

Topics in Geobiology 48

Sergio Martínez  
Alejandra Rojas  
Fernanda Cabrera *Editors*

# Actualistic Taphonomy in South America

 Springer

## Chapter 2

# The Fossil, the Dead, the Living: Beach Death Assemblages and Molluscan Biogeography of the Uruguayan Coast



Alejandra Rojas and Sergio Martínez

**Abstract** Shelly death assemblages are major sources of information for Actualistic Taphonomy studies. They preserve a sample, often biased, of the living communities, provide biostratigraphic evidence useful for taphonomic analyses, allow one to establish shell time averaging and residence time, and are valuable resources in conservation paleobiology studies. Besides these paleontologically related approaches, death assemblages have traditionally been a source for species records in a given location or area. Although a species' geographic range should be established through the collection of living specimens, there are numerous records in the literature based on dead shells from beaches. For the Uruguayan coast, there are some examples of this situation, and they are especially important when considering distributional endpoints. One cause that accounts for dead shells on a beach is the reworking of fossiliferous deposits. Increased knowledge about Uruguayan Quaternary marine deposits can provide explanations for why some species are found in modern beach death assemblages. For example, the bivalve *Anomalocardia flexuosa* has been recorded in several Quaternary outcrops, and its shells have been found on modern beaches, but no living specimens have been recorded on the Uruguayan coast. A shell collected from the Parque del Plata beach (Canelones county) yielded an accelerator mass spectrometry (AMS) radiocarbon age of circa 6,600 years before present (BP), a finding that suggests that the dated shell came from a nearby Holocene deposit. This contribution provides an insight for future research that integrates information from Quaternary and modern marine death assemblages to discuss the molluscan biogeography of the Uruguayan coast.

**Keywords** Mollusks · Range endpoints · Quaternary · Fossil assemblage · Death assemblage

---

A. Rojas (✉) · S. Martínez  
Departamento de Paleontología, Facultad de Ciencias, Universidad de la República, Iguá 4225,  
11400 Montevideo, Uruguay  
e-mail: [alejandra@fcien.edu.uy](mailto:alejandra@fcien.edu.uy)

S. Martínez  
e-mail: [smart@fcien.edu.uy](mailto:smart@fcien.edu.uy)

© Springer Nature Switzerland AG 2020  
S. Martínez et al. (eds.), *Actualistic Taphonomy in South America*,  
Topics in Geobiology 48, [https://doi.org/10.1007/978-3-030-20625-3\\_2](https://doi.org/10.1007/978-3-030-20625-3_2)

17

## 2.1 Introduction

Shelly death assemblages constitute a valuable resource for Actualistic Taphonomy research. They provide evidence of biostratigraphic processes, have been useful in time averaging and residence time studies, allow temporal, spatial, and ecological fidelity studies between living and dead counterparts, and represent a tool for applied taphonomy approaches such as conservation paleobiology (e.g., Fürsich and Flessa 1987; Flessa et al. 1993; Kowalewski et al. 1994; Kidwell 1998; 2013; Zuschin and Oliver 2003; Kowalewski and LaBarbera 2004; Kotzian and Simões 2006; Lokwood and Work 2006; Weber and Zuschin 2013; Cristini and De Francesco 2017; Dietl and Flessa 2017). The most diverse and abundant group in modern marine and transitional setting death assemblages are mollusks, due to their high representation in invertebrate communities and their resistant hard parts. Although the biogeographic range of a species should be established from living specimen records, molluscan remains found on beaches and emerged settings have been used for the detection of species in a particular region or area, because they are an accessible place for sampling. On the Uruguayan coast, empty shells (with a variable grade of preservation) had been considered as evidence for the presence of several molluscan species (see examples in Barattini and Ureta 1961; Figueiras and Sicardi 1968, 1971). These records are frequently cited in subsequent contributions, such as taxonomic lists, catalogs, or online databases, in which the original nature of the record may be lost. This situation is especially concerning when considering whether the Uruguayan coast is or may be the endpoint of a taxon's distribution.

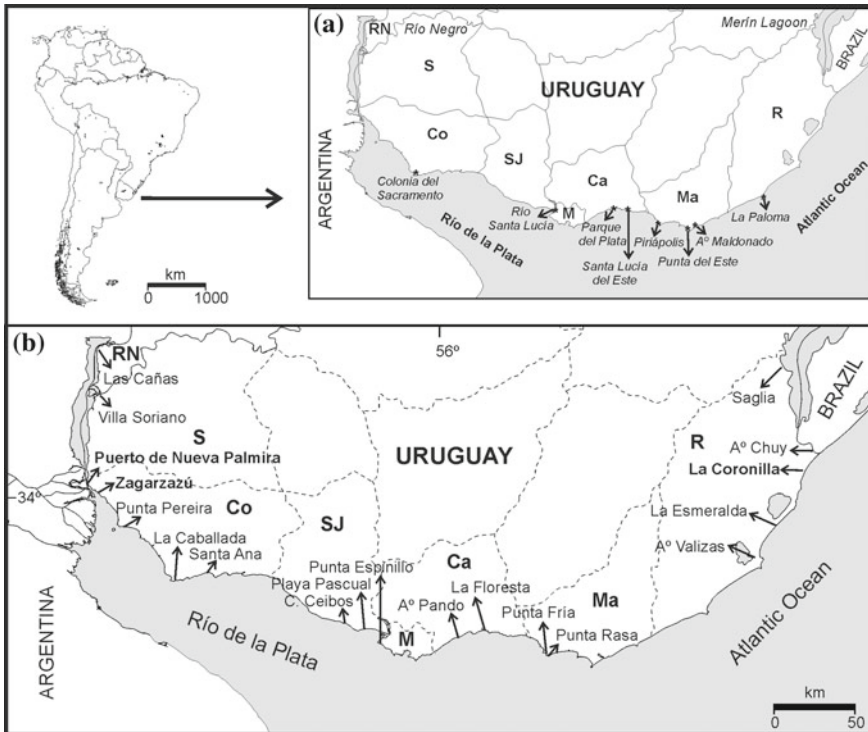
Scarabino and Zaffaroni (2004) discussed the status of 20 molluscan species cited in the literature as Uruguayan coastal residents and excluded them from the list of its living fauna. They considered several causes, such as fossil specimen inclusion, misidentified material, ballast specimens, incorrect locality labeling, and species recorded during anomalous oceanographic conditions. Of these possible explanations, our present contribution focuses on those records that may be based on fossil shells found in death assemblages. Paleontological knowledge of Quaternary littoral deposits is essential for this evaluation. Thus, our aim is to discuss how fossil shells can be recognized in Uruguayan coastal shelly death assemblages and how this information may be used to avoid misleading biogeographic assumptions in modern death assemblage studies.

