

UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL  
INSTITUTO DE GEOCIÊNCIAS  
PROGRAMA DE PÓS-GRADUAÇÃO EM GEOCIÊNCIAS

**TAFONOMIA DE MOLUSCOS COM ÊNFASE EM SISTEMAS  
ESTUARINO-LAGUNARES DA PLANÍCIE COSTEIRA DO  
RIO GRANDE DO SUL, BRASIL**

MATIAS DO NASCIMENTO RITTER

Dissertação de Mestrado

ORIENTADOR: Dr. João Carlos Coimbra

Porto Alegre, Dezembro de 2013

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## RESUMO

Acumulações de restos de moluscos são muito comuns tanto em ambientes marinhos plataformais quanto em depósitos lagunares e estuarinos da América do Sul, principalmente entre o Brasil e a Argentina. A formação destas concentrações conchíferas pode prover grande oportunidade para estudos tafonômicos, os quais ainda são raros nesta região. Existem ainda questões a serem respondidas, por exemplo, quanta informação biológica está preservada nestas concentrações? Ou, qual é a probabilidade de uma associação viva deixar um registro fóssil análogo? Os principais objetivos deste estudo foram: (i) investigar a influência dos processos ambientais na destruição de remanescentes biológicos, através da descrição das assinaturas tafonômicas presentes em conchas de moluscos de dois afloramentos da Laguna Tramandaí, nordeste do Rio Grande do Sul; e (ii) testar o potencial de preservação de associações de moluscos vivos, mortos e fósseis de lagunas e estuários da Planície Costeira do Rio Grande do Sul, com o intuito de compreender a qualidade da informação biológica preservada nestas associações fósseis de fácies lagunares holocênicas. O principal processo tafonômico é a dissolução. As conchas estão inseridas na zona tafonomicamente ativa e experimentam intensa dissolução, o que reduz a probabilidade de deixarem um registro fóssil. Todavia, a preservação de espécies da associação viva nos depósitos fósseis foi de 100% em nível regional, e as espécies presentes na associação morta não apresentaram boa preservação no registro fóssil recente (Holoceno), ao contrário do que é usualmente predito na bibliografia. Isso indica que a associação morta é enriquecida por espécies não indígenas, e parte deste aumento relativo da riqueza é transferida para a associação fóssil. O padrão observado na fidelidade de moluscos estuarinos é ocasionado pela (i) alta variabilidade temporal e espacial nas associações vivas, (ii) mistura espacial nas associações mortas e (iii) preservação diferencial, devido à destruição durante uma longa permanência na zona tafonomicamente ativa. Portanto, a dissolução é o principal processo tafonômico que altera a informação biológica em ambientes transicionais, embora a preservação seletiva possa introduzir vieses das associações vivas às fósseis.

**Palavras-chave:** assinaturas tafonômicas, fidelidade quantitativa, zona tafonomicamente ativa, dissolução, concentrações conchíferas.

## ABSTRACT

Molluscan shell accumulations (shell beds) are very common in shallow marine and estuarine environments in South America and also on the continental shelf from Southern Brazil through Argentina. The development of these shell beds can provide a great opportunity to taphonomic studies, which are uncommon in this geographic location. For example, how much biological information is preserved within these shell beds? Or, what is the actual probability a local living community has to leave a fossil record corresponding to these shell deposits? The aims of this study are (i) to investigate the influence of environmental processes on the destruction of biological remains in a subtropical lagoonal setting by describing the taphonomic signatures occurring in the mollusk shells from the Tramandaí Lagoon, northeastern Rio Grande do Sul State; and (ii) to compare living assemblages (LAs), death assemblages (DAs) and fossil assemblages (FAs) from estuaries and lagoons in the Rio Grande do Sul Coastal Plain to understand the nature and quality of biological information preserved in fossil associations in Holocene lagoon facies. Dissolution appears to be a leading taphonomic agent in lagoonal environments according to the study. The shells are within the taphonomically active zone and, due to intense dissolution, they will most likely leave no geological record. Nonetheless, the preservation of living species in FA was 100% and species present in DA are not as good preserved in recent (Holocene) fossil record as originally thought from the literature. The present results indicate that both DAs and FAs from estuarine-lagoons environments are composed basically by nonindigenous species, with live-dead mismatch than for continental shelves. The fidelity pattern here observed for estuarine mollusks have been driven by (i) high temporal and spatial variability in the LAs, (ii) spatial mixing in the DAs and (iii) differential preservation of shells, due to long residence times in the taphonomically active zone. Dissolution is the main taphonomic process altering biological information in those environments, but differential preservation may be, perhaps, the responsible for introducing bias from living to fossil assemblages.

**Key-words:** taphonomic signatures, quantitative fidelity, taphonomically active zone, dissolution, shell beds.

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## ESTRUTURA E ORGANIZAÇÃO DA DISSERTAÇÃO

Esta Dissertação de Mestrado está estruturada em torno de dois artigos publicados em periódicos e sua formatação geral segue a Norma 103 do PPGGEo/UFRGS. Conseqüentemente, sua organização compreende as seguintes partes principais:

a) introdução sobre o tema e descrição do objeto da pesquisa de mestrado, onde estão sumarizados os objetivos, a filosofia da pesquisa desenvolvida e um breve estado da arte (**Capítulo 1**);

b) artigo publicado no periódico *Quaternary International* (v. 305, p. 5-14), intitulado “TAPHONOMIC SIGNATURES IN MOLLUSCAN FOSSIL ASSEMBLAGES FROM THE HOLOCENE LAGOON SYSTEM IN THE NORTHERN PART OF THE COASTAL PLAIN, RIO GRANDE DO SUL STATE, BRAZIL”, em colaboração com o Dr. Fernando Erthal e o Dr. João Carlos Coimbra (**Capítulo 2**);

c) artigo publicado no periódico *Revista Brasileira de Paleontologia* (v. 16, n. 2, p. 225-236), intitulado “FIDELITY BIAS IN MOLLUSK ASSEMBLAGES FROM COASTAL LAGOONS OF SOUTHERN BRAZIL”, em colaboração com o Dr. Fernando Erthal (**Capítulo 3**);

d) considerações Finais (**Capítulo 4**).

## PRÓLOGO

A **Tafonomia** foi originalmente definida como as leis do soterramento, do grego “*taphós*”, enterramento, sepultura; e “*nómos*”, lei. Contudo, sua simplicidade nominal é contrariada pela sua complexidade prática e seu caráter interdisciplinar. Muito mais do que se preocupar com questões a respeito de como um fóssil foi parar em determinado local, ela busca responder o que este fóssil pode ilustrar sobre uma espécie, população ou comunidade pretérita (Behrensmeyer *et al.*, 2000). Portanto, seu verdadeiro objetivo é compreender as complexas modificações da informação biológica (e não apenas de um indivíduo), no percurso teórico que os organismos “percorrem” até “chegar” no registro fóssil (Kidwell & Flessa, 1995).

Nas últimas décadas a Tafonomia tem se tornado cada vez mais presente em diversos trabalhos paleontológicos. Alguns estudos taxonômicos, por exemplo, ilustraram que certas estruturas, antes identificadas como morfológicas, são vieses tafonômicos (Lucas, 2001).

Além disto, no contexto da Tafonomia, pesquisadores perceberam primordialmente que estudar o presente pode elucidar o passado, como afirmou James Hutton (1726-1797). Em ambientes atuais (e recentes, Holoceno) a quantidade de remanescentes biológicos é maior e é possível quantificar os vieses e observar padrões, aplicáveis ao registro fóssil (Kowalewski & Labarbera, 2004). Os moluscos, principalmente os bivalves, foram (e ainda são) o principal alvo destes estudos, por apresentarem um expressivo registro fóssil.

