the West Wind drift (WWD) define the circulation pattern in Chile: the Humboldt Current flowing northwards up to southern Perú, and the southwards Cabo de Hornos Current to the Drake Passage where it joins the Antarctic Circumpolar Current. Subantarctic waters influence the whole Chilean coast and reach Perú. The entire coast is influenced by the southeastern Pacific winds flowing towards the coast. In the Chilean coast the Humboldt Current is an oxygen minimum zone with high levels of productivity (Veas et al., 2012).

### 3. Materials and methods

Taxonomic aspects of *Tegula* from South America, and whether the Patagonian Pleistocene shells belong to the same taxonomic entity than the species living in Chile and the distribution of *T. atra*

in space and time, were assessed through a systematic review. The taxonomical framework followed classifications by Hickman and McLean (1990), specific studies of modern Trochidae from South America (Véliz and Vásquez, 2000, SEP) and molecular studies available for Trochidae (including *Tegula* sp.) from littoral areas worldwide (Ponder and Lindberg, 1997; Hellberg, 1998; Bouchet and Rocroi, 2005).

The molluscan material examined comes from coastal deposits between the Río de La Plata margin and San Julián/Rincón del Buque. A total of 130 collected bulk samples (complete sedimentary matrix and shells) contain *T. atra* (Fig. 4) and belong to more than 30 fossiliferous sites in 9 wider geographical areas: San Antonio Oeste, Puerto Lobos, Bahía Vera–Cabo Raso, Camarones, Bahía Bustamante, Caleta Olivia, Puerto Mazarredo, Puerto Deseado, San Julián (Table 3, Fig. 2). The stratigraphical range of *T. atra* in the Patagonian marine terraces was determined on the basis of occurrences in constrained deposits dated by modern methods (Table 1). Additionally, fossil and modern shells assigned to *T. atra* were examined from collections housed at several institutions: Invertebrate Palaeontology Department in the Museo de La Plata (MLP PI), Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” in Buenos Aires (MACN, Malacology Section), Zoology Department at the Museo de La Plata (MLP ZI), historical molluscan collections from South America at the Natural History Museum London (NMHUK) (Table 4); modern materials collected by oceanographic campaigns housed at the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP, Mar del Plata) and modern shells from the Chilean coast provided by Chilean colleagues (Ricardo Guíñez, Carolina Briones, Universidad de Antofagasta; Marcela Astorga, Universidad

**Table 2**

Species of *Tegula* described for the western Atlantic and eastern Pacific (South America) according to geographic areas and age periods. Earlier references available in Aguirre and Farinati (2000). Synthesis of the stratigraphical, geographical and dimensions for each species based on collected material and on bibliographic review.

Ecological Requirements	Distribution		PLIOC	LATE MIOC	PLEIST	HOLOC	SW Atlantic				ANTARCTICA	Eastern Pacific						Modern Malacological Provinces (N-S)						Habitat and Habit						DIMENSIONS (mm)	REFERENCES			
							SURINAM	BRAZIL	URUGUAY	ARGENTINA		CHILE	PERU	Others	NACA	CACA	VIRG	CARL	ANT	BRA	ARG	MAG	PAN	CALIF	BATHYMETRY			SUBS.	LIFE MODE					
										BONAE RENS.															PATA GONIA	SUPRAT	INTERT	UPPER INFRA	HARD			FREE EPIF	HERB	
<i>Tegula fasciata</i> (Born, 1778)						M	M																								12, 18, 20	1		
<i>Tegula viridula</i> (Gmelin, 1791) (#) n.n						M	M																								19-23	2		
<i>Tegula excavata</i> (Lamarck, 1822)							M																								12	1		
<i>Tegula patagonica</i> (d'Orbigny, 1835)						M	H,M	PL,H,M	PL,H,M																						3-23	2,3,4,5,6		
<i>Tegula hottentorian</i> (d'Orbigny, 1842)						M	M																								20	2		
<i>Tegula orbignyana</i> (Pilsbry, 1900)																															9	3		
<i>Tegula blakei</i> (Clench & Aguado, 1938)									H,M	PL,H, M																					5,10, 60	3		
<i>Tegula atra</i> (Lesson, 1830)									PL*	M ?	PL, PL, H,M*			H-M	M																5- 22-70	4, 5, 6, 7, 8		
<i>Tegula luctuosa</i> (d'Orbigny, 1841)											PL, M	PL, M																			26-35	7, 8		
<i>Tegula euryomphala</i> (Jonas, 1844)											PL* , M																				29-36.1	7, 8		
<i>Tegula ignota</i> Ramirez, 1976												M	M																		25	7		
<i>Tegula quadricostata</i> (Wood, 1828)												M	M																		24.7-32	7		
<i>Tegula tridentata</i> (Potiez & Michaud, 1838)											PL, M*		M																		18-20	7		
<i>Tegula brunnea</i> (Wood, 1828)														M																	35-40	1		
<i>Tegula aureocincta</i> (Potiez & Michaud, 1838)														M	M	M															25-28	1		
<i>Tegula funebris</i> (A.Adams, 1855)															M	M	M														30	1		

Most common species of *Tegula* from America described and illustrated in the traditional bibliography (local and worldwide catalogues and specific studies)

#### Western Atlantic Ocean

*Tegula fasciata* (Born, 1778)  
*Tegula viridula* (Gmelin, 1791)  
*Tegula excavata* (Lamarck, 1822)  
*Tegula patagonica* (d'Orb., 1835)  
*Tegula hottentotiana* (d'Orb., 1842)  
*Tegula orbignyana* (Pilsbry, 1900)  
*Tegula blakei* (Clench & Aguiar, 1938)  
 Note that *orbignyana* is a synonym of *T. patagonica*

#### Eastern Pacific Ocean

*Tegula atra* (Lesson, 1830)  
*Tegula luctuosa* (d'Orb., 1841)  
*Tegula euryomphala* (Jonas, 1844)  
*Tegula quadricostata* (Wood, 1828)  
*Tegula tridentata* (Potiez & Michaud, 1838)  
*Tegula blakei* (Clench & Aguiar, 1938)  
*Tegula ignota* Ramirez, 1976

#### References:

- M: modern (Chile, Perú)  
 H: Holocene (Magellan Region, Chile)  
 PL: Pleistocene (Chile, Patagonia)  
 PLI: Pliocene (Caldera, Mejillones; Chile)  
 #: Type species of *Tegula* Lesson, 1835  
 n.n.: nomen nudum  
 \*: abundant  
 Western Atlantic Ocean (northern and southern hemispheres):  
 1: Abbott (1989), Abbott & Dance (1991), historical collections at the NMHUK (London)  
 2: Rios (1994)  
 3: Carcelles (1944), Carcelles (1945), Carcelles & Williamson (1950), Castellanos (1967), Scarabino (1977), Castellanos & Landoni (1989)  
 4: Feruglio (1933), Feruglio (1950)  
 5: Aguirre (1993), Aguirre & Farinati (1999, 2000), Pastorino (2000); Aguirre et al. (2008 and other references therein)  
 Eastern Pacific Ocean–Perú and Chile:  
 6: Linse, 1999  
 7: Marinovich (1973), Ortlieb et al. (1994), Guzmán et al. (1998, 2000), Veliz & Vásquez (2000), Moreno et al. (2004), Aldea & Valdovinos (2005), Rivadeneira & Carmona (2008), Cárdenas et al. (2008); Osorio et al. (1979; 2006); Nielsen (2012) (Chile)  
 8: Cortés & Narosky (1998), Forcelli (2000)  
 Antarctica:  
 6: Linse (1999) with doubts

Austral de Chile at Puerto Montt). A survey included all available literature on fossil and living records of *Tegula* Lesson in South America, along the SWA from Surinam to Tierra del Fuego and along the Pacific from Ecuador to Chile and Juan Fernández Island. Modern records of *Tegula* in the SWA included report collections from oceanographical expeditions carried out in the Mar Argentino (campaigns SAO, Mar del Plata, OB-07/93 INIDEP, “Shinkai Maru” IV, V, X y XI B/I; Canepa, Holmberg, Oca Balda) (most available at INIDEP) together with an exhaustive bibliographic survey (complete references in Supplementary Appendix 2).

**Table 3**

Synthesis of datasets for gastropods from assemblages of Pleistocene (PL), Mid-Holocene (HOL) and modern (MOD) age from Argentina and other areas in Atlantic South America used for multivariate and cladistics analyses. See also Fig. 7A.

	PL	HOL	MOD
<b>Localities/Areas</b>			
SACA	3	3	5
BON	10	7	12
PAT	16	18	18
Total	29	28	35
Total molluscan taxa recorded: 721	95	140	721
<b>Gastropod taxa (382)</b>			
SACA	5	32	297
BON	20	46	117
PAT	39	43	76
Total	49	73	382

A geometric morphometric analysis of fossil and modern shells was performed by means of the Relative Warps (RW) method to objectively assess if differences in shell shape variation are apparent according to age and/or geographical groups. The shell outline from digital images of 67 specimens (27 fossil and 40 modern) in apertural view (more informative, exhibiting diagnostic columellar teeth, the most common features used for taxonomic discrimination at the species level) were used for a shape analysis. Comparative analyses of the spire (3–4 whorls) and of the abapertural view exhibiting the outer ornamentation and colour were dismissed, as they could produce deceiving results due to the varying preservation grades between fossil (most often altered) and modern shell specimens. The coordinates for 4 Landmarks (L, ○, soft insertion points, columellar tooth), and 11 Semilandmarks (SL, ●, regularly spaced points along the apertural shell margin) (Fig. 5), were recorded on the digital images by means of the TPSdig2 and TPSUtil programs (Rohlf, 2004a, 2004b). In landmark-based analysis, the shape is defined as the information resulted in a figure after location, scale and orientation data are removed, generally by generalized least square Procrustes superposition. The relative warps (principal component vectors of the partial warps – variables generated for thin-plate spline transformations) were used for comparison of the configuration of L and SL (Bookstein, 1989a, 1989b) and to describe the major trends in shape variation among specimens within the sample (review in Bookstein, 1991; Rohlf, 1996; Adams et al., 2004). The results of statistical analysis can be expressed as a deformation of each case over the mean form or reference. The analysis was performed by means of the Relative Warps 1.39 software (Rohlf, 2004c).

From a regional palaeobiogeographical perspective (Murray-Wallace et al., 2000; Hammer and Harper, 2006; Kreft and Jetz, 2010; Garilli, 2011), three methods were applied to the shell material and macrogeographical dataset:

- Cluster Analysis (CA) and Principal Coordinate Analysis (PCO) (Hammer and Harper, 2006) applied to gastropod presence–absence data matrices for three time spans (Pleistocene, fossil

Holocene and Modern = present; Table 3) at a macrogeographical scale (Surinam, Brazil, Uruguay, Argentina) were performed in order to reconstruct the palaeocommunities inhabiting the nearshore along the SWA since the Pleistocene. All the multivariate analyses for each dataset were conducted using the software Past version 2.02 (Hammer et al., 2001). CA was performed calculating a similarity matrix (SM) using Jaccard index and using unweighted pair-group average (UPGMA) algorithm to obtain the fenogram. Upon the same SM calculated for CA, a PCO was performed together with a Minimum Spanning Tree (MST) superimposed to the tri-dimensional graphic representation of the PCO as a distortion measure.

- Parsimony Analysis of Endemicity (PAE) (Rosen, 1988, Rosen and Smith, 1988) was applied to all the same matrices to define areas of endemism based on gastropods and to define between areas relationships. Emphasis was placed on Argentina and on the Pleistocene vs. the present, with some highlights on taxa which define areas of endemism or are displaced in the SW Atlantic today. An Area of endemism (AE) is here defined as the congruent distributional limits of two or more taxa (Platnick, 1991). PAE were performed with TNT version 1.1 (Goloboff et al., 2008) under maximum parsimony using equal weights. Tree search was performed using a Wagner tree as starting tree and 1000 random addition sequences plus TBR with 100 trees to save per replication. The trees obtained then were swapped with TBR. The results obtained in this analysis were estimated as absolute and GC (Group present/Contradicted) frequencies with 1000 replicates of jackknife symmetrical resampling plus TBR, 10 random addition sequences, and saving 100 trees per replicate.