## 2.2 The Uruguayan Coastal Quaternary Marine Molluscan Assemblages

The Uruguayan Quaternary marine deposits crop out patchily along a thin strip parallel to the present coastline, approximately from the mouth of the Río Negro River to the margin of the Merín Lagoon (Fig. 2.1). They are a consequence of global climatic oscillations and sea level changes that occurred during this period

(e.g., Lisiecki and Raymo 2005; Jouzel et al. 2007). The formal lithostratigraphic units used to recognize these deposits are the Chuy and Villa Soriano formations (see Ubilla and Martínez 2016). Molluscan shells are the most diverse and abundant fossils, although there are occasional remains of other taxa such as crustaceans, bryozoans, corals, echinoderms, annelids, and fish (e.g., de Mata 1947; Figueiras 1961, 1962; Sprechmann 1978; Rojas 2007; Ubilla and Martínez 2016).

Quaternary marine mollusks were mentioned for Uruguay since the works of Larrañaga (1819, but published in 1894), d’Orbigny (1842), and Darwin (1846). In the twentieth century, research centered on the taxonomic composition of the deposits mostly located on the coasts of Montevideo, Colonia, and Soriano (e.g., von Ihering 1907, 1923; Teisseire 1928; Frenguelli 1930; Roselli 1939, 1976; de Mata 1947; Calcaterra 1971; Figueiras 1961, 1962, 1967). Some authors took into account the molluscan ecological preferences and made interesting paleoenvironmental inferences (von Ihering 1907; Teisseire 1928; Parodiz 1962), and new information was obtained from deposits located on the eastern coast (Figueiras 1975; Sprechmann



**Fig. 2.1** Coastal area of Uruguay. **a** Geographic features mentioned in the text, **b** location of Quaternary fossiliferous marine deposits (bold letters correspond to Pleistocene assemblages and regular letters to Holocene assemblages). Counties are: RN Río Negro, S Soriano, Co Colonia, SJ San José, M Montevideo, Ca Canelones, Ma Maldonado, R Rocha

1978; Martínez 1988, 1990; Piñeiro et al. 1992). More recent approaches include radiocarbon dating of shells to provide a precise chronology of shell concentrations (Martínez et al. 2001, 2006; Rojas 2002, 2007; Rojas and Urteaga 2011; Martínez and Rojas 2013), an effort that led to the recognition of three Late Pleistocene assemblages and numerous Holocene shell beds (see Martínez et al. 2001; Martínez and Rojas 2013; Rojas and Martínez 2016; Ubilla and Martínez 2016). The malacological content and paleoecology of the Pleistocene assemblages were studied by Martínez et al. (2001), Rojas (2007, 2016), Demicheli (2015), Rojas and Martínez (2016), and Rojas et al. (2018a, b). In turn, paleontological knowledge of Holocene marine localities has increased from the report of specific deposits (e.g., Teisseire 1928; Calcaterra 1971; Alonso 1978; Martínez 1983, 1988, 1990; Piñeiro et al. 1992) to a more geographically comprehensive and integrative approach of the malacofauna and paleoecology of precise temporal frameworks (Martínez et al. 2006; Martínez and Rojas 2013; Ubilla and Martínez 2016). Taxonomic lists of Quaternary mollusks were compiled by Figueiras (1961, 1962, 1967) and Clavijo et al. (2005).

The Quaternary beds are characterized by a lithological composition that includes clay, silt, fine to coarse sands, and even conglomerates (Preciozzi et al. 1988). Most deposits are unconsolidated and exposed to the coastal dynamics, since they usually occur on the abrasion platform of sandy beaches, low cliffs, or in river margins and mouths. Due to this fact, fossil shells can potentially reenter the taphonomic active zone and mix into modern littoral death assemblages.

The Zagarzazú and La Coronilla marine assemblages in Colonia and Rocha counties are among the Late Pleistocene deposits that could be a potential source of fossil shells. These fossil beds have been found covered by sand or occasionally underwater during storms (Fig. 2.2).

Holocene molluscan-rich deposits that could provide shells to modern death assemblages are known for all littoral areas from the Río de la Plata to the Atlantic coast. Fossiliferous localities occur in Colonia county (Arroyo La Caballada and Santa Ana-Artilleros), San José county (Playa Pascual), Montevideo (Punta Espinillo), Canelones county (Arroyo Pando, La Floresta, Arroyo Sarandí, Punta Fría, and Punta Rasa), Rocha county (La Esmeralda, Arroyo Valizas, and Arroyo Chuy), and in the margin of the Merín Lagoon (Saglia) (Fig. 2.3).

### **2.3 Detection of Fossil Shells in Modern Uruguayan Coastal Death Assemblages**

Researchers use several approaches to detect fossil valves in modern death assemblages, such as numerical dating, comparison between the taxonomic composition of fossil and modern assemblages in a given area, or by the taphonomic grade exhibited by the collected shells. All approaches have advantages and disadvantages, and the suitability of each for the detection of old shells in modern death assemblages depends on the similarity or dissimilarity in their taxonomic composition, the depositional

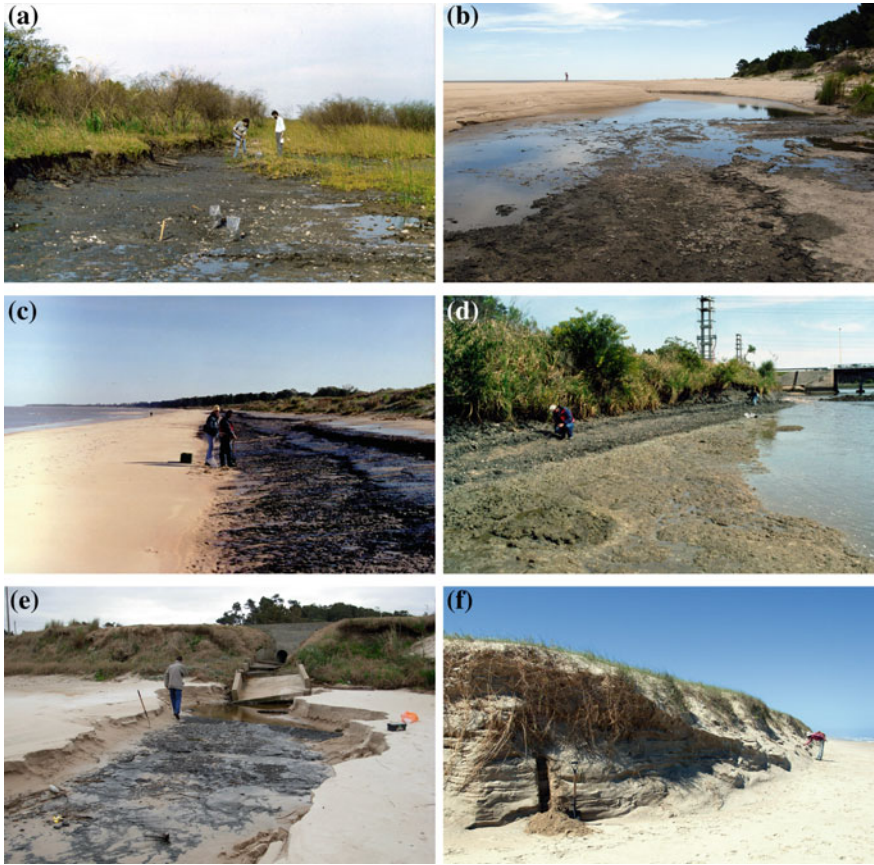


**Fig. 2.2** Late Pleistocene fossiliferous deposits located at the abrasion platform of the beach. **a** La Coronilla exposed, **b** La Coronilla covered by sand, **c** Zagarzazú exposed, **d** Zagarzazú predominantly covered

and environmental settings involved, the taphonomic history of fossil assemblages, among others.