Desde então, uma série de trabalhos explanaram o quanto uma camada sedimentar centimétrica fossilífera tem de amplitude temporal. Datações em diversas acumulações recentes permitiram a compreensão de que o registro fóssil é formado naturalmente por fósseis não contemporâneos (depósitos com mistura temporal, *time-averaged*) (Flessa & Kowalewski, 1994). Inicialmente este padrão era visto como um viés negativo, contudo seus pontos positivos imperam dependendo do objetivo do estudo. A mistura temporal capta processos mais expressivos, eliminando os ruídos das variações de pequena escala (Kowalewski, 1996).

Outro aspecto importante é que a preservação dos fósseis é influenciada por uma série de fatores, desde o hábito de vida até o ambiente deposicional. Ou seja, qualquer resto biológico (folhas, ossos, sementes, conchas) transportados de um ambiente a outro podem ser depositados num contexto geológico diferente daquele

onde viveram. Entretanto, estes ambientes deixam um registro de alteração nestes remanescentes – assinaturas tafonômicas, que analisadas de forma integrada, podem caracterizar o ambiente deposicional (Parsons-Hubbard, 2005), pelo menos o ambiente final (Davies *et al.*, 1989). Naturalmente, as características intrínsecas também influenciam: folhas têm menor probabilidade de deixar registro fóssil em relação às conchas, embora quando preservadas, apresentam um registro relativamente mais fidedigno (Kowalewski, 1997).

A tafonomia aplicada a sistemas deposicionais recentes também permitiu elucidar o quanto do registro fóssil é fiel à população (comunidade, etc.) pretérita, bem como o quanto dos organismos atuais está preservado no registro fóssil local (Kidwell, 2013). Tais estudos abordaram diversos grupos, tais como diatomáceas, ostracodes, moluscos, pequenos mamíferos e cetáceos, assim como contemplaram diferentes ambientes, como por exemplo, rios, lagos e estuários. A consolidação destes estudos, não obstante, hoje deriva para outras áreas, como a paleobiologia da conservação e estudos ecológicos de ampla escala espacial e temporal, além da utilização de estatística multivariada, comprovando a dinâmica interdisciplinar da Tafonomia (Dietl & Flessa, 2011; Kidwell & Tomašových, 2013).

Há ainda uma lacuna de conhecimento a ser preenchida sobre todos estes aspectos em ambientes fluviais, estuarino-lagunares e marinhos. Portanto, existe a necessidade de se testar hipóteses teóricas e inferir padrões. Este trabalho, que contempla algumas lagunas e estuários de ambiente subtropical, é apenas um primeiro passo neste sentido.

## CAPÍTULO 1

## 1. INTRODUÇÃO

### 1.1 FILOSOFIA E OBJETIVOS DO TRABALHO

A principal finalidade dos estudos tafonômicos é determinar a qualidade do registro fóssil, *i.e.*, compreender quali- e quantitativamente as informações biológicas preservadas em associações fósseis. Neste sentido, este trabalho visa determinar quais os fatores tafonômicos que podem enviesar o registro fóssil de moluscos em ambiente estuarino-lagunar.

Os processos tafonômicos são produzidos tanto por condições sedimentares (*e.g.* tipo de sedimento, geoquímica) e ambientais (*e.g.* temperatura, profundidade) quanto por fatores biológicos intrínsecos (*e.g.* hábito de vida, composição mineralógica da concha/osso), os quais podem ser mensurados e utilizados para reconstruções paleoambientais. A maioria dos estudos com moluscos recentes e atuais (especialmente bivalves) – pós-padronização dos métodos por Kidwell *et al.* (2001) – estão concentrados em ambientes marinhos tropicais e com sedimentação majoritariamente carbonática.

Os ambientes deposicionais modernos são excelente fonte de dados tafonômicos. Nas últimas três décadas, diversas pesquisas foram conduzidas, principalmente em ambientes marinhos atuais, demonstrando correlação positiva entre a condição tafonômica de remanescentes bioclásticos e o tipo de ambiente deposicional (Fürsich & Flessa, 1987; Best & Kidwell, 2000a, b; Parsons-Hubbard, 2005; Best, 2008; Powell *et al.*, 2011a, b, c), embora ainda não exista um padrão muito claro dos principais parâmetros que afetem o dano tafonômico.

Recentemente, o número de trabalhos tafonômicos em ambientes modernos (denominada tafonomia atualística; Kowalewski & Labarbera, 2004) aumentaram consideravelmente, com iniciativas como o SSETI (*Shelf and Slope Experimental Taphonomy Initiative*; Parsons-Hubbard *et al.*, 2011 e suas referências).

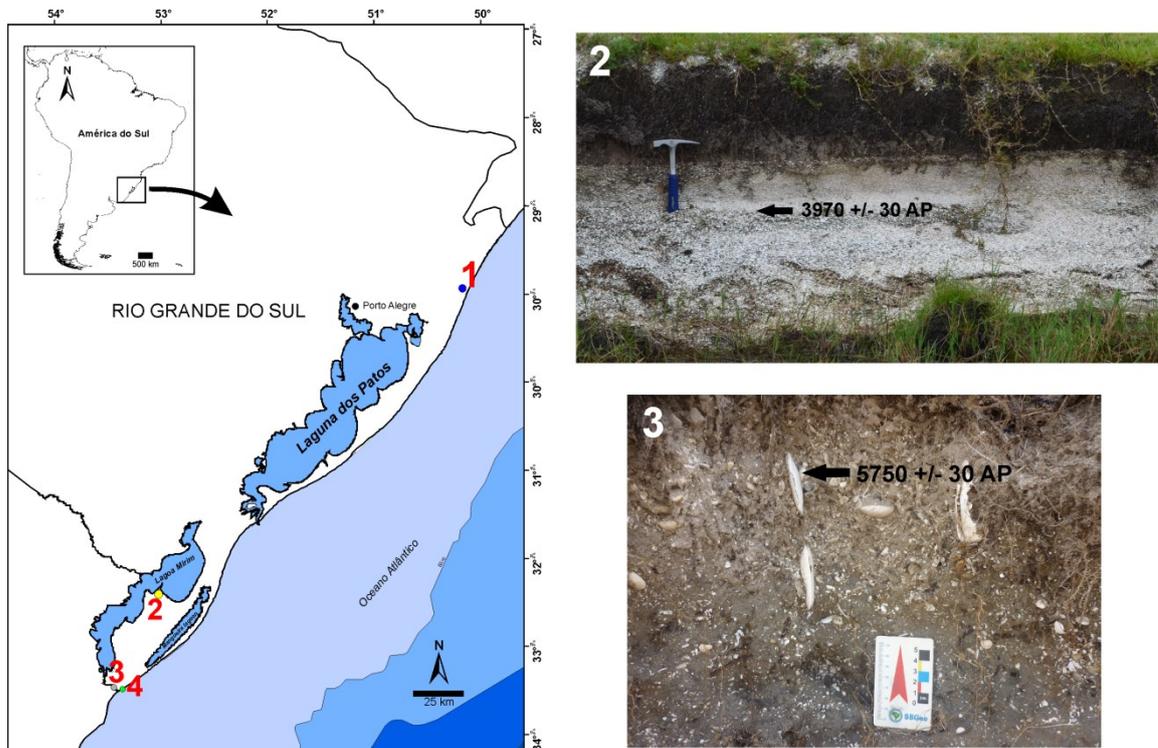
A tafonomia de moluscos para plataformas carbonáticas e siliciclásticas tropicais está relativamente bem descrita e quantificada. Por exemplo, é possível verificar que a dissolução de conchas nestes ambientes é condicionada em parte pelo ambiente deposicional, sendo maior a destruição de conchas em ambientes siliciclásticos devido a um acréscimo de íons de ferro que altera a geoquímica da