#### 4. Systematic results

The Trochidae are well known from all modern oceans worldwide, especially in shallow waters and hard substrate environments. Along the Atlantic margin of South America, they are commonly and abundantly represented, among other genera, by *Margarites* Gray, *Calliotropis* Seguenza, *Tegula* Lesson, *Calliostoma* Swainson, *Photinula* H.A. Adams, most typically in intertidal or shallow infralittoral exposed rocky habitats. Of these, *Tegula*, *Calliostoma* and *Photinula* are the most common for Argentina and occur also northwards in Uruguay, Brazil and Surinam. *Tegula* is today represented in the Atlantic and Pacific margins of South America (Carcelles, 1944; Castellanos, 1967; Keen, 1971; Abbott, 1991; Abbott and Dance, 1991; Ríos, 1994; Guzmán et al., 1998) (Table 2).

**Table 4**

Material of *Tegula atra* and related species examined. **a**, modern shells (different collections); **b**, fossil (Pleistocene) shells from the Patagonian coastal area (Argentina); **c**, locality samples used for morphometric analysis (RW) of *Tegula atra* and close species of *Tegula*. **MLP (ZI)**: Museo de La Plata, Zoología Invertebrados; **MACN**: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires; **NHMUK**: Natural History Museum London; **MLP (PI)**: Museo de La Plata (División Paleontología Invertebrados); **MLP (DCG)**: Museo de La Plata Departamento Científico Geología. **M**: modern; **H**: Holocene; **PL**: Pleistocene (See locality samples for the morphometric analysis shown on map of Figs. 1 and 7A).

a)		
Name labelled	No. MACN	Procedence
<i>Chlorostoma atrum</i> Lesson	614	Valdivia, Chile – Playa San Vicente (Canje Museo Cs. Nat.)
<i>Chlorostoma atrum</i> Lesson	10453	Calbuco, Chie (Canje Museo Catharinense)
<i>Tegula atra</i> Lesson	9040–16	Punta Arenas, Chile
<i>Tegula atra</i> Lesson	21302	Golfo San Matías (fossil)
<i>Tegula luctuosum</i> d’Orb.	1481	Chile
<i>Tegula atra</i> (Lesson)	24788	Bahía de Tongoi, Chile

Table 4 (continued)

a)		
Name labelled	No. MACN	Procedence
<i>Chlorostoma atrum</i> Lesson	25287	Puerto de San Pedro, Chiloé, Chile
<i>Tegula atra</i> var. <i>euryomphulum</i> Lesson	37942	Caldera, Chile
<i>Tegula atra</i> Lesson	9532	Puerto Inglés, al S de Caldera, Chile
<i>Tegula atrum</i> Lesson	11603	Caldera, S de Chile
<i>Tegula atrum</i> Lesson	12168	Valparaíso, Chile
<i>Tegula atra</i> Lesson	13820	Talcahuano, Chile
<i>Tegula atrum</i> Lesson	15091	Antofagasta, Chile
<i>Tegula atra</i> Lesson	19039	Canales de Smith, Magallanes, Chile
<i>Tegula atrum</i> Lesson	19574	Antofagasta, Chile
<i>Tegula euryomphulum</i>	1183	Chile
<i>Tegula atra</i> Lesson	24789	—
<i>Tegula atrum</i> Lesson	13820-1	Is. Quiriquina, Chile
<i>Tegula euromphalla</i> (Jonas)	11813	Isla Santa María – Golfo de Arauco, Concepción, Chile
<i>Tegula atra</i> Lesson	11812	Bahía Concepción, Chile
<i>Tegula atra</i> Lesson	35377	Reserva nacional de Paracas, Región de Ica, Perú, sobre rocas, intermareal
<i>Tegula atrum</i> Lesson	23266-1	San Vicente, Talcahuano, Chile
<i>Chlorostoma atrum</i>	24746	Antofagasta, Chile
<i>Tegula atra</i>	9027	Valparaíso, Chile
<i>Tegula atra</i>	11627	Calbuco, Chile
<i>Tegula atra</i>	21648	Calbuco, Chile
<i>Tegula atra</i>	21837-1	Calbuco, Chile
<i>Tegula atra</i>	1473	Chile
<i>Tegula atra</i>	24829-1	Valparaíso, Chile
<i>Tegula atra</i>	B-9027	Valparaíso, Chile
<i>Tegula atra</i>	21848	Chile
Name labelled	No. MLP (ZI)	Procedence
<i>Tegula atra</i> Lesson	3333	Puerto Americano, Chile
<i>Tegula atra</i> Lesson	3449	Puerto Americano, Chile
<i>Tegula atra</i> Lesson	10728	Puerto San Pedro, Isla Chiloé, Chile
<i>Tegula atra</i> Lesson	3333	Puerto Americano, Chile
<i>Tegula atra</i> Lesson	3343	Puerto Americano, Chile (examined by Castellanos and Landoni, 1988–1993)
<i>Tegula atra</i>	12985	? Portugal
<i>Tegula atra</i> Lesson	3246	Puerto Ballena, Chile
<i>Tegula atra</i> Lesson	12092	Playa La Cuchara, al sur de Tocopilla, Chile
<i>Tegula atra</i> Lesson	10741	Puerto Americano, Chile
Name labelled	No. NHMUK	Procedence
<i>Tegula atra</i> Lesson	1869.6.5.14	Patagonia
<i>Tegula atra</i> Lesson	1869.6.5.81	Chiloé, Chile
<i>Tegula atra</i> Lesson	2351	Papudo, Chile
<i>Tegula atra</i> Lesson	1869.6.5.83	Coquimbo, Chile
<i>Tegula atra</i> Lesson	20041038	Quitrilco, Chile
<i>Tegula atra</i> Lesson	20041037	Chile – Raleigh Expedition
<i>Tegula atra</i> Lesson	89.5.22.6.7	Chile
<i>Tegula atra</i> Lesson	1922.8.23.133.135	Calbuco, Chile – (MACN 11621)
<i>Tegula atra</i> Lesson	1563 S/L	—
<i>Tegula atra</i> Lesson	2242	Chile
<i>Tegula atra</i> Lesson	1823	—
<i>Tegula atra</i> Lesson	1563	—
<i>Tegula atra</i> Lesson	—	—
<i>Tegula atra</i> Lesson	2242	—
<i>Tegula atra</i> Lesson	—	Valparaíso, Chile
<i>Tegula aureotincta</i>	—	California
<i>Tegula brunnea</i>	—	California

b)

Name labelled	No. MLP (DCG)	Procedence
<i>Tegula atra</i> Lesson	913	Puerto Lobos
<i>Tegula atra</i> Lesson	914	Cabo Raso area
<i>Tegula atra</i> Lesson	915	North of Camarones
<i>Tegula atra</i> Lesson	916	South of Camarones

Table 4 (continued)

b)		
Name labelled	No. MLP (DCG)	Procedence
<i>Tegula atra</i> Lesson	917	North of Caleta Olivia
<i>Tegula atra</i> Lesson	918	North of Bahía Bustamante
<i>Tegula atra</i> Lesson	919	Arroyo Marea, Bahía Bustamante
<i>Tegula atra</i> Lesson	920	North of Camarones
<i>Tegula atra</i> Lesson	921	17 km south of Camarones
<i>Tegula atra</i> Lesson	922	Golfo San Jorge
<i>Tegula atra</i> Lesson	923	Camarones
Name labelled	No. MLP (PI)	Procedence
<i>Tegula atra</i> Lesson	26573	South of Camarones
<i>Tegula atra</i> Lesson	26574	South of Camarones
<i>Tegula atra</i> Lesson	26641	South of Camarones
<i>Tegula atra</i> Lesson	26642	South of Camarones
<i>Tegula atra</i> Lesson	26643	South of Camarones
<i>Tegula atra</i> Lesson	26644	South of Estancia La Ibérica, Bahía Bustamante
<i>Tegula atra</i> Lesson	26645	Bahía Bustamante
<i>Tegula atra</i> Lesson	26646	North of Las Grutas—South of San Antonio Oeste
<i>Tegula atra</i> Lesson	26647	Baliza San Matías, NE of San Antonio Oeste

c)

	AGE	Main Patagonian area (Figs. 1 and 7A)
<b>Fossil specimens of <i>Tegula atra</i> for morphometric analysis samples collected in Patagonian marine deposits</b>		
1 BUSTAMANTEPA02Q15-1	PL	Bahía Bustamante
2 BUSTAMANTEPA08Q7	PL	
3 BUSTAMANTEPA08Q8-1	PL	
4 BUSTAMANTEPA09AOMAREA	PL	
5 BUSTAMANTEPA0859-1	PL	
6 BUSTAMANTEPA0863-1	PL	
7 CABORASOPA087-1	PL	Cabo Raso—Camarones
8 CABORASOPA0812-1	PL	
9 CAMARONESaBUSTPA0863-1	PL	
10 CAMARONESPA0847-1	PL	
11 GSJ PA01042SPANAZUCAR-1	PL	Golfo San Jorge
12 GSJ PA01042SPANAZUCAR-2	PL	
13 GSJ PA01042SPAN AZUCAR-3	PL	
33 MAZARREDOPA04Y-1	PL	Puerto Mazarredo
34 MAZARREDOPA04Y-2	PL	
35 NCAMARONESPA0833-1	PL	Camarones
36 NCAMARONESPA0840bis-1	PL	
37 NCAMARONESPA0840bis-2	PL	
41 P.LOBOSCONG.GEOL.	PL	Puerto Lobos
42 P.LOBOSPA0871-1	PL	
43 P.LOBOSPA0871-2	PL	

**Modern and fossil specimens of *T. atra* and related species from museum and private collections**

14 MACN614-1	M	Valdivia, Chile Central
15 MACN614-2	M	Valdivia, Chile Central
16 MACN9040-16-1	M	Punta Arenas, sur de Chile
17 MACN9040-16-2	M	Punta Arenas, sur de Chile
18 MACN10453-1	M	Calbuco, Centro-Sur de Chile
19 MACN10453-2	M	Calbuco, Centro-Sur de Chile
20 MACN11603-1	M	Caldera, Norte de Chile
21 MACN12168-1	M	Valparaíso, Centro-Norte de Chile
22 MACN13820-1	M	Talcahuano, Centro-Norte de Chile
23 MACN15091-1	M	Antofagasta, Norte de Chile
24 MACN15091-2	M	Antofagasta, Norte de Chile
25 MACN19039-1	M	Canales Smith, Magallanes, Sur de Chile
26 MACN19039-2	M	Canales Smith, Magallanes, Sur de Chile
27 MACN23266-1	M	Talcahuano, Centro-Norte de Chile
28 MACN24788-1	M	Bahía de Tongoi, S de Coquimbo, N Chile

(continued on next page)



Table 4 (continued)

c)		AGE	Main Patagonian area (Figs. 1 and 7A)
29	MACN24788-2	M	Bahía de Tongoi, S de Coquimbo, N Chile
30	MACN35373-1	M	Ica, Perú
31	MACN35373-2	M	Ica, Perú
32	MACN37942-1	M	Caldera, Norte de Chile
38	NHMUK1869.6.5.83-1	M	Coquimbo, N Chile
39	NHMUK1869.6.5.83-2	M	Coquimbo, N Chile
40	NHMUKSINNoVALPARAISO-1	M	Valparaíso, Centro-Norte de Chile
44	TegulaaureotinctaNHMUKCalif-1	M	California, USA
45	Tegulablakeicat	Hol	San Antonio Oeste, Río Negro
46	TegulabrunneaNHMUKCalif-1	M	California, USA
47	TegulabrunneaNHMUKCalif-2	M	California, USA
48	Tegulaeuryomphala1 CHILE	M	Chile
49	Tegulaignota1CHILE	M	Chile
50	TegulaluctuosaCHILE	M	Chile
51	TegulapatagGSJ	PL	Holoceno GSJ
52	TegulapatagonicaBustamante	PL	Bustamante
53	TegulapatagonicaCamarones	PL	N Camarones (PA02Q15)
54	Tegulapatagoniacatálogo	M	MATERIAL TIPO NHMUK
55	TegulapatagonicaP.Lobos	PL	P. Lobos
56	TegulaaMODIQUIQUE(2)	M	Iquique, N Chile
57	TegulaaMODIQUIQUE(3)	M	Iquique, N Chile
58	TegulaaMODIQUIQUE(4)	M	Iquique, N Chile
59	TegulaaMODIQUIQUE(5)	M	Iquique, N Chile
60	TegulaaMODIQUIQUE(6)	M	Iquique, N Chile
61	TegulaaMODIQUIQUE(7)	M	Iquique, N Chile
62	TegulaaMODIQUIQUE(8)	M	Iquique, N Chile
63	TegulaaMODIQUIQUE(9)	M	Iquique, N Chile
64	TegulaaMODIQUIQUE(diez)	M	Iquique, N Chile
65	TegulaaMODIQUIQUE(doce)	M	Iquique, N Chile
66	TegulaaMODIQUIQUE(once)	M	Iquique, N Chile
67	TegulaaMODIQUIQUE(unos)	M	Iquique, N Chile

The genus *Tegula* has a recent origin (Neogene). It first appeared in North America in the Mid-Miocene in California (ca. 15 Ma), in the Miocene at Chile and Argentina (Hellberg, 1998; Aguirre and Farinati, 2000; Nielsen et al., 2004) and includes more than 40 modern species so far described: a group geographically restricted to subtropical and tropical waters of the eastern Pacific and the Caribbean (half of all) and another (“cool-water *Tegula*”) (e.g. *Tegula* (*Chlorostoma*) species) spread in temperate regions of East Asia and the eastern Pacific in North and South America (Hellberg, 1998).