### 2.3.1 *Taphonomic Grade*

The taphonomic signatures of fossil shells in modern death assemblages will depend on their original taphonomic conditions before their reworking into modern death assemblages (e.g., from autochthonous versus parautochthonous to allochthonous deposits), the redeposition environment (e.g., high versus low energy conditions, high or low encrustation and bioturbation incidence, and high versus low sedimentation rate), the rate of freshly dead shell incorporation, and the shell time residence in different environmental settings. For example, in a study based on *Chione* spp. from modern death assemblages of the tidal flats of Bahía la Choya, Mexico, Flessa et al. (1993) concluded that the taphonomic condition did not reliably indicate the time since death. On the other hand, De Francesco and Hassan (2008) found that in an Argentine estuary modern death assemblages were mostly composed of fossil shells



**Fig. 2.3** Holocene fossiliferous deposits exposed to erosive processes. **a** Santa Ana-Artilleros, **b** Cañada de los Ceibos, Kiyú, **c** Playa Pascual, **d** Arroyo Pando, **e** La Floresta, **f** La Esmeralda

and were worse preserved than fossil assemblages, due to reworking and exposition of these shells by modern biostratinomic processes.

### 2.3.2 Numerical Dating

Fossil shells may be detected in modern death assemblages if old ages are obtained by direct dating techniques, such as accelerator mass spectrometry (AMS) radiocarbon dating or radiocarbon calibrated amino acid racemization. One limitation for this approach is that not every collected shell will be dated. Among the dated shells, those derived from Pleistocene terraces may be successfully recognized due to the expected age differences (e.g., Wehmiller et al. 1995). However, the ages of shells that come

from young (Holocene) fossil deposits may overlap with the residence time of modern time-averaged shelly assemblages. Several studies have dealt with shell survival and estimates of time-averaging in different marine subenvironments. Kidwell and Bosence (1991) estimated that maximum scales of time-averaging in coastal environments would be on the order of a few thousand years, while in open shelf habitats it would tens-of-thousands of years. Flessa et al. (1993) found that surficial shells may be 3,500 years old in Bahia La Choya accumulations, and their long survival is explained by frequent shallow burial. Flessa and Kowalewski (1994) compiled data on radiocarbon ages from the literature and found that the median age of 128 nearshore shells was 2,465 years, and that of 158 shells from the shelf was 8,870 years. The authors interpreted that the lower shell survival in nearshore deposits (<10 m) is linked to a more active sedimentary environment where shells may be rapidly destroyed or buried, in contrast to deeper environments with a lower sedimentation rate and lower taphonomic destruction rate. Recently, Kidwell (2013) summarized the literature on shell dating from death assemblages. Dating from modern-day outer shelves yielded maximum ages of 10,000–20,000 years, whereas shells from inner shelves and beaches are typically younger, with ages of a few thousand years.

### ***2.3.3 Comparison Between the Taxonomic Composition of Fossil Assemblages and Modern Communities***

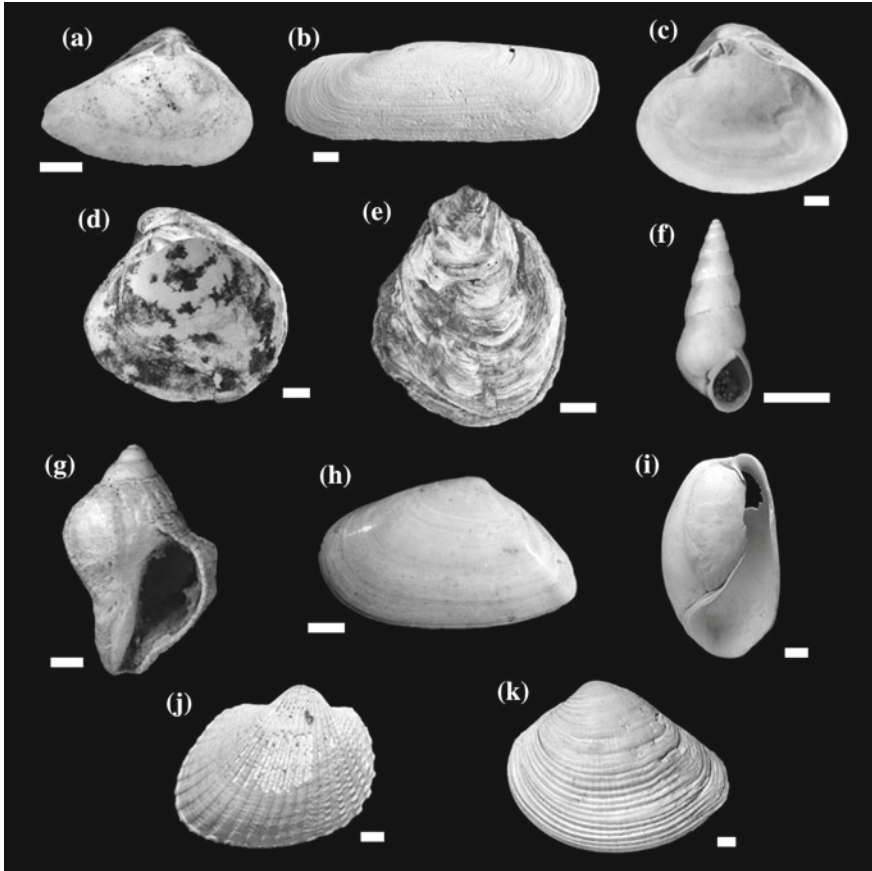
This approach may be useful if the taxonomic composition between the fossil assemblages and the adjacent living fauna from a given area differ. For example, de Francesco and Hassan (2008) found that death assemblages in the Mar Chiquita coastal lagoon were dominated by reworked fossil shells derived from Holocene beds at the lagoon margins, a finding that consequently demonstrates low ecological fidelity to the living fauna.

On the Uruguayan coast, several species are shared between the malacological fossil assemblages and the living communities. However, environmental parameters of some coastal areas have changed in the last thousand years, as well as the taxonomic composition and geographic distribution of mollusks.