água de poro, diminuindo seu pH e, conseqüentemente, favorecendo a precipitação de carbonato (Best *et al.*, 2007). Conchas da associação morta – em ambientes tropicais – apresentam um padrão de dano tafonômico em resposta ao ambiente sedimentar (Best & Kidwell, 2000a, b; Kidwell *et al.*, 2005; Best, 2008). Em áreas carbonáticas recifais predominam incrustação e bioerosão macroscópica, enquanto que para regiões não recifais dominam processos de origem química e física (Lescinsky *et al.*, 2002; Best, 2008). Não obstante, em ambientes siliciclásticos as conchas geralmente apresentam elevada alteração na superfície, com raras incrustações (Lockwood & Work, 2006; Best, 2008). Para plataformas siliciclásticas e carbonáticas temperadas, a dissolução é o principal processo tafonômico (Alexandersson, 1979; Aller, 1982; Smith & Nelson, 2003).

Em ambientes estuarinos, conchas podem ter baixo potencial de preservação, mesmo em áreas onde existem densos depósitos de conchas (Powell *et al.*, 1992). Isso acontece por que a grande quantidade aparente de conchas não significa, necessariamente, alta probabilidade de preservação, mas sim pode indicar simplesmente uma alta entrada de conchas (Davies *et al.*, 1989). A acidez da água, por exemplo, pode ser aumentada em áreas com elevada produção de CO<sub>2</sub> por organismos heterótrofos, e isso ocorre particularmente em estuários (pelo menos tropicais), onde também há uma menor atividade fotossintética que remova esse CO<sub>2</sub> da água. Portanto, áreas marinhas adjacentes às desembocaduras de rios podem ser ambientes onde, potencialmente, haja maior dissolução (Marshall *et al.*, 2008).

Para plataformas siliciclásticas subtropicais mais estudos são necessários para se compreender quanto cada fator pode contribuir para o padrão tafonômico geral (Erthal, 2012). Não obstante, ambientes estuarino-lagunares subtropicais, como a costa sul da América do Sul, carecem de estudos tafonômicos, até o momento, com exceção de trabalhos conduzidos no Uruguai, na Argentina e no sul do Brasil (Martínez *et al.*, 2006; De Francesco & Hassan, 2008; Aguirre *et al.*, 2011, Tietze & De Francesco, 2012; Ritter *et al.*, 2013).

Especificamente, no contexto de sistemas lagunares e estuarinos, objeto desta dissertação, a costa do Rio Grande do Sul apresenta elevado potencial para estudos tafonômicos, devido à expressiva quantidade de depósitos fósseis estritamente lagunares (Figura 1).



**Figura 1** – Exemplos de diferentes concentrações conchíferas lagunares da Planície Costeira do Rio Grande do Sul. **1:** Laguna Tramandaí (*Erodona mactroides*, 1060-1490 anos AP, Capítulo 2); **2:** Mineração, Lagoa Mirim (*Erodona mactroides*, 3970 +/- 30 anos AP); **3:** Margem brasileira do Arroio Chuí (*Tagelus plebeius*). Caron (2007) encontrou idade igual ao datar oito espécimes de *Tagelus plebeius* neste depósito; **4:** Praia das Maravilhas, Hermenegildo. As datações  $^{14}\text{C}$  dos afloramentos 2, 3 e 4 são de dados inéditos do autor.

Os ambientes deposicionais transicionais apresentam importância em diversas escalas (Schröder-Adams, 2006). Atualmente, são locais com expressiva pressão antrópica, assim como desempenham papel ecologicamente chave em áreas costeiras (Lötze *et al.*, 2006). Já o registro fóssil (e sedimentar) associado a sistemas deposicionais pode se tornar ótimo reservatório para petróleo e derivados. Por exemplo, em camadas abaixo do pré-sal é encontrado petróleo confinado em *shell beds* que sofreram intensa dissolução (efeito tafonômico), aumentando sua porosidade (Formação Lagoa Feia, Cretáceo Inferior, Bacia de Campos) (Bertani & Carozzi, 1985).

O principal objetivo deste trabalho, portanto, foi determinar quais processos ambientais e biológicos que podem influenciar na destruição de restos de moluscos da Planície Costeira do Rio Grande do Sul (PCRS) ao: (i) descrever as assinaturas tafonômicas identificadas em conchas de dois afloramentos pertencentes ao complexo lagunar da Laguna Tramandaí; e (ii) determinar o viés da fidelidade quantitativa em associações de moluscos das lagunas costeiras da PCRS.

Minha hipótese é que ambientes transicionais apresentam padrão de dano tafonômico mais semelhante ao ambiente fluvial, onde a dissolução predomina (veja Kotzian & Simões, 2006); e, devido a este enviesamento, a fidelidade de espécies lagunares é obliterada no registro fóssil lagunar.

## 1.2 ESTADO DA ARTE

Esta seção está estruturada nos dois eixos centrais que contemplam a dissertação: (i) assinaturas tafonômicas em bivalves, com ênfase em sistemas lagunares ou análogos; e (ii) estudos de fidelidade quantitativa em associações de moluscos costeiros e/ou marinhos. Trata-se de breve revisão com objetivo de contextualizar os capítulos posteriores. Adicionalmente, a introdução dos capítulos subsequentes (2 e 3) contempla os dois eixos centrais de forma mais específica, bem como a área de estudo.

### 1.2.1 Assinaturas tafonômicas

De forma geral, o registro fóssil – apesar de pobremente preservado e naturalmente enviesado – pode prover informações úteis e confiáveis sobre condições pretéritas, tanto ecológicas quanto ambientais (veja Kidwell, 2013). Naturalmente, tais estudos obtêm melhores resultados quando conduzidos com organismos que deixem restos refratários, e para moluscos de modo geral, os resultados são aparentemente bons: pelo menos 76% dos gêneros de bivalves viventes estão representados no registro fóssil (Behrensmeyer *et al.*, 2000; Valentine *et al.*, 2006).

Os processos de destruição de qualquer remanescente biológico (*e.g.* concha, osso) deixam um registro e, por se tratarem de dano pós-morte, podem ser considerados tafonômicos. Estas marcas são denominadas assinaturas tafonômicas e são o registro dos processos que modificam esqueletos mortos e que indicam processos de destruição pós-morte (Tabela 1). As assinaturas são mais amplamente

mensuradas em restos de moluscos, por serem estes facilmente preserváveis e coletáveis (Kowalewski & Hoffmeister, 2003; Behrensmeyer *et al.*, 2005).

Tabela 1 - Resumo das principais assinaturas tafonômicas e suas interpretações (adaptado por Erthal, 2012 de Kidwell & Bosence 1991; Parsons-Hubbard 2005; Best 2008).