#### 4.1. Records of *Tegula* in South America

In the SEP, the available oldest fossil records of *Tegula* date to the Miocene (Navidad Formation; Nielsen et al., 2004; no sufficient dating) and then appeared in the Pliocene (27–28°S, Caldera area, Guzman et al., 2000; Mejillones area, Nielsen, 2012). For the SWA it is well documented since the Late Miocene (ca. 10 Ma): “Entrerriense” = Paraná Fm. in Entre Ríos province; Puerto Madryn Fm. in Chubut province; approximately equivalent sediments in Río Negro province (Aguirre and Farinati, 1999; del Río, 2004; Pérez et al., pers. comm. 2010; Reichler, 2010; Supplementary Appendix 1). In the marine Quaternary it occurs in the Pleistocene and Holocene along both sides of South America, and in Argentina it is outstanding for its abundance in the Pleistocene from Patagonia (Aguirre and Farinati, 2000; Aguirre et al., 2011).

Six species of *Tegula* have been described as living in the SWA (Table 2): *T. fasciata* (Born, 1778), *T. viridula* (Gmelin, 1791), *T. excavata* (Lamarck, 1822), *T. patagonica* (d’Orb., 1835),

*T. hotessieriana* (d’Orb., 1842), *T. blakei* (Clench and Aguayo, 1938). On the other hand, in the SEP side six species have most often been cited living from the Magellan Strait northwards: *T. quadricostata* (Wood, 1828), *T. atra* (Lesson, 1830), *T. tridentata* (Potiez and Michaud, 1838), *T. luctuosa* (d’Orb., 1841), *T. euryomphala* (Jonas, 1844), *T. ignota* Ramirez, 1976, of which *T. atra* is most common in Chile (Carcelles and Williamson, 1951; Guzmán et al., 1998; Moreno, 2004). In Argentina, the most common living species are *T. patagonica* (d’Orb.) and *T. blakei* (Clench and Aguayo), typical of the Argentine Malacological Province (Fig. 1) (Carcelles, 1944, 1945; Castellanos, 1967), although *T. patagonica* has also been recorded in scarcer numbers in southern Patagonia (Magellanean Province) (Aguirre et al., 2006, 2009; Castellanos & Landoni, 1989, as *Tegula orbignyana*).

#### 4.2. Taxonomy and distribution of *Tegula atra*

**Phylum Mollusca** Linné, 1758

**Class Gastropoda** Cuvier, 1795

**Clade Vetigastropoda** Ponder and Lindberg, 1997

**Superfamily Trochoida** Rafinesque, 1815

**Family Trochidae** Rafinesque, 1815

**Subfamily Tegulinae** Kuroda, Habe and Oyama, 1971

**Genus *Tegula*** Lesson, 1835

Type species: *Trochus viridulus* Gmelin, 1791 (original designation).

Geographical distribution: Eastern Pacific: Northern Hemisphere; Tropical Indo-Malaysia: Australia (N), Arafura Sea; Tropical Indo-West Pacific: Indo-Malaysia: Australia (N), Timor Sea; Philippines; Central and East Indian Ocean: Indo-Arabia: Persian Gulf (=Arabian Gulf); Indo-China; Japan; East China Sea (Hellberg, 1998; ANSP OBIS, <http://clade.ansp.org/obis/search.php/43648>); Western Atlantic coast (North, central and South America) (Castellanos, 1967; Emerson and Jacobson, 1976; Andrews, 1981; Castellanos and Landoni, 1988–1993, this study; Ríos, 1994). This restricted geographical distribution is represented by two groups: species typical of warmer waters (subgenus *Agathistoma*) and cool-water species (subgenus *Chlorostoma*).

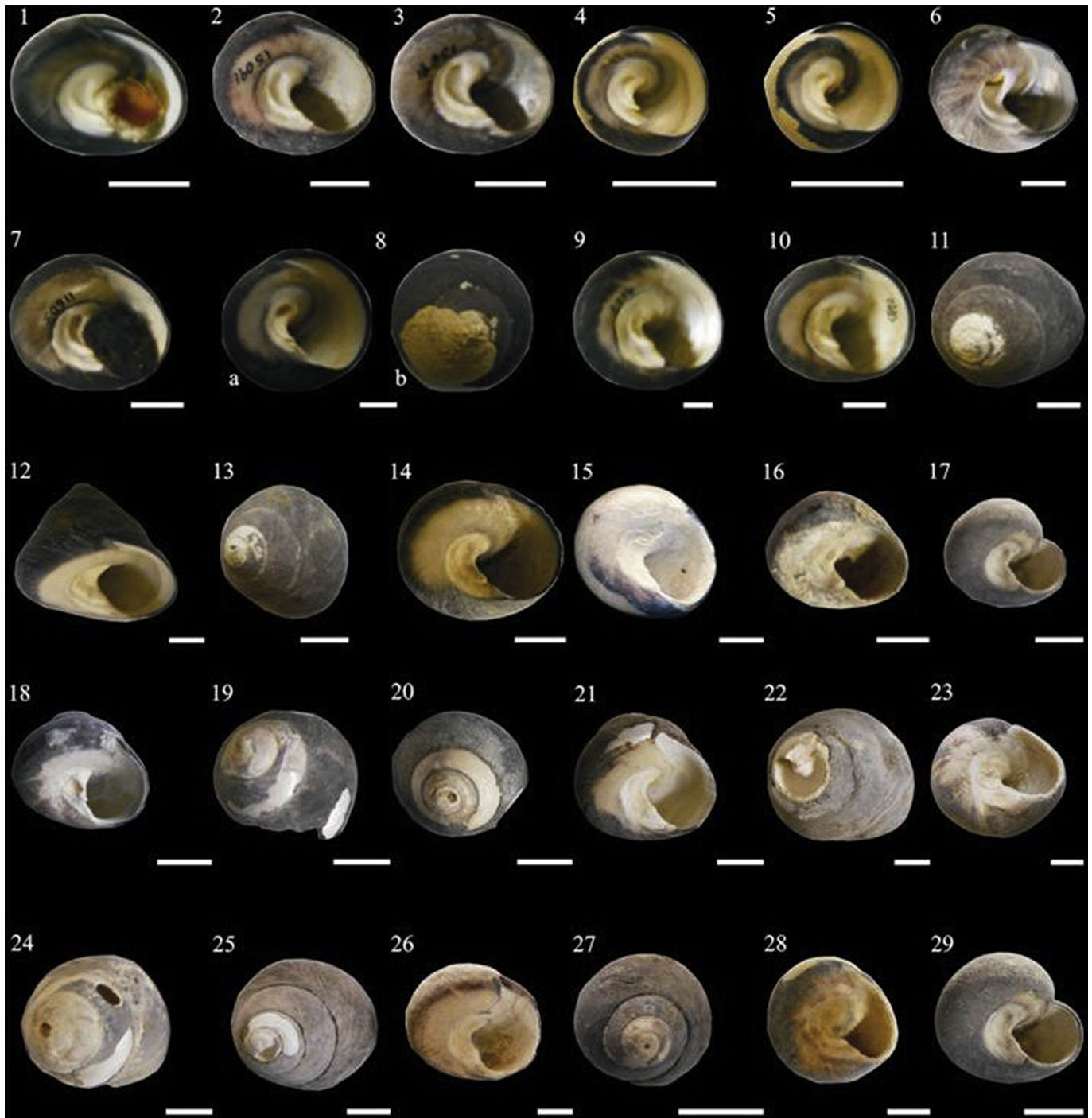
Stratigraphical distribution: Miocene–Recent. In North America Miocene records are available for California (Addicott, 1970; Hellberg, 1998). In South America fossil records are available since the Miocene in the SWA (Aguirre and Farinati, 1999; Aguirre et al., 2008) and SEP (Nielsen et al., 2004).

Habitat and life mode: intertidal and shallow subtidal, rocky shores, lecithotrophic larvae, free epifaunal adults feeding on algae.

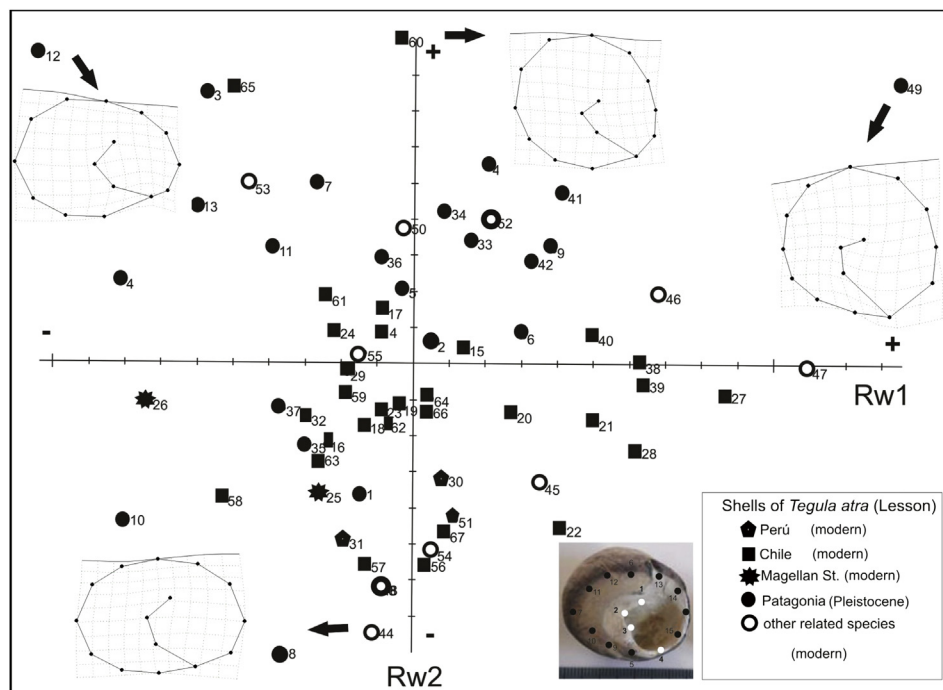
**Subgenus *Chlorostoma*** Swainson, 1840

Type species: *Trochus argyrostomus* Gmelin, 1791 (subsequent designation, Hermannsen, 1846), living in Japan.

Remarks: the species included in *Tegula* (*Agathistoma*) form a cold and temperate-zone group that has well documented records in Japan, California, Chile and other areas in the Southern Hemisphere (Keen, 1971; Hellberg, 1998). The modern geographical distribution of this group is strongly linked to the worldwide distribution of macroalgae among the most abundant floating items dispersing by rafting worldwide (Thiel and Gutow, 2005a; Fig. 15). Its oldest confirmed records in South America belong to the Pliocene from northern Chile (Caldera and Mejillones areas) where it also occurs in the Pleistocene and Holocene (scarce) and modern representatives are very abundant. It is absent today in the SWA (Tables 2 and 3).