#### **2.3.3.1 Small-Scale Shifts in Geographical Distribution Due to Salinity Changes**

The most noticeable difference between past and present environmental conditions is salinity. While there is currently an increasing salinity gradient from west to east (e.g., Urien 1972; Nagy et al. 1998), fossil assemblages indicate the prevalence of marine conditions into what is now the Rio de la Plata estuary (Martínez et al. 2001, 2006; Rojas 2007). In the present Atlantic region, Quaternary assemblages indicate,





**Fig. 2.4** Mollusks from Late Pleistocene and Holocene assemblages from Uruguay. **a** *Erodona mactroides*, **b** *Tagelus plebeius*, **c** *Macra isabelleana*, **d** *Pitar rostratus*, **e** *Ostrea stentina*, **f** *Heleobia australis*, **g** *Stramonita haemastoma*, **h** *Tellina gibber*, **i** *Bulla occidentalis*, **j** *Anadara brasiliana*, **k** *Anomalocardia flexuosa*. Scale bars equal 2 mm except in b that equal 5 mm

as expected, that marine littoral environments developed (Martínez et al. 2001, 2006; Rojas and Urteaga, 2011; Rojas et al. 2018b).

If past and present species geographical distributions with specific salinity preferences do not overlap, this criterion may allow for the detection of fossil specimens in modern death assemblages. For example, *Erodona mactroides* and *Tagelus plebeius* are estuarine bivalves which currently reside in the Río de la Plata, coastal lagoons, and river mouths of the Canelones, Maldonado, and Rocha counties (Scarabino et al. 2006b, 2015). Both species are commonly found in Holocene deposits (Fig. 2.4a, b), in which, for example, *E. mactroides* is sometimes dominant (Martínez et al. 2006). Contrarily, both species are rare in Pleistocene assemblages (Rojas et al. 2018a).

Marine euryhaline species such as *Macra isabelleana* and *Pitar rostratus* are also found in Río de La Plata estuarine environments and in unconsolidated coastal and shelf area substrates. Fossil specimens for these species are present in both Pleistocene and Holocene coastal deposits, where *M. isabelleana* is more abundant than *P. rostratus* (Fig. 2.4c, d). While *Ostrea stentina* is another abundant species in the Pleistocene assemblages, and frequently found in Holocene deposits (Martínez et al. 2006; Rojas et al. 2018a), it is currently recorded in consolidated Atlantic coast substrates (Scarabino et al. 2006b) (Fig. 2.4e). A common microgastropod of the Río de La Plata and other estuarine environments is *Heleobia*. Specimens are often referred to the species *Heleobia australis*, as found in the Quaternary records. This gastropod is common and usually abundant in Holocene assemblages from different coastal sectors (Martínez et al. 2006) (Fig. 2.4f). For Pleistocene deposits, it is abundant in the Zagarzazú assemblage but rarely occurs in Puerto de Nueva Palmira and La Coronilla (Rojas et al. 2018a). All of these frequently or abundantly represented species in Quaternary assemblages demonstrate partially overlapping ranges with their current distribution in the Uruguayan coastal zone. Thus, in the latest areas, it is difficult to know whether the shells correspond to fossil specimens or members of modern death assemblages. However, where the current and fossil geographic distribution does not overlap, it is probable to identify shells reworked from Quaternary deposits. The reason is that mollusks responded to environmental changes during the last thousand years by modifying their biogeographic distribution on the Uruguayan coast.

The salinity inferences along the coast during the Quaternary, and especially in the Late Pleistocene, show a high marine influence in the western sector, where marine species are recorded (Martínez et al. 2001, 2006; Rojas and Martínez 2016). For instance, species found in the Pleistocene deposits of Puerto de Nueva Palmira, such as *Diodora patagonica*, *Lottia subrugosa*, *Lunarca ovalis*, and *Plicatula gibbosa*, are currently restricted to the Atlantic coast, about 400 km to the southeast of these deposits. *Stramonita haemastoma*, currently found to the east of Punta del Este, was recorded both in Puerto de Nueva Palmira and Zagarzazú (Fig. 2.4g); a similar situation occurs with *Tellina gibber* (Rojas and Martínez 2016) (Fig. 2.4h). Regarding marine species found in western Holocene deposits, *Buccinanops globulosus*, *Olivella tehuelcha*, and *T. gibber* were reported in La Caballada (Colonia del Sacramento). Even westwards, *L. ovalis* was recorded from the Villa Soriano locality, close to the Río Negro (Martínez et al. 2006).

Similar range displacements occur for estuarine species, such as *E. mactroides* and *T. plebeius*, since they were found westward of their current distribution boundary in the Río de La Plata. Colonia del Sacramento is nowadays the western endpoint for *E. mactroides* (Olazarri 1966), and Montevideo for *T. plebeius* (Scarabino et al. 1975). Both species are rare in the Puerto de Nueva Palmira and Zagarzazú Pleistocene deposits. However, *E. mactroides* is very abundant in most Holocene assemblages (Martínez et al. 2006). In deposits to the west of Colonia del Sacramento, *E. mactroides* is a dominant species. For instance, in Las Cañas (Río Negro county) the assemblage is monospecific. In Punta Pereira, this species represents more than 80% of the recorded specimens, and in Villa Soriano it comprises about the 60% of the

recorded mollusks (see Martínez et al. 2006). The presence of *E. mactroides* shells in modern death assemblages to the west of Colonia del Sacramento is probably due to the erosion of fossil deposits, as commented by Olazarri (1966), based on the finding of highly abraded shells.

For other species, such as euryhaline taxa, a similar pattern was verified since they are recorded as displaced from their present distribution. Meanwhile, *M. isabelleana* decreases its abundance to the west of the mouth of the Río Santa Lucía (Scarabino et al. 2006b), but it is recorded in several fossil assemblages towards the northwest, reaching Villa Soriano (Martínez et al. 2006). Similarly, *P. rostratus* is found in the eastern coast up to Montevideo, while in the Holocene assemblages it is also recorded in Villa Soriano (Martínez et al. 2006).

### 2.3.3.2 Out-of-Range Warm Water Taxa Currently Displaced Northwards from the Uruguayan Coast

Besides the small-scale biogeographic modifications within the Uruguayan coast due to salinity changes, Quaternary molluscan assemblages record species not currently living at this latitude. These warm-water taxa are extralimitals (see Roy et al. 1995), since their southern biogeographic boundary is located at the Brazilian coast. Extralimitals were reported in both Pleistocene and Holocene assemblages (Martínez et al. 2001, 2006; Rojas and Martínez 2016; Rojas et al. 2018b) and corresponded to micro- and macromollusks. Several of these extralimitals were traditionally included among the living Uruguayan molluscan fauna and their status has been a matter of uncertainty since the records come from dead shells collected on beaches. Scarabino and Zaffaroni (2004) clarified the status of *Bulla occidentalis* (as *Bulla striata*), *Anadara chemnitzii* (as *Scapharca chemnitzii*), *Anadara brasiliana* (as *Scapharca brasiliana*), *Anomalocardia flexuosa* (as *Anomalocardia brasiliana*), *Littoraria flava*, and *Melampus coffeus*. The last species was not reported from fossil assemblages, unlike the others.

The *B. occidentalis* record in Rocha county by Barattini and Ureta (1961) and Figueiras and Sicardi (1974) was considered to be due to their presence in Holocene assemblages from the same region, as reported by Figueiras (1967) and later by Martínez et al. (2006) from Saglia (Fig. 2.4i). Further, this species was recently found in the La Coronilla Pleistocene assemblage (Rojas et al. 2018b).