Aspecto tafonômico	Descrição/Significado
Abrasão	Indica energia ambiental, mas também pode ser resultado de processos biológicos como bioerosão. É diagnóstica em ambientes de praia.
Arredondamento de margem	Combinação de fragmentação, dissolução, bioerosão e abrasão; dá uma estimativa de tempo após a fragmentação.
Bioerosão	É o resultado de processos corrosivos de organismos epibiontes, principalmente microperfuração (algas, briozoários) e raspagem. Em conchas pode deixar traços característicos da espécie/táxon que o causou (icnofósseis). É ótimo indicativo do tipo de ambiente.
Cor	Indica estado de oxirredução do sedimento; deposição de minerais tanto alóctones quanto autigênicos.
Dissolução	Nem sempre os esqueletos estão em equilíbrio químico com a água ambiente, então a insaturação da água em CaCO <sub>3</sub> (assim como flutuações no pH, PCO <sub>2</sub> e temperatura) pode levar à dissolução de conchas carbonáticas.
Fragmentação	Produzida principalmente em ambientes de alta energia, mas também pode ser o resultado de processos biogênicos, como predação.
Incrustação	Indica exposição acima da interface sedimento-água. Também é um ótimo indicador de ambientes, pois os táxons incrustantes tendem a ser bem específicos.

Em ambientes estuarinos (e lagunares), de forma geral, são escassos os estudos que utilizaram assinaturas tafonômicas, muito embora alguns trabalhos abordem questões relacionadas à tafonomia. Wiedemann (1972), por exemplo, estudou a preservação de depósitos de conchas em sedimentos estuarinos (quaternários e paleógenos) na Geórgia, EUA. O autor afirma que conchas com calcita têm maior probabilidade de serem preservadas que as compostas por aragonita, pois encontrou extensos depósitos de ostreídeos. Em relação ao transporte, elenca que há depósitos retrabalhados e que estes geralmente estão próximos à desembocaduras, provavelmente misturando conchas de idades diferentes.

Já Trewin & Welsh (1976) relataram a adição de conchas fragmentadas pela predação de aves e bioturbação na formação de *shell beds* estuarinas, no estuário Ythan, Escócia. Eles também afirmaram que a “diagênese” dentro da camada

sedimentar varia com a espécie, ilustrando um exemplo de preservação diferencial. Além disso, identificaram a presença de *pits* (pequenos furos, 30-60 µm de diâmetro) em conchas do bivalve do gênero *Cardium* e os atribuiu à destruição da camada superficial das conchas, contudo, não apontaram sua origem. A “diagênese”, apontada pelos autores, é a alteração tafonômica de remanescentes biológicos na zona tafonomicamente ativa (ZTA) (Davies *et al.*, 1989). A ZTA é o intervalo físico abaixo, mas também incluindo a interface sedimento-água, onde os distintos processos formam as assinaturas tafonômicas. Em plataformas temperadas, a ZTA é um lugar bastante agressivo. Os primeiros poucos centímetros (às vezes dezenas de centímetros) da ZTA hospedam processos químicos, físicos e biológicos, que alteram os bioclastos carbonáticos (Smith & Nelson, 2003). Em lagoas ela pode se estender até 25 cm, sendo que a maior destruição acontece nos primeiros 10 cm, ocorrendo, então, a diminuição gradativa da alteração tafonômica (Cristini & De Francesco, 2012).

Ambientes estuarino-lagunares são contíguos a dois ambientes que apresentam distintas assinaturas tafonômicas: enquanto que em ambientes fluviais a dissolução predomina (Kotzian & Simões, 2006), no meio marinho a bioerosão e incrustação são mais expressivas (Kidwell & Bosence, 1991). Não obstante, as espécies que formam depósitos lagunares apresentam mistura espacial entre estes ambientes. Portanto, uma concha pode trazer do seu ambiente de origem uma assinatura específica (e.g. incrustação), que poderá ser obliterada ou reforçada no ambiente lagunar. Dentro desta perspectiva, o objetivo do capítulo 2 é responder: quais são as principais assinaturas tafonômicas em ambiente estuarino-lagunar e quais suas possíveis consequências para o registro fóssil?

### 1.2.2 Fidelidade quantitativa

Fidelidade quantitativa ou composicional estima o quanto o registro fóssil capta da informação biológica original (em termos ecológicos *lato sensu*) da associação viva correspondente (Behrensmeyer *et al.*, 2000). Contudo, a comparação direta entre associação viva e associação fóssil nem sempre é possível. Por isto, estudos que comparam a associação viva com a morta (estudos vivo-morto) são predominantes e têm se tornado o método mais comum para quantificar o

potencial de preservação de informações ecológicas, porém de forma análoga (Kidwell & Flessa, 1995; Kidwell, 2013 e suas referências).

Os estudos que comparam vivo e morto quantificam o número de espécies encontradas vivas (presença/ausência de espécies, grupos funcionais, classes de idade) que também ocorrem em acumulações de restos mortos. Esta comparação pode ser realizada em um dado local de um hábitat, num hábitat inteiro, ao longo de um gradiente, bem como para um grupo específico ou genérico de organismos (moluscos, bivalves, macrozoobentos, folhas, sementes; Kidwell, 2013).

Os primeiros trabalhos em ambientes estuarino-lagunares e baías que realizaram esta abordagem tinham como objetivo principal responder se os fósseis são comumente soterrados onde vivem, ou se foram transportados a curtas ou longas distâncias. Um dos primeiros trabalhos a comparar (e separar) a associação viva com a morta foi o de Johnson (1965). Neste trabalho, a partir de 260 amostras da Baía Tomales, Califórnia, ele concluiu que “todas ou próximo de todas as conchas mortas são encontradas na associação viva” (Johnson, 1965, p. 121). Também percebeu que a relação entre o número de indivíduos vivos e mortos (abundância) é mais complexa de se comparar, ilustrando a dificuldade de interpretações biológicas de espécies fósseis de localidades diferentes.

Warne (1969) comparou “conchas vazias” com moluscos vivos a partir de 55 amostras coletadas na Laguna Magu, costa meridional da Califórnia. O autor identificou que o transporte a curtas distâncias é comum na laguna e que, de forma geral, muitas das conchas vazias foram soterradas no ambiente onde viviam. Assim como Johnson (1965), Warne (1969) concluiu que os táxons coletados vivos são adequadamente refletidos por conchas vazias acumuladas na laguna. Além disto, o autor afirma que “o transporte pós-morte, dentro do ambiente, é insignificante para muitas resoluções paleoecológicas” (p. 148-149).

Já Peterson (1976) analisou amostras coletadas em dez momentos ao longo de um período de 37 meses. De acordo com o autor, são três os fatores que podem causar diferenças entre a associação viva e a morta: (i) transporte pós-morte e mistura espacial de diferentes comunidades; (ii) diferentes taxas de dissolução e fragmentação de remanescentes biológicos; e (iii) *time-averaging*. Suas conclusões sobre a importância do transporte, entretanto, são consoantes com as de Johnson (1965) e Warne (1969): “(...) o transporte pós-morte é insignificante dentro do hábitat [e.g. laguna, estuário] (...)” (p. 146). Contudo, o trabalho de Peterson (1976)

confirmou que a dissolução seletiva e o *time-averaging* alteram negativamente a fidelidade.

Zenetos (1990), a partir de comparações vivo-morto, visou identificar associações de espécies estritamente lagunares com elementos alóctones no estuário Eden (Escócia). Seus resultados corroboram a alta correlação entre a associação morta com a fauna viva do estuário, inclusive ao longo do gradiente de salinidade. Embora conchas alóctones sejam onipresentes, segundo o autor, não obliteraram a correspondência entre a associação viva e a morta. Em outras palavras, Zenetos quis afirmar que embora a associação morta contenha expressivo número de conchas de outros habitats, isto não altera a correlação positiva entre a associação viva e a morta.