**Fig. 4.** Variability of fossil and modern *Tegula atra* in South America since the Pleistocene. **1–14:** Modern specimens from the Pacific littoral (Chile and Perú); **15–29:** fossil specimens from Atlantic coastal deposits of Pleistocene age along Patagonia (Argentina). All are apertural views. Scale: 1 cm. Abbreviations for repositories in museum collections and location of samples taken in the field are as follows: MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” in Buenos Aires (Argentina); MLP, Museo de La Plata (Argentina); NHMUK, Natural History Museum in London (UK); **PA**..., samples collected in several campaigns along Patagonia. **1** – Ica, Perú (MACN 35373); **2** – Antofagasta, Chile (MACN 15091); **3** – Antofagasta, Chile (MACN 15091); **4** – Coquimbo, Chile (NHMUK N° 1869.6.5.83); **5** – Coquimbo, Chile (NHMUK N° 1869.6.5.83); **6** – Caldera, Chile (MACN 37942); **7** – Caldera, Chile (MACN 11603); **8** – Valparaíso, Chile (NHMUK S/N°); **9** – Valparaíso, Chile (MACN B/9027); **10** – Talcahuano, Chile (MACN 13820-1); **11** – Calbuco, Chile (NHMUK N° 1922.8.23.133.135); **12** – Chiloé, Chile (NHMUK N° 1869.6.5.81 S/N); **13** – Quirralco, Chile (NHMUK N° 20041038); **14** – Puerto Angosto, Estrecho de Magallanes (MLP 3343); **15** – Puerto Lobos, Patagonia, Argentina; PA0871 (Pleistocene SCIII, +8 m) (42° 01'55"S–65° 03' 38"W) (MLP-DCG 913); **16** – Cabo Raso area, Patagonia, Argentina; PA08-12 (Pleistocene, +16 m) (44° 19'49"S–65° 16'8.6"W) (MLP-DCG 914); **17** – North of Camarones, Patagonia, Argentina; PA08-33 (Pleistocene) (44° 41'36.3"S–65° 40'23.8"W) (equivalent to Pa47 of Schellmann and Radtke, 2000: MIS5, 117–135 ka B.P.) (MLP-DCG 915); **18** – South of Camarones, Patagonia, Argentina; PA08-63 (Pleistocene, +40 m) (MLP-DCG 916); **19** – North of Caleta Olivia, Supe Locality, Patagonia, Argentina; PA010-42 (Pleistocene) (MLP-DCG 917); **20** – North of Caleta Olivia, Supe Locality, Patagonia, Argentina; PA010-42 (Pleistocene) (MLP-DCG 917); **21** – North of Bahía Bustamante, South of Estancia La Ibérica, Patagonia, Argentina; PA08-59 (Pleistocene) (MLP-DCG 918); **22** – North of Bahía Bustamante, South of Estancia La Ibérica, Argentina; PA08-59 (Pleistocene) (MLP-DCG 918); **23** – Bahía Bustamante, Arroyo Marea, Patagonia, Argentina; PA09-Ao. Marea (Pleistocene) (MLP-DCG 919); **24** – Bahía Bustamante, Arroyo Marea, Patagonia, Argentina; PA09-Ao. Marea (Pleistocene) (MLP-DCG 919); **25** – 14 km North of Camarones, Patagonia, Argentina; PA02Q15 (Pleistocene) (MLP-DCG 920); **26** – 14 km North of Camarones, Patagonia, Argentina; PA02Q15 (Pleistocene) (MLP-DCG 920); **27** – 7 km South of Camarones, Patagonia, Argentina; PA08-44 (Pleistocene) (MLP-DCG 921); **28** – Golfo San Jorge, Patagonia, Argentina; PA010-42 (Pleistocene) (MLP-DCG 922); **29** – Camarones, Patagonia, Argentina; PA08-33 (Pleistocene, +12–13 m). Same as Pa47 Schellmann and Radtke (2000). MIS 5, 117–135 ka B.P.) (MLP-DCG 923).



**Fig. 5.** Results of the morphometric analysis of *Tegula atra* (Lesson) and related species. Scatterplot of the first two principal component axes (analysis based on proportions – shape) for morphs identified (27 fossil and 40 modern shells): Rw = RWarps. Other related species: 44, *aureotincta*; 45, *blakei*; 46–47, *brunnea*; 48, *euryomphala*; 50, *luctuosa*; 51–55, *patagonica*. The remaining numbers refer to *T. atra* (references for geographical precedence and age inside the graph and in Table 4).

### *Tegula (Chlorostoma) atra* (Lesson, 1830)

(Fig. 4, 1–29)

\* [1830] *Trochus ater* Lesson: 344.

[1831] *T. ater* Lesson pl. 16, Fig. 2.

V [1840] *T. ater* Lesson. d'Orbigny: 409.

V 1933 *Chlorostoma atrum* (Lesson). Feruglio pl. 11, Fig. 11ab, 12ab.

V 1945 *Tegula atra* (Lesson). Carcelles: 32.

V 1994 *T. (Chlorostoma) atra* (Lesson). Pastorino: 65, Pl.II, Figs. 1a,b; 3a,b

2000 *T. (Chlorostoma) atra* (Lesson). Aguirre and Farinati: 256, Pl. 2, Figs. 18–19.

2005 *Tegula atra* (Lesson). Aldea and Valdovinos: 389, Fig. 8B

2009 *Tegula atra* (Lesson). Aguirre et al.: 423, Fig. 6.

**Type Material:** not found at the NHMUK where most of Lesson's type material is deposited.

**Type Locality:** Bahía Concepción, Quiriquina Island, Chile (ca. 37°S).

**Description:** Shell thick, medium-sized, trochoid, mostly larger than height (more globose) or sometimes higher than wide (more conic). Spire short. Whorls (3–4) convex. Aperture subovate, umbilicate or imperforate (adults). Labial region with one prominent tooth in a columellar fold (not well seen in eroded specimens). External surface smooth, only with oblique colabral growth lines, spiral lines feeble. Dark (blackish). Internal surface brilliant nacreous.

**Range Dimensions:** H: 13–40 mm; Dm: 12–63 mm (Table 2).

**Material studied (Table 4a–c):** 1080 shells, fossil (130 samples, 16 SWA sites) and modern (15 southeastern Pacific sites). Fossil collections (more than 250 specimens) from Quaternary MT along Patagonia (MIS5, 7, 9; Pleistocene): 30 from Golfo San Matías (PA04Q4; PA04Q3), 60 from Bahía Vera–Camarones (PA02I2, PA02Q15; PA02Q10), 70 from Bahía Bustamante area (PA02Q7, PA02Q8, PA02Q9), 65 from central Golfo San Jorge area (PA04I2;

PA3; PA04A7) and 20 from Puerto Deseado area (PA010-1, 2, 3). Approximately 840 modern specimens from localities of Chile (Antofagasta, Coquimbo, Caldera, Valparaíso, Talcahuano, Concepción, Valdivia, Pucatrihue, Puerto Montt, Calbuco, Isla Chiloé, Quitraco, Punta Arenas, Magallanes) and southern Perú (Ica) housed in museum collections (320 specimens housed at the MACN, 60 specimens housed at the NHMUK, 50 housed at the MLP ZI).

**Stratigraphical range:** Pliocene to Recent (South America). Pacific margin: Pliocene, Pleistocene, Holocene (Chile); Recent from southern Perú to Magellan region (Chile) (Osorio, 1979; Véliz and Vásquez, 2000; Moreno, 2004; Aldea and Valdovinos, 2005; DeVries, 2007; Cárdenas Mancilla et al., 2008; Nielsen, 2012). Atlantic margin: Pleistocene, exclusively in Patagonia (Argentina) Golfo San Matías area down to southern Santa Cruz province, most abundantly in Golfo San Jorge area (Aguirre et al., 2005, 2006, 2008, 2009 and other references therein), especially within MIS5 and 7. It is absent in MIS11 (warmer than present *sensu* Ortlieb et al., 1996; sea level close to the modern position, *sensu* Bowen, 2010) and MIS1. Mentions of a few shells from Holocene sediments (San Antonio Oeste by Pastorino, 1994; south of Camarones by Aguirre et al., 2006) are now confirmed to be Pleistocene in age (MIS5?) (San Antonio Oeste area) or to have been reworked from nearby Pleistocene ridges (Camarones area). Other Holocene mentions (Aguirre et al., 2008) are copy-paste proof error.

**Modern Geographical distribution:** Pacific coast of South America from Southern Peru southwards to the Magellan region (Chile) (Carcelles, 1945; Guzmán et al., 1998; Hellberg, 1998; Véliz and Vásquez, 2000; Osorio and Reid, 2004). According to the molluscan materials and inventories from oceanographic expeditions carried out in the Mar Argentino and to modern collections from several museums, *T. atra* does not live in the SWA. Modern unconfirmed records (no illustrations provided) are available, however, for Antarctica, Malvinas (Falkland) Islands and Atlantic Tierra del Fuego southern beaches (Linse, 1999; Isla et al., 2005). It is absent in central South Atlantic and Subantarctic islands (Tristan de Cunha; Kerguelen, Crozet, Prince Edward, Bouvet) and in



Australia, New Zealand (Dell, 1971; Loodbruck, 1984; Hellberg, 1998; Reid and Osorio, 2000; Troncoso et al., 2001; Rosenberg, 2005; Linse et al., 2006; Griffiths et al., 2009; Beu, 2009; Griffiths, written comm., 2010, 2012) and in Southeastern Pacific islands (Easter Island and Juan Fernandez Island; Colomina et al., 2004; Osorio et al., 2005; Osorio, written comm. 2012) (Fig. 1, Table 2). A mention of this species collected from Easter Island (to two specimens housed at the Museo Nacional de Historia Natural in Santiago in Chile) was probably carried there by antropochoria or in ballast (Rehder, 1980). Interestingly, the modern range of *T. atra* matches the geographical distribution of kelp macroalgae (*Durvillaea antarctica*) (Thiel and Gutow, 2005a; Boraso and Zaiuso, 2009; Liuzzi et al., 2011) which allow its dispersion by rafting in the SEP (Vásquez et al., 2006).

**Remarks:** There is a wide variability of both modern and fossil shells (Fig. 4). Maximum sizes and most globose shells arise from Valdivia–Chiloé Island area (38–43°S), probably where optimum physical parameters (sea surface temperature, light, water oxygenation, substrate nature, nutrient availability) are prevalent. A wide morphological range of shape variation (modern and fossil shells) can be observed (see morphometric results below, Fig. 5). Height–width proportions can vary according to available optimum habitat conditions (larger, more globose forms in optimum colder, hard substrate, intertidal water column). The extensive latitudinal range of *T. atra* in the SEP could be a result of very similar littoral conditions found locally at different latitudes all along the Chilean coast (Camus, 2001).

**Comparisons:** Several species living along the Chilean coasts are very similar to *T. atra* in shell shape and dimensions and share approximately the same geographical distribution, habitat and ecological requirements: *T. luctuosa* (d'Orb., 1841), *T. euryomphala* (Jonas, 1844), *T. ignota* Ramirez, 1976 (Abbott and Dance, 1991; Guzmán et al., 1998; Véliz and Vásquez, 2000; Aldea and Valdovinos, 2005) (Table 2). The shape of the aperture (more acute-subquadrangulate) is the main difference between these species and *T. atra* (more rounded–subovate). It is outstanding that *T. luctuosa* and *T. euryomphala* are dominant in central and northern Perú (Guzmán et al., 1998), where *T. atra* has its northern endpoint. These forms could be regarded as synonyms of *T. atra*. However, until their type material is found and compared this remains undocumented. Studies to decipher whether these could represent clinal variations of the same species or a replacement (species turnover) and phylogeographic approaches are still needed.

Other Chilean species including *T. tridentata* (Potiez and Michaud, 1838) and *T. quadricostata* (Wood, 1828) also strongly resemble *T. atra*, but the number of columellar teeth (three or four, respectively) is a stronger distinct taxonomic character. *Homalopoma cunninghami* Smith, living in southern Chile (as illustrated by Cárdenas Mancilla et al., 2008, Fig. 2) is only superficially similar in shape to *T. atra*. However, this species shows marked spiral cords. On the other hand, other two species living in Pacific waters of the Northern Hemisphere (Panamic and Californian provinces), *Tegula brunnea* (Philippi, 1841) and *Tegula aureotincta* (Forbes, 1852), as illustrated by Abbott (1991, p. 42) and examined in the collections of the NHMUK, show similar contour and dimensions (ca. 40 mm) but different colour and commonly quite distinct sculpture (marked concentric growth lines). *Tegula funebris* (A. Adams, 1853), living in intertidal rocky habitats along the western coast of Canada southwards to Baja California (Abbott and Dance, 1991) is another similar species.

*Diloma nigerrima* (Gmelin, 1791) (= *Tegula niger sensu Hellberg* (1998)) is another Pacific species recorded at present in Japan, New Zealand, Juan Fernandez Island and the Chilean coast (as illustrated for Chile by Guzmán et al. (1998, Fig. p. 36) and Aldea and Valdovinos (2005, Fig. 8A) and for the Magellan province by

Forcelli (2000) is strongly similar both in shell shape and dimensions, a similarity already pointed out by Pastorino (1994). However, it is thought to exhibit a larger umbilical callus, apparently lacking columellar teeth (abraded?) and showing fine spiral striae (both conditions also found in many *T. atra* shells). This species was placed in the genus *Tegula* by Hellberg (1998).