Incomplete *A. brasiliana* specimens were reported by Barattini and Ureta (1961) on the La Coronilla beach, while *A. chemnitzii* loose valves were found by Figueiras and Sicardi (1968) between La Coronilla and Chuy. Despite these findings, and the fact that the latter authors mention the presence of these two arcids in Holocene deposits (see Figueiras 1961), they cited the eastern Uruguayan coast as the geographic boundary for these species. Later, Scarabino and Zaffaroni (2004) excluded both records from the living Uruguayan malacofauna and indeed further commented that the living distribution of *Anadara* (as *Scapharca*) in southern Brazil was not yet been established by the record of living specimens. The shells from *A. brasiliana* and *A. chemnitzii* found in death assemblages of La Coronilla and eastward locali-

ties can be more confidently regarded as fossils due to the record of both species in the La Coronilla Pleistocene deposit (Rojas and Martínez 2016; Rojas et al. 2018b) (Fig. 2.4j).

*L. flava* was included among the Uruguayan coast living mollusks by Parodiz (1962) without providing any distribution detail. Later, Figueiras and Sicardi (1971) mentioned this species (as *Littorina nebulosa flava*) on the basis of a deteriorated specimen found by the authors in the Puerto de La Paloma in Rocha and by records in private collections. These authors attributed the occasional presence of this species in the Uruguayan coast to special oceanographic conditions. Based on a preliminary communication by Rojas (2003) on the presence of *L. flava* in the Zagarzazú Pleistocene deposit, Scarabino and Zaffaroni (2004) considered that the record of empty shells could be fossil specimens since it was never found alive on the Uruguayan coast.

Another example is *Finella dubia*, a microgastropod reported by Figueiras and Sicardi (1980) and Layerle and Scarabino (1984) in Rocha and Maldonado counties, and therefore considered among the living Uruguayan coast malacofauna (e.g., Scarabino 2003). Only empty and abraded shells from this species were found by Scarabino et al. (2006a), and for this reason the authors cast doubt on the living status of *F. dubia*. Moreover, Forcelli and Narosky (2015) excluded the Uruguayan coast from the southern boundary of this species' distribution. Similar to the examples cited above, *F. dubia* was found in all Pleistocene assemblages (Martínez et al. 2001; Rojas and Martínez 2016) and in the Arroyo Chuy Holocene deposit (Martínez et al. 2006). Therefore, these records can explain the presence of its shells on the coast.

*Eurytellina angulosa* was regarded as a living Uruguayan species by Boss (1968) on the basis of material from the Arroyo Pando in Canelones. Scarabino and Zaffaroni (2004) considered the record as erroneous because no specimens were reported from the Uruguayan Atlantic area. Moreover, the Arroyo Pando Holocene deposit, mentioned by Broggi (1967) and more recently studied by Rojas (2007), does not contain any similar species. However, *E. angulosa* was recently found in the La Coronilla Pleistocene assemblage (Rojas et al. 2018b), and consequently it cannot be completely ruled out that the record reported by Boss (1968) corresponds to a fossil specimen.

Barattini and Ureta (1961) regarded the Uruguayan coast as the southern boundary of the *A. flexuosa* distribution, because complete specimens were found at La Coronilla beach and Arroyo Maldonado. Figueiras and Sicardi (1969) referenced the previous work and mentioned that *A. flexuosa* is very common in Holocene assemblages, and thus the reported shells could come from nearby fossil deposits. Despite this assertion, the authors still considered that the mouth of the Río de la Plata was the boundary of this species' distribution. *A. flexuosa* is indeed a common species in Quaternary assemblages along the Uruguayan coast (Fig. 2.4k). It was found in the Pleistocene marine assemblages (Martínez et al. 2001; Rojas and Martínez 2016) and Holocene beds from Soriano, Colonia, San José, Montevideo, Canelones, and Rocha counties (Figueiras 1961; Martínez et al. 2006). Besides considering that *A. flexuosa* shells could come from fossil assemblages, Scarabino and Zaffaroni (2004) also allowed for the possibility that the record by Barattini and Ureta (1961) could

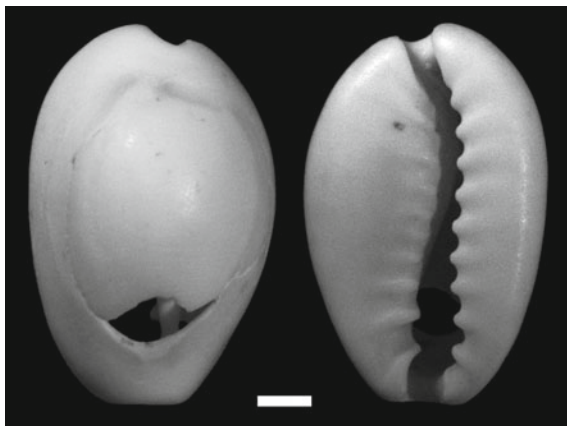
**Table 2.1** Radiocarbon ages obtained for *A. flexuosa* from a modern death assemblage and ages from nearby Holocene deposits. Calib 7.10 was used for calibration (Stuiver et al. 2018)

Species dated	Locality	$^{14}\text{C}$ age	95.4% (2 $\delta$ ) cal. age BP	Lab. Nr.	Age source
<i>Anomalocardia flexuosa</i>	Modern death assemblage on Parque del Plata beach	6,650 $\pm$ 50	7,418–7,618	AA93851	This work
<i>Maetra isabelleana</i>	La Floresta (Holocene deposit)	4,790 $\pm$ 80	5,316–5,700	LP-904	Martínez et al. (2006)
<i>Anomalocardia flexuosa</i> (in life position)	Arroyo Pando (Holocene deposit)	6,630 $\pm$ 60	7,398–7,625	LP-1464	Rojas (2007)

be due to incorrect labeling or the existence of anomalous oceanographic conditions that favored the transport of *A. flexuosa* to the Uruguayan coast. Recently, Rojas et al. (2018a, b) reported articulated *A. flexuosa* specimens from the La Coronilla fossil assemblage, a finding which may explain the shell record of Barattini and Ureta (1961) at the same beach. The absence of living *A. flexuosa* records at the Uruguayan coast, and even from the adjacent Rio Grande do Sul State in Brazil, has been well established (see Scarabino et al. 2015). Despite this fact, recent research based on modern death assemblages still included *A. flexuosa* in analyses regarding molluscan composition and diversity of Maldonado beaches (as *A. brasiliiana*; Boretto et al. 2018).