Os trabalhos acima citados ilustram que o transporte não altera de forma significativa a correspondência entre associação viva e associação morta. Assim, o *time-averaging* e a dissolução são os principais agentes que enviesam a informação biológica na rota vivo-morto. Contudo, tais análises importaram-se somente com a relação direta entre as espécies lagunares, minimizando o efeito da adição de conchas de outros habitats (e.g. Warne, 1969). Ou seja, a adição de conchas “inter-habitats” não oblitera o sinal biológico do registro das espécies lagunares. Porém, quanto da associação viva (número de espécies, abundância, classes de idade) é preservado no registro fóssil? Os trabalhos citados compararam apenas vivo-morto. De forma geral, a motivação do Capítulo 3 é a inclusão da associação fóssil nestas análises.

Todos os trabalhos citados não apresentam padrão comparativo. Mas, Kidwell & Bosence (1991) descreveram um método lógico e empírico de se comparar quantitativamente associações vivas com mortas (e fósseis também, veja adaptação no Capítulo 3), utilizando tanto dados de presença e ausência quanto abundância relativa de espécies. Este método permitiu comparações entre ambientes e escalas temporais diferentes. Assim, as comparações passaram a ser quantitativas e não apenas qualitativas. Estes autores, por exemplo, a partir do trabalho de Warne (1969), estimaram que 51% das espécies encontradas na associação morta também são parte da viva, mostrando que aproximadamente metade das espécies da associação morta são alóctones. Ou seja, há um acréscimo de riqueza na passagem vivo-morto. Mas, pode ser questionado se esta tendência está ou não presente no registro fóssil local.

Além dos questionamentos, a base empírica foi sustentada pelo crescente número de trabalhos para ambientes marinhos (áreas marinhas plataformais, <200 m de profundidade) após esta padronização metodológica. A partir disto, também, alguns padrões foram verificados. Por exemplo, Kidwell (2002) afirmou que a associação morta apresenta, aproximadamente, 25% mais espécies do que qualquer censo único da comunidade, devido principalmente ao *time-averaging* (para áreas não impactadas; veja Kidwell 2007 para resultados de fidelidade em áreas com alteração antrópica). Ainda, recente compilação pode ser encontrada em Kidwell & Tomašových (2013).

Outra aplicação dos estudos de fidelidade é estimar o quanto dos organismos atuais de determinado grupo também são encontrados no registro fóssil, em nível de espécie, gênero, família ou qualquer outra categoria taxonômica ou ecológica. Valentine *et al.* (2006), por exemplo, relataram que 76% dos 1292 gêneros atuais de moluscos marinhos são também encontrados no registro fóssil. Entre os 24% não presentes há similaridades: tamanho pequeno (< 1 cm), estruturas das conchas mais reativas (aragoníticos, alto conteúdo orgânico e alta relação superfície-área), hábito parasítico e/ou comensal, gêneros que habitam regiões profundas (> 200m, protobrânquios e carnívoros septibrânquios) e gêneros com distribuição geográfica restrita.

De forma geral, nos últimos anos o número de trabalhos que abordam fidelidade é crescente, e com os mais variados grupos taxonômicos, como por exemplo, pequenos mamíferos (Terry, 2010a, b) e cetáceos (Pyenson, 2010, 2011). Não obstante, o número de trabalhos também é crescente em ambientes fluviais (Cummins, 1994; Martello *et al.*, 2006; Erthal *et al.*, 2011; Tietze & De Francesco, 2012). Os diversos refinamentos estatísticos e a utilização de conceitos de metapopulações, metacomunidades e partição da diversidade (Leibold *et al.*, 2004; Holland, 2010; Tomašových & Kidwell, 2010) também foram incorporados, visto que a fidelidade e suas aplicações não são restritas à paleontologia. Duas recentes revisões sobre o assunto podem ser encontradas em Kidwell (2013) e Kidwell & Tomašových (2013).

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## CAPÍTULO 2

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# Taphonomic signatures in molluscan fossil assemblages from the Holocene lagoon system in the northern part of the coastal plain, Rio Grande do Sul State, Brazil



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## ABSTRACT

Molluscan shell accumulations (shell beds) are very common in shallow marine and estuarine environments in South America and also on the continental shelf between Argentina and southern Brazil. The development of these shell beds is restricted to the Quaternary, and can provide a great opportunity for taphonomic studies, which are rare in this geographic location. This study investigates the influence of environmental processes on the destruction of biological remains in a subtropical lagoonal setting by describing the taphonomic signatures occurring in the mollusk shells from the Tramandaí Lagoon, northeastern Rio Grande do Sul State, Brazil. This lagoon system originated during the regressive phase that followed a transgressive maximum at 6.0–6.5 ka BP. The taphonomic variables (fragmentation, margin modification, surface alteration, hinge fine scale alteration and corrosion degree) and their damage states were recorded for 1000 shells of *Erodona mactroides*. The shells were recovered from two outcrops 8 km apart. <sup>14</sup>C-AMS dating were performed on the shells of *E. mactroides* from those outcrops, which yielded similar ages (from 1060 to 1490 cal yrs BP). The ages would indicate that the Tramandaí Lagoon occupied a larger area and must have been subjected to very rapid progradation towards its present position. Several taphonomic variables, such as fragmentation, surface alteration, and corrosion extent and oxidation, presented significant differences ( $p < 0.01$ ) between the two outcrops. This may be due to some natural variation of the estuarine and lagoonal environments or differences within the taphonomically active zone (TAZ). Dissolution seems to be a leading taphonomic agent in lagoonal environments. The shells from the two outcrops are within the TAZ and, due to intense dissolution, they will most likely leave no geological record.

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## 1. Introduction

The main destructive processes that modify the biological remains in marine sediments are rather well understood (Best and Kidwell, 2000a; Smith and Nelson, 2003; Best, 2008; Hauser et al., 2008; Powell et al., 2011a), but the biases introduced in the molluscan fossil assemblages from fluvial and estuarine settings require further study (Kidwell and Flessa, 1996; De Francesco and Hassan, 2008; Erthal et al., 2011; Tietze and De Francesco, 2012). The taphonomic destruction due to differential preservation of mollusk shells in contemporary and Quaternary fluvial environments seems to be

mostly promoted by dissolution, which occurs at or very close to the sediment–water interface (Kotzian and Simões, 2006).

Information on taphonomic processes that act on estuarine mollusk assemblages in South America is rare. Two papers by De Francesco and Hassan (2008) and Farinati et al. (2008) are important studies on this subject and are therefore discussed briefly. The first study indicates that the fossil assemblages from Mar Chiquita lagoon are mainly composed of reworked shells that were carried through tidal currents and mixed with modern shells. Any ecological or environmental parameter inferred from these reworked assemblages would therefore reflect Late Holocene rather than Modern indices (De Francesco and Hassan, 2008). Furthermore, the study by Farinati et al. (2008) discriminates estuarine shell deposits based on taphonomic signatures related to high-energy and storm events.

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The quality of preservation in transitional bay settings seems to depend on intrinsic shell factors such as organic content and shell mineralogy. For example, Lockwood and Work (2006) described some taphonomic signatures of bivalves from Chesapeake Bay (North America): disarticulation, fragmentation, edge alteration, periostracum loss and fine scale surface alteration were found to be most pervasive, while encrustation and bioerosion were rare. Lockwood and Chastant (2006) showed that 70%–100% of the living molluscan species were also found dead in Chesapeake Bay.