*Diloma zelandica* (Quoy and Gaimard, 1834), living in New Zealand, and *Austrocochlea rudis* (Gray, 1826), living in southern Australia, are very similar species, similar in shell shape, dimensions (average 14–26 mm) and external colour. To decide on whether they could be posterior synonyms of *T. atra* requires examination of their type material, not available at this stage of study.

Six species of *Tegula*, most commonly found living in the SWA, represent closely related forms but clearly distinct from *T. atra*, to judge from the general sculpture (spiral lines, sometimes nodulose ribs) and size (smaller): *T. excavata* (Lam., 1822), living from Florida to West Indies (Abbott and Dance, 1991: 42); *T. fasciata* (Born, 1778) living from southern Florida to Brazil (Abbott and Dance, 1991, p. 42); *T. hortesseriana* (d'Orb., 1842), living from North Carolina to Surinam and Brazil (Ríos, 1994, Pl. 9, Fig. 84); *T. viridula* (Gm., 1791), living from eastern Panama down to Surinam and Brazil (Ríos, 1994: Pl. 9, Fig. 86); *T. patagonica* (d'Orb., 1835), living from southern Brazil to northern Patagonia (Carcelles, 1944: pl.1, Figs. 12–17; Carcelles, 1945: pl.1, Figs. 1–5, 8–11, 16–19; Aguirre and Farinati, 2000: pl. 2, Figs. 14–15) and *Tegula blakei* (Clench and Aguayo, 1938), with the same geographical range (southern Brazil–Golfo San Matías, northern Patagonia) (Aguirre and Farinati, 2000: pl. 2, Figs. 16–17).

*Tegula patagonica* (d'Orbigny, 1835) is a well differentiated smaller (5–23 mm) species, with typical ribbed spiral sculpture (Aguirre and Farinati, 2000: 255, Pl. 2, Figs. 14–15), which lives in the Argentine Province and can less frequently found in Patagonian waters south to Golfo San Jorge. It belongs to the subgenus *Agathistoma* Olsson and Harbison, 1953 and is the most common *Tegula* in the Argentine Province, with confirmed records since the Late Miocene in Argentina (Aguirre and Farinati, 1999). *T. blakei* (Clench and Aguayo, 1938) is also smaller (3–15 mm), more depressed and eventually with spiral sculpture, *T. blakei* only occurs in the Holocene of Patagonia (Golfo San Matías).

Another Trochidae which has often been confused with *T. atra* is *Photinula caerulea* (King and Broderip, 1831), typical of the Argentine Province and with Holocene records in Patagonia (Aguirre and Farinati, 2000: Pl. 2, Figs. 20, 21). Scarce modern material of this species recorded in the Mar Argentino and within the outer zone (marine) of the Río de La Plata was examined in 2009 from collections housed at the Inidep (Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, Argentina) which were labelled as *T. atra*. Also, most “modern” specimens illustrated or mentioned for Argentina (Castellanos and Landoni, 1988–1993) are shells washed ashore along the modern beach from nearby fossiliferous marine terraces and beach ridges.

**Ecological requirements** (Supplementary Appendix 3): intertidal, typical of hard rocky substrates or coarse sediments, high energy, clean cold waters. In the intertidal zone along the Chilean coasts it lives preferably on rocky shores and in variable oxygenated cold waters of the Patagonian Estuarine Front (Chile) and in the Peru–Chile Upwelling Front/System, controlled by the cold Cabo de Hornos Current and the Humboldt Current System (Acha et al., 2004; Bogazzi et al., 2005; Thiel et al., 2007). It has a lecithotrophic planktonic larva and adults are free epifaunal feeding on algae (generalist diet of microalgae; Hellberg, 1998; Moreno, 2004). They can be found attached to brown macroalgae (e.g. *D. antarctica*, *Macrocystis pyrifera*; Thiel and Gutow, 2005a, 2005b; Liuzzi et al., 2011) and their shell surface is often covered by calcareous algae (Coralinaceans). Having lecithotrophic (non-feeding larvae) makes

*T. atra* a perfect candidate for dispersion mechanisms by rafting (Fraser et al., 2010). During ENSO episodes in Chile, the larvae of *T. atra* can be transported offshore towards warm subtropical waters, metamorphosing in high numbers when warm waters reach the coastal zone; then adults return to colder waters near the coast (Moreno, 2004). Environmental stress produced by marked rise in temperature directly and strongly affects heart physiology of closely related species of *Tegula* (i.e., *T. brunnea*, *T. funebris*, *T. montereyi*) that inhabit discrete vertical zones in California, in the marine intertidal down to the shallowest subtidal, leading to their immediate death (Stenseng, 2005).

#### 4.3. Morphometric results

Morphometric results are based on 67 shells of *T. atra* and other close species from different SWA and Pacific sites (Table 4c, Fig. 1): 27 fossil shells (20 Pleistocene *T. atra*, 6 fossil Holocene *T. patagonica* and 1 fossil Holocene *T. blakei*) and 40 modern shells (*T. atra* from Chile and Perú and other close species from Chile and California). The lack of morphometric differences between modern shells of *T. atra* (SEP) and the Pleistocene Patagonian specimens (SWA) reinforce that they belong to the same taxonomic unit and presumably to the same habitat preferences in oceanic physical conditions (substrate, salinity, sea surface temperature, productivity along the modern Humboldt system).

Fig. 5 displays the two first RW of the analysis performed on L and SL marked on the apertural view (most used for taxonomic discrimination at the species level), with the cases grouped by traditional morphs, *T. atra* and the remaining species: Pacific: *T. aureotincta*; *T. brunnea*; *T. euryomphala*; *T. luctuosa*; Atlantic: *T. patagonica*, *T. blakei*. In this figure the variation observed for the modern and Pleistocene *T. atra* clearly overlap. All the variation in shell shape is included in one same group, confirming that the SEP and SWA specimens belong to the same morphological group/species. Regarding remaining close “species”, they are mostly intercalated within the same major morphological range. At least some of the *Tegulas* spread in the Pacific (e.g., *luctuosa*, *euryomphala*) could be posterior synonyms, but this needs to be checked by comparisons of the type material and phylogeographic studies.

Apart from the shell variation, observations of the abundant whole specimens collected in the field (Fig. 4), and specimens examined from museum collections (Table 4), indicate that smaller shells and more depressed (less developed spire) are most common in northern Chile and Perú. By contrast, most numerous, larger, globose shells are typical of colder and estuarine waters in rocky exposed coasts (ca. 33–44°S; Fig. 1), coinciding with the type locality for *T. atra* (Concepción, Chile; see taxonomic results above), an area which represents approximately the latitude where the WWD, Fig. 3A) diverges northwards in the Humboldt cold current and southwards in the Cabo de Hornos cold current.

### 5. Palaeobiogeographical results

Overall, the gastropod records considered include a total of 382 taxa from the SWA coastal area between Argentina and Surinam (Fig. 6A): 297 taxa from Surinam–Brazil–Uruguay; in Argentina: 117 from the Bonaerensian area and 76 from Patagonia; a total of 49 taxa occur in Pleistocene sediments, 73 are from fossiliferous Holocene sites and 382 belong to sites along the modern littoral. Solely for Patagonia, a total of 39 taxa correspond to the Pleistocene and 43 to the Holocene. The molluscan taxonomic composition for Patagonia is based on samples from selected localities between San Antonio surroundings in northern Golfo San Matías and southern Santa Cruz province, according to better preservation and deposits

dated by modern methods or correlated with them (Table 3, Supplementary Appendix 1).

Results based on multivariate (CA, PCO) (Fig. 6A, B) and cladistic (PAE) (Fig. 6C) methods are in general terms congruent for the three age periods considered. Three main groups of localities/areas can be discriminated: I, marginal marine areas; II, oceanic northern South America–oceanic Bonaerensian localities, and III, Patagonian coastal sector. Overall, they are coincident with previous results obtained for bivalve taxa from the same area and dataset (Aguirre et al., 2011).

#### 5.1. Results of multivariate analyses

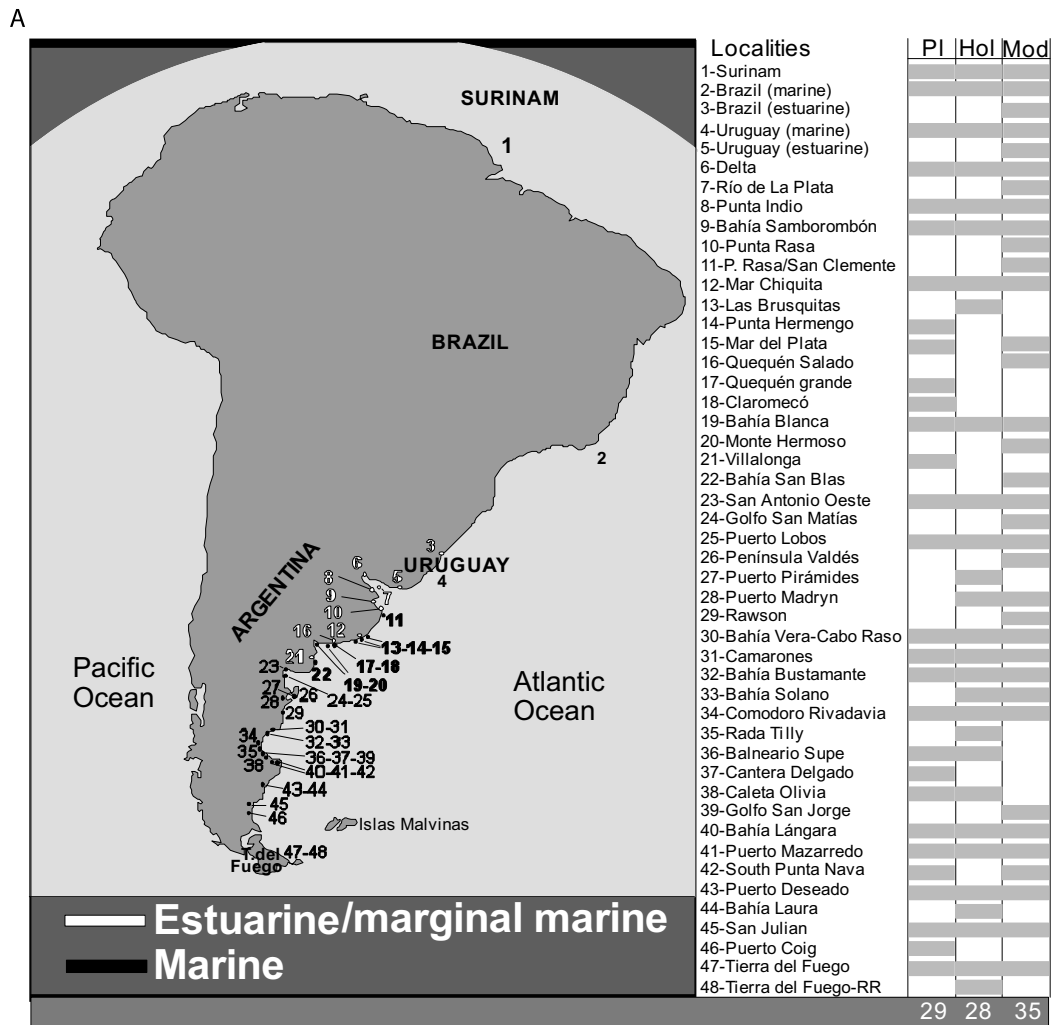
The multivariate results by CA and PCO through time (Modern, fossil Holocene, Pleistocene) are in agreement, showing that Northern South American coastal areas (Surinam, Brazil, Uruguay) and the Bonaerensian sector in Argentina are not linked with Patagonia. A key area is represented by San Antonio Oeste (SAO, northernmost Patagonia, Fig. 1) which is at present a transitional (ecotonal) region, between the Bonaerensian and Patagonian sites, controlled by salinity and thermal fronts (Fig. 3C) which are responsible for the occurrence and abundance of varied taxonomic groups (among others Carcelles, 1944; Castellanos, 1967; Bogazzi et al., 2005; Balech and Ehrlich, 2008). The same pattern is apparent for the fossil Holocene sites, but SAO is not clearly separated from the remaining localities during the Pleistocene. Moreover, SAO is closely linked to central and southern Patagonian localities which are characterized by species typical of cold temperate and cold water masses (Fig. 3B).