We found *A. flexuosa* shells on the Parque del Plata and Santa Lucía del Este beaches, and in Piriápolis in Maldonado. One valve of this species from Parque del Plata was AMS dated 6,650  $\pm$  50 radiocarbon years before present (BP) (Table 2.1). Considering the calibrated age interval (median probability of 7,520 years BP), and taking into account that the range of ages represented by shells in recent beach death assemblages is a few thousand years (e.g., Kidwell 2013), it is probable that the dated *A. flexuosa* shell was eroded from a nearby Holocene deposit. This hypothesis is plausible since Holocene assemblages are known to occur at a short distance from Parque del Plata. Approximately 5 km to the east, the La Floresta assemblage was studied by Martínez et al. (2006) in which a radiocarbon age of 4,790  $\pm$  80 years BP (cal. age of 5,316–5,700 years BP) was obtained. Although the mollusks originally reported from La Floresta deposit were *H. australis* and *M. isabelleana*, we recently recorded the presence of *A. flexuosa* (unpublished). Additionally, about 14 km to the west of Parque del Plata, the beds exposed at the margin of the Arroyo Pando were studied by Rojas (2007). Among the molluscan species recorded, life position specimens of *A. flexuosa* were used for standard  $^{14}\text{C}$  dating. The obtained radiocarbon age, 6,630  $\pm$  60 years BP (calibrated age range between 7,398–7,625 years BP), is almost identical to *A. flexuosa* shell age collected from the death assemblage of Parque del Plata.

**Fig. 2.5** Specimen of the alien species *Monetaria annulus* found in the modern death assemblage of Piriápolis beach, Maldonado county



## 2.4 Alien Molluscan Shells in Beach Death Assemblages

In January 2018, during an inspection of the death assemblage from the Piriápolis beach (Maldonado county), a shell from the Cypraeidae family was found. Despite its small size and abraded condition, it was identified as *Monetaria annulus*, a species from the central and western Pacific and Indian Oceans (Simone 2004) (Fig. 2.5). This taxon, and other alien cypreids such as *Monetaria moneta*, and western Atlantic representatives such as *Erosaria acicularis* and *Luria cinerea*, were found on several Uruguayan beaches (Juan Carlos Zaffaroni pers. comm. 2018). According to compilations by Ríos (2009) and Rosenberg (2009), the southernmost reaching species of this family in the southwestern Atlantic is *Macrocypraea zebra*, which occurs off the Santa Catarina coast in Brazil. Considering the living specimen records, *E. acicularis* was reported at the northern Saõ Paulo coast (Simone and Gonçalves 2006). Among the Uruguayan Quaternary assemblages, no Cypraeidae family members have been reported. However, as mentioned above, extralimital warm water species are common in fossil deposits. The presence of the alien *M. annulus* in Uruguayan coastal death assemblages may be explained by diverse anthropic activities, such as religious rituals that take place on beaches, as a part of pieces of craftsmanship or ballast remains. Beyond the finding of alien species shells, the extralimital shell record of western Atlantic taxa must then be carefully evaluated to avoid misleading biogeographic interpretations when studying death assemblages.

## 2.5 Final Remarks

The geographic distribution of the Uruguayan Quaternary marine assemblages allow for the possibility that fossil mollusk shells may be reworked into modern beach death assemblages. This has complicated the literature concerning the living Uruguayan

molluscan fauna, since species recorded by empty shells were assumed to be part of living communities. Inaccurate information was afterwards amplified in subsequent publications, taxonomic lists, inventories, and webpages. The status of several species was clarified and referred to the possibility that living records may be based on fossil shells (Scarabino and Zaffaroni 2004). The current increased and improved knowledge on the taxonomic composition, location, and age of littoral Uruguayan Quaternary molluscan assemblages becomes a relevant source of information when studying death assemblages. Detection of fossil shells as part of modern death assemblages by means of numerical dating or their geographical displacement may help recognize them and assess the importance of fossil deposit erosion. Being aware of this phenomenon will contribute to the correct interpretation of the taxonomic composition of modern beach death assemblages, and their use in different actualistic approaches.

**Acknowledgements** We deeply thank Juan Carlos Zaffaroni for his comments on alien molluscan species found on Uruguayan beaches, and for his help in the identification of the *M. annulus* specimen.

## References

- Alonso C (1978) La fauna de moluscos del yacimiento de Playa Pascual con referencia a otros yacimientos estuáricos y marinos del Cuaternario de Uruguay. *Com Soc Malac Uruguay* 4(34):365–380
- Barattini LP, Ureta EH (1961) La fauna de las costas uruguayas del este (invertebrados). Publicaciones del Museo Dámaso Antonio Larrañaga, Montevideo
- Boretto GM, Rouzaut S, Cioccale M, Gordillo S, Benitez Y (2018) Dinámica costera y antropización en playas uruguayas. Un análisis integrado para su conservación. *Rev Mex Ciencias Geol* 35(3):291–306
- Boss KJ (1968) The subfamily Tellininae in the Western Atlantic. The Genera *Tellina* (Part II) and *Tellidora*. *Johnsonia* 4(46):273–344
- Broggi J (1967) Primera cita de *Pholas (Thovana) campechiensis* Gmelin para el Querandino uruguayo. *Com Soc Malac Uruguay* 2(12):47–48
- Calcaterra A (1971) Algunas observaciones sobre la fauna de moluscos de la Formación Querandina (Deptos de Colonia y Soriano, Uruguay). *Com Soc Malac Uruguay* 3(20):79–82
- Clavijo C, Scarabino F, Rojas A, Martínez S (2005) Lista sistemática de los moluscos marinos y estuarinos del Cuaternario del Uruguay. *Com Soc Malac Uruguay* 9(88):381–411
- Cristini PA, de Francesco CG (2017) Molluscan taphonomic patterns below the sediment-water interface in freshwater shallow lakes from the southeastern Pampa plain, Argentina. *Palaios* 32(8):528–542
- Darwin C (1846) Geological observations on South America, being the third part of the geology of the voyage of the Beagle, under the command of capt. Fitzroy RN during the years 1832–1836. Smith, Elder & Co., London
- de Francesco CG, Hassan GS (2008) Dominance of reworked fossil shells in modern estuarine environments: implications for paleoenvironmental reconstructions based on biological remains. *Palaios* 23(1):14–23
- de Mata O (1947) La formación holocena en el Departamento de Montevideo (República Oriental del Uruguay). Imprenta Nacional, Montevideo