In marine molluscan shells, taphonomic processes have demonstrated to be a good indicator of the depositional environment (Fürsich and Flessa, 1987; Meldahl and Flessa, 1990; Best and Kidwell, 2000a; Kidwell et al., 2005; Powell et al., 2011b), although there seems to be more preservation of sample-level characteristics, as opposed to facies-level (Lescinsky et al., 2002; Cai et al., 2006; Powell et al., 2011a). This finding implies that local geochemical and biological conditions, as opposed to the general depositional setting, play a major role in influencing the preservation of biological remains. The major directionality of shell preservation and time averaging appear to be strongly linked to the sediment type (carbonate vs. siliciclastics) (e.g., Kidwell et al., 2005) but also depend on geochemical features, such as sedimentary iron content (Canfield and Raiswell, 1991; Best and Kidwell, 2000a; Parsons-Hubbard, 2005; Best et al., 2007; Cherns et al., 2008, 2011) and time of exposure along the Taphonomically Active Zone (TAZ). In this respect, there is little information on particular environmental conditions that could lead to differential preservation of biological remains in different environments and the preservation potential in moderate to high latitudes, as most taphonomic

evaluations involving mollusk remains are from tropical latitudes (e.g., Best and Kidwell, 2000a,b; Kidwell et al., 2001, 2005; Parsons-Hubbard, 2005; Best et al., 2007; Olszewski and Kidwell, 2007; Best, 2008; Powell et al., 2011a,b).

Molluscan shell accumulations (shell beds; Kidwell, 1986) are very common in marine (mainly) and estuarine sediments along the coastal region of South America and also on the continental shelf between Argentina and southern Brazil (Aguirre, 1993; Aguirre and Whatley, 1995; Corrêa et al., 1996; Aguirre and Farinati, 1999, 2000; Calliari et al., 1999; Caruso, 1999; Aguirre et al., 2005, 2008, 2009, 2011; Fucks et al., 2005; Martínez et al., 2006; Dillenburg et al., 2009). However, most studies in the Holocene lagoon system from the northern coastal plain of Rio Grande do Sul State only list the mollusk species that were recovered from the drill holes (e.g., Closs and Forti, 1971; Forti-Esteves, 1974), or the studies were targeted to constraining the age of the mollusks obtained from the outcrops or in the drill holes (radiocarbon dating; see Dillenburg et al., 2009). These assemblages dominated by the shallow marine species near the surface, are found within elongated banks aligned approximately parallel to the present coastline, which are interpreted as submerged ancient coastal lines (Forti-Esteves, 1984; Corrêa et al., 2007).

This paper determines how past environmental processes may have influenced the destruction of carbonate biological remains in the Southern Brazilian coastal plain by describing the taphonomic signatures occurring in shells from the Tramandaí Lagoon, northeastern part of Rio Grande do Sul State. This lagoon system originated during the regressive phase that followed a transgressive maximum at 6.0–6.5 ka BP, which marked a sea level 2.5 m above

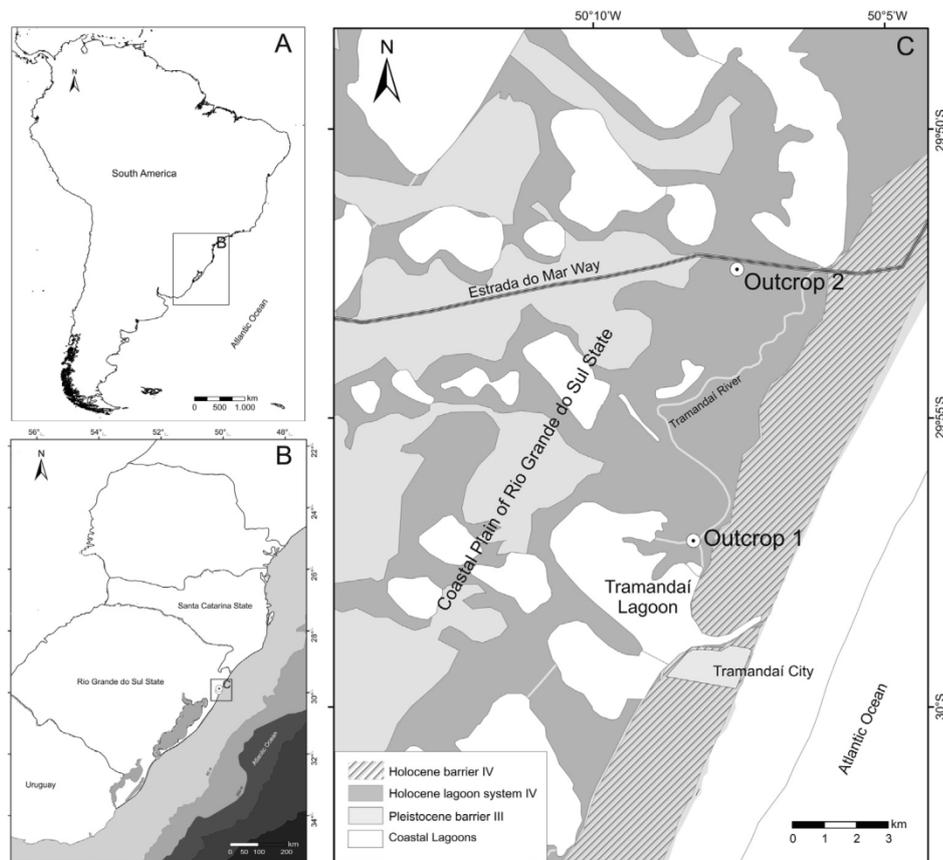


Fig. 1. Overview of the study area (A and B). Geology of the study area (C), modified from Villwock et al. (1984).

the present level (Dillenburger, 1996; Dillenburger et al., 2009). The fossil mollusks deposited in the lagoon system may record meaningful taphonomic alterations that can be correlated with processes typical of transitional environments.

## 2. Regional setting: study area

The study area lies in the northern part of the coastal plain of Rio Grande do Sul (CPRS) (Fig. 1). The CPRS was formed during the Quaternary by the juxtaposition of sedimentary deposits from four barrier-lagoon systems designated as I (oldest) to IV (youngest) by Villwock et al. (1986). The first three are Pleistocene (Villwock et al., 1986) while the younger barrier-lagoon system (Barrier-Lagoon IV) formed during the Holocene (Villwock et al., 1986; Tomazelli and Villwock, 2000). At the final stages of the Post-Glacial Marine Transgression (PMT), when the sea level was rising at low rates, coastal evolution was strongly influenced by the antecedent topography (Dillenburger et al., 2000).

The northern part of the CPRS lacks precise paleoenvironmental information because data on the sea level oscillation after the PMT are scarce (Angulo et al., 2006; Martinho et al., 2008; Dillenburger et al., 2009). Nevertheless, there is consensus that the sea began

rising by the early Holocene, reaching 1–3 m above the present level during the PMT (6–5 ka BP) and then receding to the present-day level (Angulo et al., 1999; Martins et al., 2003; Angulo et al., 2006; Dillenburger et al., 2009).

The most recent lagoon-barrier depositional system of CPRS is represented by a suite of coastal lakes and lagoons, which were fully developed by the maximum Holocene transgression (Tomazelli and Villwock, 2000; Dillenburger et al., 2009). After the PMT, most of the lowlands, presently constituting the Holocene lagoon plain, were flooded and formed large lagoon bodies that were connected to the ocean (Tomazelli and Villwock, 1991).