#### 5.2. Results of Parsimony Analyses of Endemicity (PAE)

Similarly, the results based on PAE for the Modern, mid-Holocene and Pleistocene datasets (46, 73 and 382 taxa, respectively; Table 3) show relationships and changes through time between areas more clearly. For the modern and fossil Holocene, SAO is clearly disconnected from the remaining Patagonian sites and transitional with the Bonaerensian localities, while for the Pleistocene it is joined with the remaining Patagonian areas.

For the modern PAE (Fig. 6B), the same three main groups are discriminated (I, II, III) and the estuarine and marginal marine sites (I) are apart and do not share more than one species. In the north (II, northern South America and Bonaerensian littoral) the following sites form an AE: Monte Hermoso, Mar del Plata, Quequén, Bahía Blanca, Bahía San Blas, Uruguay, Brazil and Surinam. Two nested AE are also distinguished: P. Quequén and Bahía Blanca, supported by 39 species, and Uruguay, Brazil and Surinam supported by 15 species. Among the most characteristic taxa appear *Urosalpinx* spp., *Natica isabelleana*, *T. patagonica*, *Epitonium tenuistriatum*, *Lucapinnella* spp., *Adelomelon brasiliensis*, *Zidona dufresnei*, *Olivancillaria* spp., *Littoridina australis*. Patagonia is more homogeneous and outlines an AE supported by a larger number of gastropod species. Except for the SAO site, *L. australis* does not occur in Patagonia (not reached by the freshwater influence of the Rio de La Plata plume), and the most characteristic species are *Epitonium georgettinum*, *Fissurella radiosa*, *Trophon geversianus*, *Trophon* spp., *Nacella* spp., *Pareuthria plumbea* (all typically marine). Two nested AE in central Patagonia are represented by Cabo Raso Camarones, supported by 46 species, and C. Rivadavia–Golfo San Jorge by 38 species.

The PAE for the fossil Holocene (not shown) confirms the results based on the modern dataset regarding the three major groups (I, II, III). In the Bonaerensian area (II) a few species displaced northwards at present occur (e.g., *Triphora nigrocincta*, *Anachis avara*, *Urosalpinx rushi*, *Triphora nigrocincta*) and the most characteristics are *A. brasiliensis*, *Z. dufresnei*, *Buccinanops* spp., *T. patagonica*. Within



**Fig. 6.** Multivariate (CA, Cluster Analysis, UPGMA, Jaccard Index, PCO, Principal Coordinate Analysis) and cladistic analyses based on gastropod data matrixes for the SWA (Surinam down to Tierra del Fuego). Modern sites and fossiliferous deposits (Holocene and Pleistocene) sampled in Buenos Aires, Río Negro, Chubut and Santa Cruz provinces (Argentina) and from bibliographic sources. Details for each locality can be obtained from Feruglio (1950), Codignotto et al. (1988, 1992), Aguirre and Whatley (1995), Aguirre et al. (2008, 2009) and other references in Aguirre et al. (2011). Dataset showing the number of records and sites according to Table 3 and Supplementary Appendix 1 (geographical location and temporal range for the sites considered). **A:** Localities sampled in Argentina. Other areas from Southwestern Atlantic compared; **B:** PCO (top) and CA (beneath) through time. Results are in agreement and discriminate between three main groups: I, estuarine and marginal marine coastal sectors; II, North, oceanic Bonaerensian–Northern South American sectors (Uruguay, Brazil, Surinam) and III, oceanic Patagonian area. **C:** PAE (Parsimony Analysis of Endemicity) showing patterns between localities for the Pleistocene (only time span with records of *Tegula atra*) compared to the present (absent). - - - : Areas of endemism (*sensu* Morrone, 1994). Locality areas shown in Supplementary material Appendix 1b. *Tegula atra* characterizes and is dominant in the marine Pleistocene of Patagonia, especially south of SAO (San Antonio Oeste).

Patagonia (III), a whole AE, the most characteristic are *Fissurella* spp., *Trophon* spp., *Nacella* spp., *Pareuthria plumbea*, *Adelomelon ferussacii*, *Odontocymbiola patagonica* but no *T. atra* occurs, and at least three nested AE are well supported (Camarones–Tierra del Fuego supported by 11 species; SAO–P. Lobos by 12 species; B. Bustamante–P. Deseado by 15 species). Some southern sites (P. Deseado, P. Mazarredo, San Julián) are associated with central and northern localities (Bustamante, Cabo Raso). Altogether the pattern implies slightly higher SST in agreement with the “Thermal Maximum” documented in many areas worldwide (Briner et al., 2006) during the mid-Holocene and congruent with similar results based on bivalves (Aguirre et al., 2011).

The Pleistocene PAE gave a less clear pattern, uninformative in the SWA outside Patagonia (Groups I and II), where in fact the Pleistocene records are patchy and the assemblages less well preserved. The trend shows that only Patagonia (III) is as a whole an AE where *T. atra* together with *Fissurella* spp., *Nacella*, spp. are the most characteristic taxa. One well supported (14 species) nested area is

recognized (C. Raso, P. Mazarredo, B. Bustamante, San Julián, Camarones, P. Deseado). Apart from the fact that SAO is linked with southern Patagonian sites, it is outstanding that the entire AE is characterized by *T. atra*, especially south of San Antonio Oeste. SAO is southwards shifted, linked to southern sites (P. Mazarredo, P. Deseado) implying a different relationship between localities and colder waters, likely the thermal front seen at this place today (Fig. 3C) was not active or not as important. The southern shift of Camarones and B. Bustamante in a well-supported AE, together with the constant presence of *T. atra* within marine Pleistocene terraces from Patagonia (especially within MIS7 and MIS5), in huge quantities and with maximum size shells, associated with abundant large shells of cold *Fissurella* spp. or *Mulinia edulis* and *Eurhomalea exalbida* (Bivalvia), form an independent source of evidence for a predominantly cold coastal scenario during the Pleistocene as a whole, probably through a more intensified and extensive cold Malvinas (Falkland) current. These results suggest that the same or very similar nearshore environmental conditions



as those observed in the SEP must have prevailed in this area, in terms of SST (cold), nutrient availability (high) and productivity (increased), but differing from the Holocene settings, including the present. By contrast, *T. atra* is absent: 1) during the warmer MIS5e near SAO localities where *Chama* spp. (warm water bivalves northwards displaced today) occur; and 2) during MIS11 (warmest and largest in South America; Burckle, 1993; Ortlieb et al., 1996), where no *T. atra* is documented.

## 6. Discussion

Until the type material of *T. luctuosa* and *T. euryomphala* is found and compared, a possible synonymy with *T. atra* remains undocumented. To verify whether they could represent clinal variations of the same species, or a replacement (species turnover), phylogeographic approaches are still needed.

There is no doubt that the fossil shell materials preserved in the Patagonian Pleistocene beach ridges and marine terraces belong to the same species living in the SEP. The fossil specimens are identical to the modern representatives, as illustrated in local catalogues and specific taxonomic or biological studies (e.g., Marincovich, 1973; Osorio, 1979; Guzmán et al., 1998; Véliz and Vásquez, 2000; Aldea and Valdovinos, 2005) and judging from specimens examined from museum collections (MLP, MACN, NHMUK; Table 4). Furthermore, the lack of morphometric differences (Fig. 5; Relative Warps, apertural view of whole shells) between the modern shells of *T. atra* and the Patagonian shells reinforce the same taxonomic unit and habitat preferences (substrate, sea surface temperature, salinity, nutrient availability, productivity similar to that observed along the modern Humboldt System in the SEP). Among the three methods applied (CA, PCO, PAE), the PAE is confirmed as the most useful, graphic, quick and objective to recognize natural patterns of benthic gastropod distribution within the marine Quaternary, in agreement with results shown previously for bivalves from the same deposits.

Considering that the Patagonian records are exclusively Pleistocene (during MIS9, 7, 5) and the results of PAE (Fig. 6C), at first glance it could be assumed that similar physical conditions prevailed after MIS11 along the SWA, where colder than present littoral scenarios with higher productivity levels may be the main reason for the occurrence and abundance of *T. atra*. Indirectly, the evidence suggests that the littoral settings along Patagonia during MIS9, 7, and 5 were colder than during MIS11 and 1.

### 6.1. Origin of *Tegula* in the Pacific

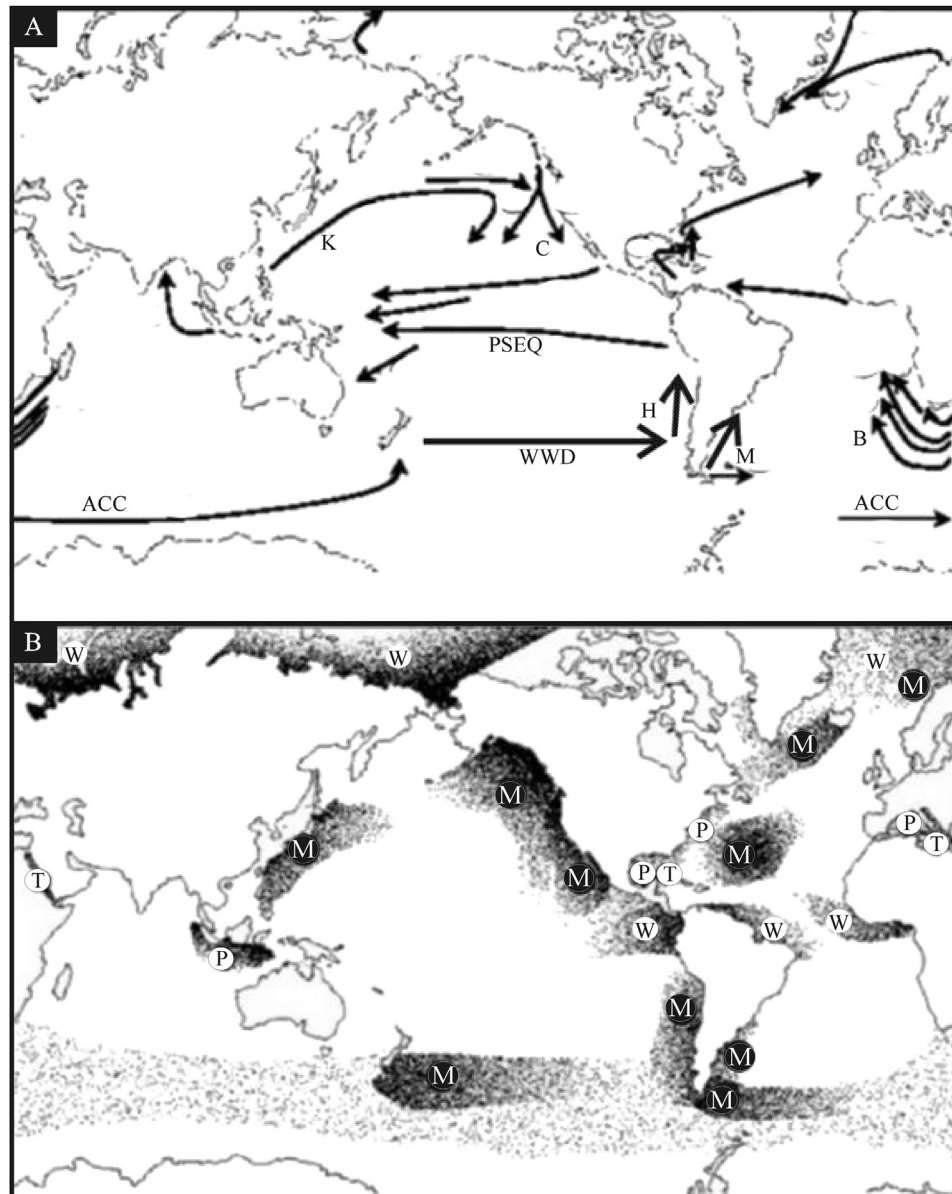
The origin of *Tegula* in the Pacific and the origin of *T. atra* in the SEP can bring light to the explanations for the occurrence and abundance of *T. atra* during the Late Pleistocene MIS9–5 in Patagonia and is strongly linked to the main question: What is the reason for its extinction in the Mar Argentino?