- Demicheli M (2015) Moluscos fósiles del Puerto de Nueva Palmira, Pleistoceno Tardío de Uruguay. Bachelor dissertation, Facultad de Ciencias, Universidad de la República
- Dietl GP, Flessa KW (2017) Conservation paleobiology. Science and practice. The University of Chicago Press, Chicago
- d'Orbigny A (1836–1843) Paléontologie. In: Voyage dans l'Amérique méridionale (le Brésil, la République orientale de l'Uruguay, la République Argentine, la Patagonie, la République du Chili, la République de Bolivie, la République du Pérou), exécuté pendant les années 1826–1833, t.3(4). Paris/Estrasburgo
- Figueiras A (1961) Contribución al conocimiento de la malacofauna holocena del Uruguay. Com Soc Malac Uruguay 1(1):15–21
- Figueiras A (1962) Sobre nuevos hallazgos de moluscos subfósiles de la Transgresión Querandina. Com Soc Malac Uruguay 1(3):53–68
- Figueiras A (1967) Contribución al conocimiento de los moluscos marinos del Holoceno uruguayo. Com Soc Malac Uruguay 2(12):61–76
- Figueiras A (1975) Sobre la existencia de un banco de ostréidos de probable edad pleistocénica media en el departamento de Rocha, Uruguay. Com Soc Malac Uruguay 4(28):59–92
- Figueiras A, Sicardi OE (1968) Catálogo de los moluscos marinos del Uruguay. Parte II. Com Soc Malac Uruguay 2(15):255–275
- Figueiras A, Sicardi OE (1969) Catálogo de los moluscos marinos del Uruguay. Parte III. Com Soc Malac Uruguay 2(16):355–378
- Figueiras A, Sicardi OE (1971) Catálogo de los moluscos marinos del Uruguay. Parte VI. Com Soc Malac Uruguay 3(21):101–130
- Figueiras A, Sicardi OE (1974) Catálogo de los moluscos marinos del Uruguay. Parte IX. Com Soc Malac Uruguay 3(26):323–360
- Figueiras A, Sicardi OE (1980) Catálogo de los moluscos marinos del Uruguay. Parte X. Revisión actualizada de los moluscos marinos del Uruguay con descripción de las especies agregadas. Sección II—Gastropoda y Cephalopoda. Com Soc Malac Uruguay 5(38):179–272
- Flessa KW, Kowalewski M (1994) Shell survival and time-averaging in nearshore and shelf environments: estimates from the radiocarbon literature. *Lethaia* 27:153–165
- Flessa KW, Cutler AH, Meldahl KH (1993) Time and taphonomy: quantitative estimates of time-averaging and stratigraphic disorder in a shallow marine habitat. *Paleobiology* 19(2):266–286
- Forcelli D, Narosky T (2015) Uruguayan seashells. Moluscos marinos Argentina, Uruguay, Brasil. Vázquez Manzini Editores, Buenos Aires
- Frenguelli J (1930) Apuntes de Geología Uruguaya. *Bol Inst Geol Perf* 11:1–47
- Fürsich FT, Flessa KW (1987) Taphonomy of tidal flat molluscs in the Northern Gulf of California: paleoenvironmental analysis despite the perils of preservation. *Palaaios* 2(6):543–559
- Jouzel J, Masson-Delmotte V, Cattani O, Dreyfus G, Falourd S, Hoffmann G, Minster B, Nouet J, Barnola JM, Chappellaz J, Fischer H, Gallet JC, Johnsen S, Leuenberger M, Loulergue L, Luethi D, Oerter H, Parrenin F, Raisbeck G, Raynaud D, Schilt A, Schwander J, Selmo E, Souchez R, Spahni R, Stauffer B, Steffensen JP, Stenni B, Stocker TF, Tison JL, Werner M, Wolff EW (2007) Orbital and millennial Antarctic climate variability over the past 800,000 years. *Science* 317:793–796
- Kidwell SM (1998) Time-averaging in the marine fossil record: overview of strategies and uncertainties. *Geobios* 30(7):977–995
- Kidwell SM (2002) Time-averaged molluscan death assemblages: palimpsests of richness, snapshots of abundance. *Geol Soc Am* 30(9):803–806
- Kidwell SM (2013) Time-averaging and fidelity of modern death assemblages: building a taphonomic foundation for conservation palaeobiology. *Palaeontology* 56(3):487–522
- Kidwell SM, Bosence DW (1991) Taphonomy and time averaging of marine shelly faunas. In: Allison PA, Briggs DEG (eds) *Taphonomy: releasing the data locked in the fossil record*. Plenum Press, New York
- Kotzian CB, Simões MG (2006) Taphonomy of recent freshwater molluscan death assemblages, Touro Passo stream, southern Brazil. *Rev Bras Paleontol* 9(2):243–260



- Kowalewski M, Labarbera M (2004) Actualistic taphonomy: death, decay, and disintegration in contemporary settings. *Palaios* 19(5):423–427
- Kowalewski M, Flessa KW, Aggen JA (1994) Taphofacies analysis of recent shelly cheniers (beach ridges), Northeastern Baja California, Mexico. *Facies* 31:209–242
- Larrañaga DA (1894) Memoria geológica sobre la formación del Río de la Plata, deducida de sus conchas fósiles, escrita por los años 1819. *Anales del Museo Nacional de Montevideo* 1(2):3–12
- Layerle C, Scarabino V (1984) Moluscos del frente marítimo uruguayo entre 9 y 78 m de profundidad: análisis biocenológico. *Contribuciones (Departamento de Oceanografía, Facultad de Humanidades y Ciencias)* 1(9):1–17
- Lisiecki LE, Raymo ME (2005) A Pliocene-Pleistocene stack of 57 globally distributed benthic  $\delta^{18}\text{O}$  records. *Paleoceanography* 20:PA1003
- Lockwood R, Work LA (2006) Quantifying taphonomic bias in molluscan death assemblages from the Upper Chesapeake Bay: patterns of shell damage. *Palaios* 21:442–450
- Martínez S (1983) Invertebrados fósiles holocenos del Departamento de Rocha, Uruguay (Mollusca y Crustacea). *Resúmenes y Comunicaciones de las Jornadas de Ciencias Naturales* 3:46–47
- Martínez S (1988) Moluscos fósiles holocenos de la margen occidental de la Laguna Merín (Formación Villa Soriano, Uruguay). *Com Soc Malacol Uruguay* 6:409–418
- Martínez S (1990) Taphonomy and Palaeoecology of Holocene mollusks from the western margin of the Merin Lagoon (Villa Soriano Fm., Uruguay). *Quat South Am Ant Pen* 7:121–135
- Martínez S, Rojas A (2013) Relative sea level during the Holocene in Uruguay. *Palaeogeogr Palaeoclimatol Palaeoecol* 374:123–131
- Martínez S, Ubilla M, Verde M, Perea D, Rojas A, Guèrèquiz R, Piñeiro G (2001) Paleoeecology and geochronology of Uruguayan coastal marine Pleistocene deposits. *Quat Res* 55:246–254
- Martínez S, Rojas A, Ubilla M, Verde M, Perea D, Piñeiro G (2006) Molluscan assemblages from the marine Holocene of Uruguay: composition, geochronology, and paleoenvironmental signals. *Amegh* 43(2):385–397
- Nagy GJ, Martínez CM, Caffera RM, Pedrosa G, Forbes EA, Perdomo AC, López Laborde J (1998) Capítulo 2. Marco hidrológico y climático del Río de la Plata. In: Wells PG, Daborn GR (eds) *El Río de la Plata –Una revisión ambiental. Un informe del Proyecto ECOPLATA*. Dalhousie University, Halifax, Nova Scotia
- Olazarri J (1966) Los moluscos de agua dulce del Depto. de Colonia, Uruguay. Parte I: Pelecypoda. *Com Soc Malac Uruguay* 2(11):15–37
- Parodiz JJ (1962) Los moluscos marinos del pleistoceno rioplatense. *Com Soc Malac Uruguay* 1(2):29–46
- Piñeiro G, Scarabino F, Verde M (1992) Una nueva localidad fosilífera del Holoceno marino de Uruguay (Punta Rasa, Departamento de Maldonado). *Bol Soc Zool Uruguay* 7:61–62
- Preciozzi F, Spoturno J, Heinzen W, Rossi P (1988) Memoria explicativa de la Carta Geológica del Uruguay a la escala 1: 500.000. DINAMIGE, Montevideo
- Ríos E (2009) Compendium of Brazilian sea shells. *Evangraf*, Rio Grande
- Rojas A (2002) Tafonomía y cronología de nuevos depósitos fosilíferos del Holoceno marino de Uruguay. *Actas de las II Jornadas Uruguayas del Cenozoico* 2:80–82
- Rojas A (2003) Moluscos marinos cuaternarios del Balneario Zagarzazú, Departamento de Colonia, Uruguay. *Pub Esp Soc Zool Urug* 1:83
- Rojas A (2007) Moluscos de aguas cálidas del Cuaternario Marino del Uruguay. Master thesis dissertation, Universidad de la República
- Rojas A (2016) Asociaciones fósiles del Pleistoceno marino de Uruguay. PhD thesis dissertation, Universidad de la República
- Rojas A, Urteaga D (2011) Late Pleistocene and Holocene chitons (Mollusca, Polyplacophora) from Uruguay: palaeobiogeography and palaeoenvironmental reconstruction in mid latitudes of the Southwestern Atlantic. *Geobios* 44:377–386
- Rojas A, Martínez S (2016) Marine Isotope Stage 3 (MIS 3) versus Marine Isotope Stage 5 (MIS 5) fossiliferous marine deposits from Uruguay. In: Gasparini GM, Rabassa J, Deschamps MC, Tonni