Three evolutionary stages can be identified in the Tramandaí lagoon system, with respect to the geomorphology: (i) stage I, from 10895 to 7355 yrs BP; (ii) stage II, from 7355 to 5430 yrs BP; and (iii) stage III, from 5430 yrs BP to present-day (Travessas et al., 2005; Dillenburger et al., 2009). During stage I, the present Tramandaí lagoon system was flooded after the onset of the post-glacial transgressions, approximately 11000 yrs BP, when the coastline was located 16 m below the present level. The oldest age found in the lagoon sediments is 10895 yrs BP (Travessas et al., 2005; Dillenburger et al., 2009). This facies presents abundant marine

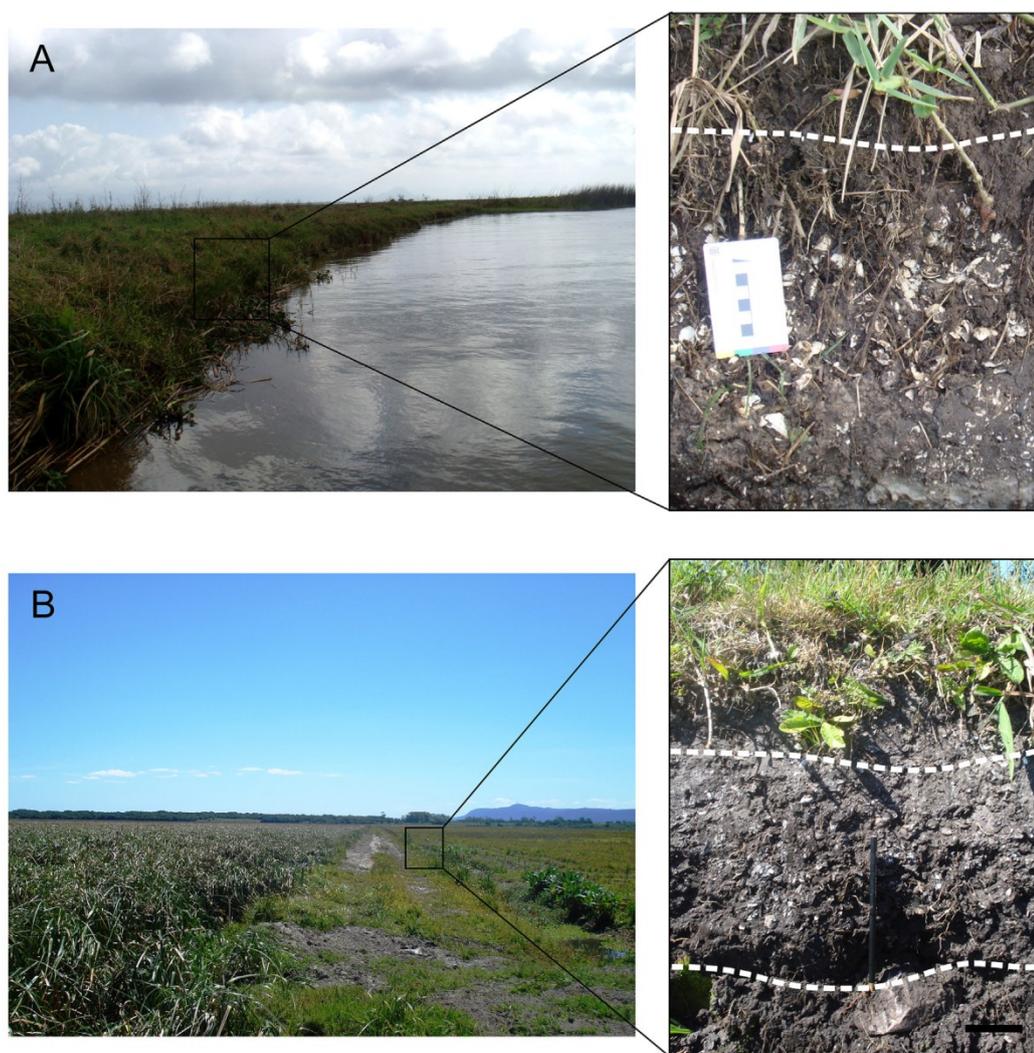


Fig. 2. Detail of the outcrops, 1 (A) and 2 (B). The dashed line delineates the layer of shells. In outcrop 1 the lower limit is not shown. Scale bars: 10 cm.

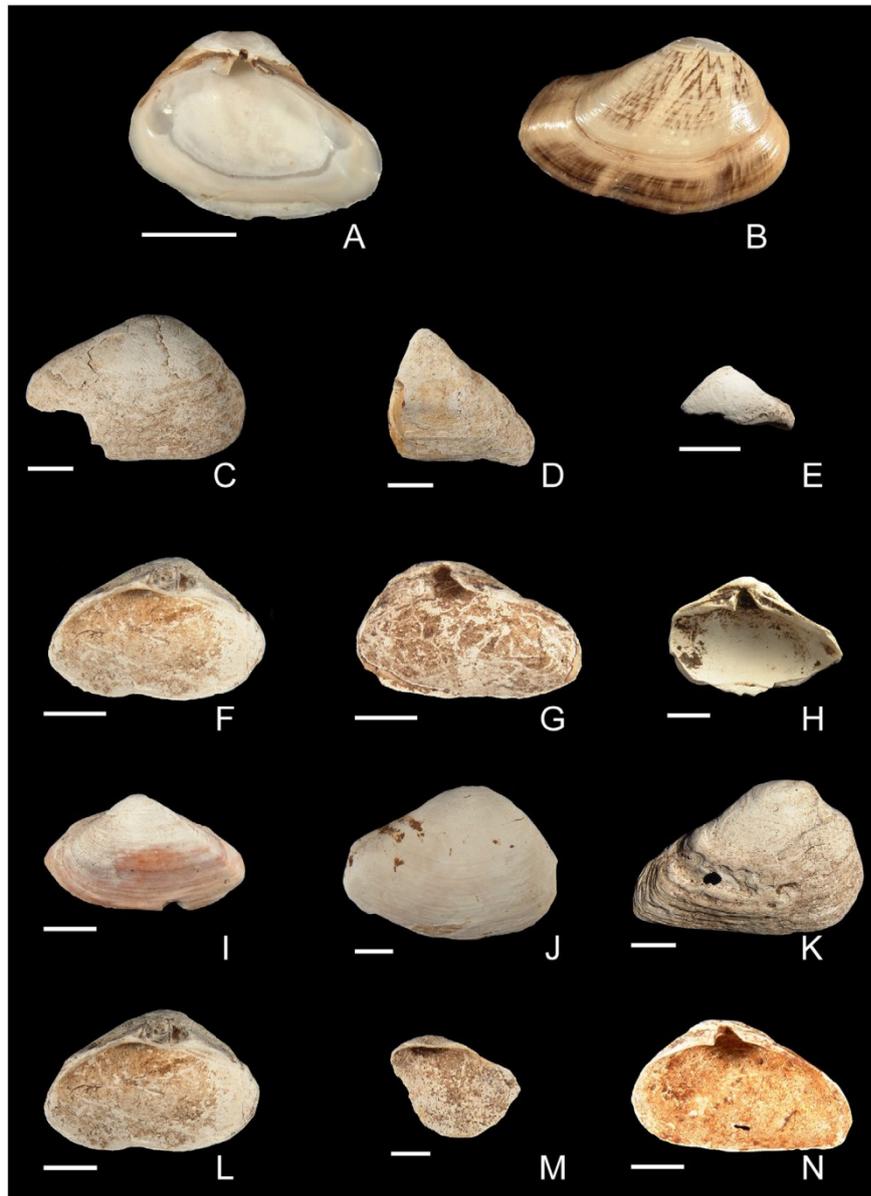
palynomorphs, corroborating the idea that the lagoon was initiated during a sea level rise (Medeanic et al., 2003).