The earliest appearance dates to the Mid-Late Miocene (ca. 15 Ma) at California, where the fossil shells are very similar to the modern shells of *T. aureotincta* living in the same geographical area (Hellberg, 1998). The Pacific shallow oceanic circulation pattern was at that moment quite different from today. In a globally warmer Neogene world (ca. 19.5–17 Ma, Crame, 1998; ca. 17 Ma in the Pacific, Tsuchi, 2002; ca. 10 Ma in the SWA, Scasso et al., 2001) the northern Pacific cold currents were less well developed (both in length and intensity) influencing only the coastal areas around Japan and California. Stronger and more extensive warm currents flowed westwards from the Atlantic into the Pacific and Indian Oceans. A free interchange of cold and warm species was thus possible between the Pacific and the Atlantic, a palaeoceanographical pattern that could account for the occurrence of two

distinct groups of *Tegula* as suggested by Hellberg (1998): 1) a “warm tropical and subtropical” set of species of the equatorial Pacific, Atlantic and Caribbean (subgenus *Agathistoma*; e.g., *T. fasciata*, *T. excavata*, *T. patagonica*, *T. blakei* in the Caribbean and Atlantic; Table 2), and 2) the so-called “cool-water *Tegula*” (subgenus *Chlorostoma*) within the Pacific (e.g., among others *T. atra*, *T. luctuosa*, *T. brunnea*, *T. aureotincta*). The “warm” *Tegula* could easily disperse from the Atlantic into the Pacific until before the closure and constriction of the Central American Seaway (Isthmus of Panama; ca. 4.6–3.8 Ma) and into the South China Sea and Indian Ocean before the closure of the Indonesian Seaway (ca. 5–3 Ma) (Karas et al., 2011) (but after 3 Ma, Filippelli and Flores, 2009). Both palaeogeographical events were responsible for the climatic transition from a warmer and wetter Mid-Pliocene epoch (Raymo et al., 1996, 2011; Wara et al., 2005; Salzmann et al., 2011) towards the onset of a dominantly cooling scenario during the late Pliocene in the Pacific (Lisiecki and Raymo, 2005; Klotz et al., 2006) and at least since ca. 3.5–3.2 Ma in the Southern Ocean (Hodell and Warnke, 1991). A stronger influence since the Pliocene and throughout the whole Pleistocene of the cold current systems (Kuroshio, Californian, Pacific South equatorial, West Wind Drift, Humboldt and Cabo de Hornos; Fig. 7A) can explain the high abundance of cold *Tegula* (*Chlorostoma*) species in the Pacific, such as *T. aureotincta* in the NEP (California) and *T. atra* in the SEP (Chile, southern Perú).

During cold periods of more intense circumpolar circulation, oceanic dispersal of benthic forms with planktonic larvae, such as *T. atra*, was favoured (Crame, 1998). Considering the affinities of *T. atra* with other species living in the Pacific and taking into account that the oldest records of *T. atra* in the SEP date back to the Pliocene (Mejillones and Caldera areas, northern Chile), it probably colonized the SEP during the Pliocene from the north, through the Kuroshio (northeastwards) and Californian (southwards) intensified cold currents; then along the Pacific South Equatorial current, afterwards surrounding New Zealand (with modern records of *Diloma zelandica*, probably another synonym) and, lastly, through the West Wind Drift (WWD, a branch of the ACC) to finally reach western South America and dispersing along Chile and southern Perú through the Humboldt Current (northwards) and Cabo de Hornos Current (southwards), both branches of the WWD.

Alternatively, another possible origin could be during the distinct Pliocene cooling that characterized the SO after ca. 3.5–3.2 Ma enhancing the shallow cold currents. Thus, *T. atra* could also have originated somewhere in the Southern Pacific along the WWD, as in the area between New Zealand and Concepción (Chile) or around Juan Fernandez Island (but with no records of *T. atra*, only of the close *Diloma nigerrima*). A third possibility could be an origin in any of the Subantarctic islands (Bouvet, Prince Edward, Crozet, Kerguelen). However, no published molluscan records are available from these islands (due to the lack of studies?), except for those by Troncoso et al. (2001) from Kerguelen Islands (with no records of *T. atra*). Lastly, because Western and Eastern Antarctica (Weddell and Ross Seas) were not completely isolated during the Pliocene (Clarke et al., 2005) but, on the contrary, trans-antarctic connections are well documented (Barnes and Hillenbrandt, 2010; invertebrate taxa) and the palaeontological evidence appears to be indicative (although still a matter of debate) of open marine conditions in the interior Antarctic basins during the middle Pliocene (Webb and Harwood, 1991), a recent origin somewhere in Antarctica is plausible as well, followed by dispersal along different regions of the SO through the intensified Circum-Antarctic current system. This system is known to have aided dispersal of benthic organisms with planktonic larval stages between southern high latitude regions (e.g., Crame, 1998). In contrast to this, the only published record of *T. atra* from Antarctica was



**Fig. 7.** Main current trajectories (A) and distribution of main floating elements (B) worldwide: References for 7A: K: Kuroshio; C: Californian; PSEQ: Pacific South Equatorial; H: Humboldt; WWD: West Wind Drift; ACC: Antarctic Circumpolar Current; M: Malvinas (Falkland); B: Benguela. M: References for 7B: M: macroalgae; W: wood; P: plastic litter; T: tar lumps (modified from Thiel and Gutow, 2005a).

supplied by Linse (1999) but no material of *T. atra* is available in the Antarctic collections at the British Antarctic Survey (Cambridge) (Linse et al., 2006; Barnes and Griffiths, 2007; Griffiths et al., 2009; Huh Griffiths written communication, 2010 and 2012).

The available data at the present state of knowledge are not sufficient to objectively conclude whether the different “species” of *Tegula* from the Pacific could have had different independent origins neither about the precise origin of *T. atra* in the SEP, which could only be clarified through a phylogeographic study of modern Pacific representatives. However, regardless of any of the plausible origins in the SEP (from the North Pacific, inside the SEP, in any of the Subantarctic islands or through East–West trans-antarctic connections), it can be assumed that its origin in the SWA took place during the Pleistocene after MIS11, continuing its dispersal from the SEP through the Cabo de Hornos current and then through the cold Malvinas (Falkland) current into the Mar Argentino (Fig. 3), where the youngest records belong to the Last Interglacial (MIS5)

south of SAO, an area where there is a thermal front today (San Matias Frontal System, Fig. 3).

## 6.2. Why is *Tegula atra* extinct from the Mar Argentino (SWA)?

In oceanic contexts, the available evidence on range shifts compared with modern patterns has been linked to different mechanisms including plate tectonics, changes in climate, circulation patterns and oceanographical variables, and ocean biology (Hellberg et al., 2001; Rex et al., 2005; Valentine et al., 2008; Roy et al., 2009; Drinkwater et al., 2010; Vermeij, 2012). For the Late Neogene–Quaternary, it has been shown that climate has a key role in regulating phytoplankton by controlling nutrients and the availability of light in shallow water masses, especially during growing seasons (Behrenfeld et al., 2006, 2008; Etourneau et al., 2009), thus modelling spatial patterns of the marine biota and determining severe ecosystem changes. Even slight changes in

winds, carbon, nitrate, and phosphate cycles can trigger changes in stratified vertical water mixing regimes, altogether subsequently responsible for taxonomic and biogeographical changes (e.g., Etourneau et al., 2009; Filippelli and Flores, 2009).

The dispersal of shallow marine organisms such as *T. atra* depends on extrinsic factors (climate, winds, currents, substrates, depth within intertidal waters) and also on their intrinsic characteristics (larval stages, dispersal mechanisms, capacities of these mechanisms, feeding types) (Lomolino et al., 2010). Of these, abrupt climate changes (mainly SST) seem the most plausible key factor triggering its shift and subsequent extinction from the Mar Argentino after MIS5 (Last Interglacial).

Strong SST variability is well documented for the last 400 ka in the South Atlantic, with glacial-to-interglacial contrasts to 8 °C and rapid shifts of the Subtropical Front. Sea ice followed by nutrients and SST were the first parameters to change at Termination I (Hodell et al., 2002), the so-called Southern “Ocean Tunnelling” operated during deglaciation (Ivanova et al., 2012) and the post LGM warming trend was much more rapid and drastic in central-south Atlantic than in the Pacific (Roemmisch et al., 2012). Could this climate scenario (unfavourable) have triggered a range shift of *T. atra* after the LGM in South America?

In the first place, temperature controls the physiology and survival of *Tegula* in the Pacific. Studies by Stenseng (2005) and Stenseng et al. (2005) through laboratory experiments showed that several *Tegula* from California (namely *T. funebris*, *T. brunnea* and *T. montereyi*) occurring at different vertical positions in the shallow marine littoral (upper intertidal to low-intertidal and upper subtidal, respectively) are negatively influenced by a rise in water temperature. Apart from shape shell variations, these *Tegula* are physiologically altered at different rates by environmental changes in response to daily tidal cycles (temperature fluctuations, desiccation stress, wave force, salinity). Shallower specimens more exposed to heat stress live much closer to their upper cardiac limits than their deeper relatives, and have limited abilities to acclimate to rising temperature changes. A 1–2 °C increase in average global temperatures could strongly compromise their physiology, leading to death.

The average SST was 2–3 °C higher during interglacial maxima relative to glacial maxima according to different sources of evidence for oceanic settings worldwide (e.g., Zachos et al., 2001; Hodell et al., 2002; Clarke et al., 2005; Lomolino et al., 2010) and during the so-called mid-Holocene Thermal Maximum (Briner et al., 2006). Over the SO during the Early and Mid-Holocene, temperatures were higher than at present (Renssen et al., 2005); near Bouvet Island the delivery of ice rafting debris (resulting from ice melting) increased abruptly during the Holocene Hypsithermal at 5.5 ka (Hodell et al., 2002). In Argentina, after the last Glacial/Interglacial transition (ca. 11 ka) the amelioration trend led to a SST rise of ~2 °C during the Mid-Holocene Climatic Optimum (ca. 7.5–4.5 ka B.P.) in comparison with the modern average oceanic temperatures (Hoffmann et al., 1997). A rise of 2 °C in SST is sufficient to have displaced winds and currents. A latitudinal shift of shallow water masses of ~300–400 km southwards along Patagonia regarding the modern position is supported by the palaeobiogeographical pattern of stenothermal gastropods and bivalves, suggesting a southern shift of the Atlantic anticyclonic centre and of the Brazilian and Malvinas (Falkland) currents (Aguirre, 1993b; Aguirre et al., 2009; Cavalotto et al., 2011; Rabassa et al., 2011). During Quaternary climatic cycles, atmospheric circulation patterns were altered through shifts in the position of the oceanic anticyclonic centres in the Pacific and the Atlantic. Most models suggest greater wind speeds over the SO during glacial times (Boyle, 2000). During glacial periods, the South Pacific anticyclonic centre was northwards displaced, and thus the shifts of the westerlies played a

major role in glacial accumulation areas (Ponce et al., 2011). Compagnucci (2011) showed changes in the westerlies and in the semipermanent anticyclones of the Pacific and the Atlantic strongly influencing Patagonia during the LGM and at the glacial–interglacial transition; after the LGM a general decrease in surface wind speeds characterized the SO. Simulation models suggest stronger westerlies during the Early–Middle Holocene than today over Patagonia (Wagner et al., 2007).

Secondly, the drainage network pattern drastically changed in Patagonia when the glaciers melted due to the temperature rise after the LGM (Sudgen et al., 2005; Glasser et al., 2008; Rabassa et al., 2011). The great volume of water discharged into the Atlantic along Patagonia is linked to a drastic climate change responsible for the occurrence of innermost Holocene beach ridges very rich in gravels and almost sterile in terms of molluscan composition in many coastal areas (e.g. Bahía Laura, Ensenada Ferrer) (Codignotto, personal communication; authors’ observations).

Thirdly, the timing and quantity of nutrient availability can be altered by local variations in climate and ocean circulation (Roy et al., 1998; Romero et al., 2006; Paparazzo et al., 2010). Light and the distribution of nutrients (nitrogen, phosphate, iron) affect primary production and depend on physical parameters of oceanic circulation. In general, an increase in SST is linked to decreased nutrients (Behrenfeld et al., 2006, 2008; O’Malley et al., 2009). Primary production is directly affected by temperature and salinity, vertical density stratification and depth of mixing of the upper layer, light and availability of nutrients, winds and currents (Drinkwater et al., 2010). Interestingly, a net increase of primary production was documented for the SEP during the Pleistocene in contrast with the warmer mid-Pliocene period and the present (e.g., Filippelli and Flores, 2009).