- EP (eds) Marine Isotope Stage 3 in Southern South America 60 KA B.P.-30 KA B.P. Springer Earth System Sciences, Cham
- Rojas A, Demicheli M, Martínez S (2018a) Taphonomy of the Late Pleistocene marine molluscan assemblages from Uruguay. *N Jahrb Geol Paläontol - Abhandlungen* 289(2):217–235
- Rojas A, Zaffaroni JC, Martínez S (2018b) New molluscan records and palaeoecology of the Late Pleistocene marine assemblage from La Coronilla (Rocha, Uruguay). *J Sediment Environ* 3(4):220–233
- Roselli FL (1939) Apuntes de Geología y Paleontología uruguayas. *Bol Soc Am Cs Nat "Kraglievich-Fontana"* 1(2):29–102
- Roselli FL (1976) Contribución al estudio de la Geo Paleontología Departamentos de Colonia y Soriano (República Oriental del Uruguay). Imprenta Cooperativa, Montevideo
- Rosenberg G (2009) Malacolog 4.1.1: A Database of Western Atlantic Marine Mollusca. [WWW database (version 4.1.1)]. <http://www.malacolog.org/>. Accessed 26 Nov 2018
- Roy K, Jablonski D, Valentine JW (1995) Thermally anomalous assemblages revisited: patterns in the extraprovincial latitudinal range shifts of Pleistocene marine mollusks. *Geology* 23(12):1071–1074
- Scarabino F (2003) Lista sistemática de los Bivalvia marinos y estuarinos vivientes de Uruguay. *Com Soc Malacol Uruguay* 8(80–81):229–259
- Scarabino F, Zaffaroni JC (2004) Estatus faunístico de veinte especies de moluscos citadas para aguas uruguayas. *Com Zool Mus Nac Hist Nat Antr* 13(202):1–15
- Scarabino V, Maytía S, Cachés M (1975) Carta bionómica litoral del Departamento de Montevideo. I Niveles superiores del Sistema Litoral. *Com Soc Malac Uruguay* 4(29):117–129
- Scarabino F, Zaffaroni JC, Carranza A, Clavijo C, Nin M (2006a) Gasterópodos marinos y estuarinos de la costa uruguaya: faunística, distribución, taxonomía y conservación. In: Menafrá R, Rodríguez L, Scarabino F, Conde D (eds) Bases para la conservación y el manejo de la costa uruguaya. Vida Silvestre, Montevideo
- Scarabino F, Zaffaroni JC, Clavijo C, Carranza A, Nin M (2006b) Bivalvos marinos y estuarinos de la costa uruguaya: faunística, distribución, taxonomía y conservación. In: Menafrá R, Rodríguez L, Scarabino F, Conde D (eds) Bases para la conservación y el manejo de la costa uruguaya. Vida Silvestre, Montevideo
- Scarabino F, Zelaya DG, Orensanz JM, Ortega L, Defeo O, Schwindt E, Carranza A, Zaffaroni JC, Martínez G, Scarabino V, García-Rodríguez F (2015) Cold, warm, temperate and brackish: Bivalve biodiversity in a complex oceanographic scenario (Uruguay, southwestern Atlantic). *Am Malacol Bull* 33(2):1–18
- Simone LRL (2004) Morphology and phylogeny of the Cypraeoidea (Mollusca, Caenogastropoda). *Papel Virtual, Fapesp, São Paulo*
- Simone LRL, Gonçalves EP (2006) Reanalysis of the southernmost distribution of *Erosaria acicularis* (Caenogastropoda, Cypraeidae) in Brazil. *Strombus* 13(2):13–14
- Sprechmann P (1978) The paleoecology and paleogeography of the Uruguayan coastal area during the Neogene and Quaternary. *Zitt* 4:3–72
- Stuiver M, Reimer PJ, Reimer RW (2018) CALIB 7.1 [WWW program] at <http://calib.org>. Accessed 18 Oct 2018
- Teisseire A (1928) Contribución al estudio de la geología y la paleontología de la República Oriental del Uruguay. Región de Colonia. *Anales Univ* 122(series 37):319–469
- Ubilla M, Martínez S (2016) Geology and paleontology of the quaternary of Uruguay. Springer Brief in Earth Sciences, South America and the Southern Hemisphere, Springer, Basel
- Urien CM (1972) Río de la Plate estuary environments. In: Nelson BW (ed) Environmental framework of Coastal Plain Estuaries. Boulder; Geol Soc Am Mem 133, pp 213–234
- von Ihering H (1907) Les mollusques fossiles du Tertiaire et du Crétacé Supérieur de l'Argentine. *An Mus Nac Buenos Aires* 7(3 Série):1–611
- von Ihering H (1923) Transgression des Meeres während der Ablagerung der Pampas. *Archiv für Molluskenkunde* 55(5):183–193

- Weber K, Zuschin M (2013) Delta-associated molluscan life and death assemblages in the northern Adriatic Sea: implications for paleoecology, regional diversity and conservation. *Palaeogeogr Palaeoclimatol Palaeoecol* 370:77–91
- Wehmiller JF, York LL, Bart ML (1995) Amino acid racemization geochronology of reworked quaternary mollusks on U.S. Atlantic coast beaches: implications for chronostratigraphy, taphonomy, and coastal sediment transport. *Mar Geol* 124:303–337
- Zuschin M, Oliver PG (2003) Fidelity of molluscan life and death assemblages on sublittoral hard substrata around granitic islands of the Seychelles. *Lethaia* 36:133–150