Finally, considering the abiotic factors mentioned, changes in salinity are disregarded as a key factor leading to the extinction of *T. atra*. Although enhanced drainage during the ice melting after the LGM could have altered the salinity gradients near the few river outlets along Patagonia, this cannot be the reason for the extinction of *T. atra*, which lives along the Patagonian Cold Estuarine Zone in Chile (Fig. 3). In turn, an enhanced river discharge is expected to drive to higher nutrient discharge modifying productivity and changing phosphate contents of sea water (Glacial Shelf-Nutrient Hypothesis; variations in the phosphorous cycle can play a major role on marine biological productivity; Filippelli et al., 2007). Even slight changes could have been drastic and a key-factor in the survival of *T. atra*, which has lecithotrophic larvae (planktonic larvae that gain nutrition from phospholipoproteins in the yolk) which are known to increase with falling temperatures (Beu, 2012).

Drastic and rapid change in SST, wind velocities, oceanic currents, phosphorous content (among other nutrients) and productivity following the Pleistocene/Holocene transition must have been responsible for a geographical shift leading to the extinction of *T. atra*, physiologically unable to survive in 2 °C higher SST and to obtain the optimum quality and quantity of nutrients needed mainly for larval feeding. At the same time, the strong association between *T. atra* and macroalgae (kelps) is the main reason why *T. atra* could not survive the Holocene amelioration. A restriction during the Holocene of kelp macroalgae (e.g., *D. antarctica*) (see beneath) must have prevented its dispersion by rafting and can explain why *T. atra* was unable to survive in the Mar Argentino while other cold water gastropod taxa (e.g., *Fissurella* spp., *Nacella* spp., *Trochita pileus*, *Colisella cecilianae*, *Pareuthria plumbea*, *Xymenopsis muriciformis* among others) were able to persist in the Magellan Malacological Province along the SWA until the present (Supplementary Appendix 3).

The absence of *T. atra* in the SWA today can be gathered as a case study undoubtedly linked to changes in temperature-oceanic-



atmospheric circulation patterns at the Pleistocene/Holocene transition, which in continental settings were drastic enough to have triggered also the dramatic extinction of numerous native megamammal groups (e.g., *Megatherium*, *Glossotherium*, *Glyptodon*, *Doedicurus*, *Pampatherium* among other taxa) (e.g., Cione et al., 2003 and references therein). What still cannot be ruled out is whether this dispersal-extinction mechanism could have occurred some other time/s during Pleistocene transitions after MIS11. A search is required for records of this species in sediment cores from the Argentine continental shelf at 100 m or deeper which could correlate with MIS2, 4, 6 or 8.

### 6.3. Can brown macroalgae explain the extinction of *Tegula atra* in the SWA?

An independent source of explanation for oceanographical changes and for the modern occurrence of *T. atra* in the SEP vs. its absence after the LGM in the SWA is the modern distribution of macroalgae (kelps). Brown macroalgae (among others, *Durvillaea*, *Macrocystis*, *Sargassum*) are the dominant floating seaweeds in the world's oceans (Fig. 7B). Rafting through these large seaweeds represents an important dispersal mechanism for floating objects over huge distances, both alongshore and across the open ocean (e.g., ca. 400–600 km to more than 7000 km) (Fraser et al., 2010, 2011; Rothäusler et al., 2012). Macroalgae are concentrated in convergence zones (fronts) and eddies, and their trajectories match with the trajectories of major current systems and winds, which in turn determine the floating direction, velocities and distances that algae can cover (Thiel and Gutow, 2005a, 2005b; Rothäusler et al., 2012).

Trans-oceanic rafting of assemblages of intertidal organisms, including numerous coastal invertebrate taxa, is common today (Waters, 2008; Fraser et al., 2010). Among different groups forming part of the associated holdfast-dwelling invertebrates, molluscan species are easily transported, including *Ostrea chilensis* (Bivalvia) (Ó Foighil et al., 1999), *Diloma nigerrima* (Donald and Kennedy, 2005; Waters, 2008) and several *Tegula* from California (Lindberg, 1991) and the SEP (Vásquez et al., 2006). Not only is this a fascinating phenomenon occurring worldwide today (among others Watanabe, 1984; Lindberg, 1991; Thiel and Gutow, 2005a, 2005b; Vásquez et al., 2006; Villegas et al., 2008; Fraser et al., 2010; Hinojosa et al., 2011; Liuzzi et al., 2011; Rothäusler et al., 2012), but also the fossil evidence suggests that it occurred in palaeo-oceans as well (Ó Foighil et al., 1999).

The coastal zones where *Tegula* (*Chorostoma*) species are recorded and where *T. atra* occurs in the Pacific (SEP), match geographical regions with most abundant macroalgae (Japan, California, New Zealand, Chilean coasts) (Thiel and Gutow, 2005a, 2005b) and are all interconnected by cold oceanic currents (Kuroshio, California, Southeastern Pacific, ACC, WWD, Humboldt, Cabo de Hornos). Rafting is the most convincing mechanism for the dispersal of *Tegula* in the Pacific during the Pliocene and Pleistocene through the enhanced cold current systems and, during the Pleistocene, for *T. atra* from the SEP into the SWA through the WWD, which plays a major role in transporting algae eastwards between South America and Subantarctic islands, and the Cabo de Hornos and Falkland currents.

The most common floating seaweeds in cold waters of the SH are two brown algae, *Macrocystis pyrifera* and *D. antarctica* (Phaeophyceae). *M. pyrifera* occurs in cold waters of the Pacific and Atlantic: California, Tasmania, New Zealand, the southern Pacific, Chile, Scotia Arc, and the SWA at Tierra del Fuego, Malvinas (Falkland) Islands and Patagonia (from southern Santa Cruz province northwards to Península de Valdés in Chubut province; Boraso de Zaixso and Quartino, 1993; Liuzzi et al., 2011) reaching

northwards ~34°S (Uruguay). *D. antarctica* is typical of Pacific cold waters: south of Tasmania, New Zealand, the southern Pacific, Chile extending southwards to the Magellan Straits, Subantarctic islands (e.g., Kerguelen) (Thiel and Gutow, 2005a, 2005b; Liuzzi et al., 2011; Rothäusler et al., 2012). In the SWA, *D. antarctica* has only patchy intertidal records documented in the southern tip of South America (Tierra del Fuego) and in Malvinas (Falklands) Islands (Boras de Zaixso and Zaixso, 2008), but is absent in Patagonia or anywhere else along the cold Malvinas (Falkland) Current. No records are either known for the Southeastern Atlantic (SAE) along the trajectory of the cold Benguela Current (Thiel and Gutow, 2005a; Fig. 15).

*D. antarctica* contains gas-filled tissues, enabling their persistent floating on the sea surface and their transport by currents and winds. Patellacean gastropods in New Zealand and barnacles in Chile are transported by *D. antarctica* (Thiel and Gutow, 2005b; Waters, 2008). *D. nigerrima* (a very close species or synonym of *T. atra*?) living in Japan, New Zealand, Juan Fernandez Island and Chile, suffer dispersal by rafting on *D. antarctica* from New Zealand to Chile (Donald and Kennedy, 2005) and across trans-Tasmanian routes (Waters et al., 2006). Overall, the available evidence indicates that *D. antarctica*, sharing its modern distribution with *T. atra*, was most likely the floating substrate allowing its dispersal into the SWA during the Pleistocene.

Successful rafting depends on a number of factors: rafting organism, availability and suitability of floating substrate, trajectories of currents and winds, kind of floating item of biotic origin (e.g., macroalgae) which provides resources to the rafting organism (e.g., long-lasting food source for herbivorous passengers), convenient substrates of arrival (preferably rocky bottoms), oxygenated waters, light, SST. Among all, temperature is the primary controlling factor regulating growth and persistence of floating seaweeds. Increased water temperature conditions together with highest irradiant light can determine lower persistence of macroalgae: a SST rise directly affects their range expansion through thermal stress that provokes a loss in biomass and, consequently, of floating capacity during dispersal into warmer waters. Elevated temperatures during ENSO events also can lead to local extinction of macroalgae whereas upwelling of cold waters high in nutrients is favourable for the establishment and persistence of kelp assemblages. Overall, changes in oceanographic conditions can trigger series of local trophic variations leading to changes in the structure of kelp communities (Thiel and Gutow, 2005a; Vásquez et al., 2006; Rothäusler et al., 2012).

Unfavourable substrates cannot explain the biogeographical pattern of *T. atra* after the LGM. Various hard and rocky coasts favourable to *D. antarctica* are available along the Patagonian littoral today (Parker et al., 1997; Aguirre et al., 2011, Fig. 3) and since at least ca. 11 ka B.P. (Ponce et al., 2011). By contrast, elevated SST and light-nutrient conditions could have constrained its occurrence during the Holocene. A restriction in intensity and range expansion (southwards shift) of the cold Malvinas (Falkland) current after the Pleistocene/Holocene transition, due to the amelioration trend must have prevented the survival of both *D. antarctica* and *T. atra*, which could not retreat to colder waters within the SEP as no other current flows southwards in the SWA (at least since the Oligocene/Miocene (Crame, 1998)). In Patagonia, south of 42°S, the direction of winds and of the cold current is northwards (Bogazzi et al., 2005; Lucas et al., 2005; Palma et al., 2008; Piola et al., 2010).

In summary, to judge from its fossil distribution along Patagonia, *T. atra* could be indirectly indicative of: 1) favourable environments for the occurrence of *D. antarctica* during the Pleistocene in the SWA; 2) a different (dominantly colder, enhanced winds, higher productivity) palaeoceanographical pattern in Patagonia during MIS9, 7 and 5, in agreement with the results for the Pleistocene PAE

and of the systematic review, which showed that *T. atra* characterized the Patagonian littoral settings even during interglacial episodes assigned to MIS9, 7, and 5 (south of SAO).

## 7. Conclusions

*T. atra* is a Pleistocene biostratigraphical tool for Patagonia. In addition, it is a signal for changes occurred in the SWA after the LGM in palaeoclimate (warmer SST) and palaeoceanographical conditions (current trajectories, winds, productivity). Its records suggest that during MIS9, 7, and 5 the littoral settings along Patagonia were colder than during MIS11 and 1.

*T. atra* is a typical intertidal species living in hard/rocky coasts and cold waters of high productivity where macroalgae (mainly *D. antarctica*) are most abundant in the Pacific. It first appeared in the SEP during the cooling Pliocene trend, colonized the SWA during the Late Pleistocene after MIS11 by dispersal through the cold current systems (WWD, Cabo de Hornos Current, ACC, Malvinas (Falkland) Current; and/or trans-antarctic pathways?) but became extinct from Patagonia after MIS5 due to changes in abiotic parameters which altered intrinsic factors. Its absence in the Mar Argentino can be regarded as a biotic response to climate-oceanic-atmospheric changes mainly at the Pleistocene/Holocene transition: increased SST (ca. 2 °C higher than at present; more rapid and drastic in the Atlantic than in the Pacific), less strong winds, less light and less nutrient availability (mainly phosphorous), less productivity. Lower productivity levels, less phosphorous concentrations in the shallow littoral area and unavailability of the appropriate kelp communities (*D. antarctica*) prevented feeding of the larval stages, survival of adults and dispersal by rafting along the SWA.

The implications of large-scale (spatial and temporal) consistent responses to relatively low average rates of climate change (ca. 2 °C higher SST comparing the period after the LGM vs. the Holocene Hypsithermal) can be large for nearshore intertidal benthic associations, dramatically affecting their physiology (e.g. gastropod cardiac physiology), geographical ranges, and composition, structure and dynamics within macrobenthic communities. The results show one of the possible consequences of global warming within a predicted future scenario (ca. 2 °C higher for 2042–2050; [Walthers et al., 2002](#); IPCC reports) for benthic, free-epifaunal, herbivorous taxa, especially those which easily disperse through passive rafting.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quaint.2013.02.011>.

## Abbreviations

ACC	(Antarctic Circumpolar)
ACS	(Argentine Continental Shelf)
LGM	(Last Glacial Maximum)
MC	(Malvinas (Falkland) Current)
BC	(Brazil Current)
NH	(Northern Hemisphere)
PC	(Patagonian Current)
SEP	(Southeastern Pacific)
MIS	(Marine Isotope Stage)
SH	(Southern Hemisphere)
SO	(Southern Ocean)
SST	(Sea surface temperature)
SWA	(Southwestern Atlantic)
SWAS	(Southwestern Atlantic Shelf)
WWD	(West Wind Drift).

## Synonymy list

*	original designation
V	material examined.

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