In Stage I, the barrier-lagoon was essentially dominated by lagoonal depositional processes (Dillenburg et al., 2009). The fossil record (bivalves, foraminifera and ostracods) indicates a mixohaline environment (Dillenburg, 1996). There is no Holocene sedimentary record of marine origin overlying the basal (Pleistocene) deposits, which indicates lagoonal flooding due only to the stagnation of the lagoon waters as a consequence of barrier development in response to the sea level rise (Dillenburg et al., 2009).

Stage II (7355 to 5430 yrs BP) is characterized by the configuration of the lagoon-barrier system in its present position (Holocene Lagoon System IV; Fig. 1) and subsequent to barrier migration

and lagoon fill during the final stages of the PMT (Dillenburg et al., 2009). During this process, there was a large lagoon that extended parallel to the present coastline. According to Dillenburg (1996), in this stage and as a consequence of the sea level rise, the lagoon depth increased, which resulted in a characteristic transgressive facies succession; sandy sediments underlying an approximately 3 m thick muddy lagoonal facies.

The third stage (stage III; 5430 to present) is a regressive phase. The facies succession illustrates aeolian deposits overlying beach sediments; a typical progradational barrier sequence (Hesp et al., 2007; Dillenburg et al., 2009). The siltation and segmentation of a large lagoon that had once been a prominent geomorphological feature in the region fragmented into smaller and connected



**Fig. 3.** Taphonomic attributes of the shells of *Erodona mactroides* from outcrops 1 and 2 (except A and B). A and B) specimens without modification (Recent specimen from Mangueira Lagoon, southern CPRS – Museum of Paleontology – UFRGS, MP-I-4289) (both sides present, none damaged); C) low fragmentation; D) moderate fragmentation; E) severe fragmentation; F) edge margin rounded and hinge worn; G) edge margin chipped and oxidation more than 50%; H) broken margin chipped; I) surface alteration up to 20%; J) surface alteration from 20 to 70%; K) surface alteration more than 70%; L) worn, fine-scale hinge alteration; M) lost hinge; N) oxidation more than 50%. In some cases, multiple signatures are observed in a single shell. For example, the specimen in (K), which has a moderate extent of corrosion (frequency of small and large pits and holes), also displays a high degree of surface alteration. More information about figure is explained in Table 1. Scale bars: 5 mm.

coastal lagoons (Dillenburg et al., 2009). The same siltation process can now be found in the northeastern Tramandaí Lagoon, caused by the high sedimentation rate in the mouth of the Tramandaí river (4.2–4.4 mm/yr), where its delta progrades rapidly (Dillenburg and Burnett, 1995).

Despite the well-known geological evolution of the CPRS (Dillenburg et al., 2009), the third phase of Tramandaí Lagoon evolution requires more information, especially for the final regressive period. A more robust geochronology is also needed to better understand the paleoenvironmental evolution of the northern part of the CPRS. The existing stratigraphic framework for the entire coastal depositional system of Rio Grande do Sul State can be better constrained to paleoclimatic and paleobiological information with better age estimates.

### 3. Material and methods

#### 3.1. Outcrops

The shells used for this study were recovered from two outcrops located in the northern part of the CPRS (Fig. 1). As it cannot be assumed that both outcrops are replicates of a strictly identical environment, or that they constitute some extremes within a larger (and therefore, at least slightly, different) depositional setting, the decision was made to test their taphonomic features by treating them independently.

Outcrop 1 is located in the Tramandaí river delta, situated approximately 3 km landwards from the present coastline. The shell bed, mostly constituted by *Erodona mactroides* and *Heleobia australis* is 50 cm thick, with variable depth (but probably not exceeding 1–2 m) and tabular geometry, traceable for long distances. Vegetation, mostly grasses, is abundant on the uppermost sediments that are composed of aeolian sand. In the shelly bed, sediments are sandy to silty, and rich in organic matter (Fig. 2A).

Outcrop 2 is ~5 km landward from the present coastline and located at the margin of road RS 389 (regionally known as “Estrada do Mar”) and near the roundabout access to Imbé and Tramandaí municipalities. The sedimentary constitution is the same as outcrop 1, except for a tuffaceous layer in the upper part (Fig. 2B). The shell bed is approximately 75 cm thick, with a discontinuous lateral extension that is traceable for at least 1000 m.

These deposits were formed as a consequence of the rapid progradation of the Tramandaí River delta, with some contribution of aeolian sedimentation and palaeosol formation during the Middle to Late Holocene. These shell beds reflect episodic environmental changes, as neither evidence of bioturbation, nor transported or reworked marine/euryhaline species (e.g., *Nucula*, *Mactra*) were found in the studied area.

#### 3.2. Shell sampling

Fossil specimens were extracted from the sediment using cubic sampling units (20 cm × 20 cm × 20 cm), yielding a total of approximately 8 L of bioclast-rich sediment. Shells were carefully removed from the sediment. Each bioclast-rich block was divided into 16 subunits, from where 4 were sorted for analysis. Shells from these 4 subunits were carefully washed with current water to remove sediment excess, yielding a variable number of shells. As there is no standardized method for taphonomic analysis of fossil shells from estuarine deposits, and to avoid any analytical bias, 4 subsamples were randomly selected, each containing 50, 100, 150 and 200 shells, from each subunit. This procedure was adopted to test whether the recorded intensity of the taphonomic signatures varies over different sample sizes, as observed for marine bivalves (Kidwell et al., 2001; Kowalewski and Hoffmeister, 2003). In this

analysis, no variation according to subsample sizes was found, and therefore the shells from each outcrop were pooled. Consequently, 500 shells were analyzed from each of the outcrops.

#### 3.3. Taphonomic analysis

The damage states were tallied in the shells and the fragments of *Erodona mactroides* according to a taphonomic score system adapted from the available literature (Davies et al., 1989; Best and Kidwell, 2000a,b; Kidwell et al., 2001; Parsons-Hubbard, 2005; Best, 2008). Eight taphonomic variables (fragmentation, commissure and broken margin modification, surface alteration, fine-scale hinge alteration, extent and degree of corrosion, and oxidation) and their damage states were selected as the study parameters for characterizing the inner and outer surfaces of the shells. A 10× magnification stereomicroscope was used for this purpose (Table 1; Fig. 3).

**Table 1**

Taphonomic variables and scoring systems used to assess shell damage in the fossil assemblage. Fragmentation was scored based on the proportion of shell lost: 0 – no fragmentation (100% of the valve); 1 – low fragmentation (large fragment, at least 80% of the valve present); 2 – moderate fragmentation (average fragment, ~50% of the valve present); and 3 – severe fragmentation (small fragment, less than 20% of the valve present). Edge modification was ranked accordingly for commissure: 0 – no edge modification; 1 – slight damage (rounded shell edge); and 2 – severe damage (chipped shell edge). Broken margin modification was scored using the same scale as for commissure. Surface alteration was scored as follows: 0 – shell with no dissolution (i.e., with periostracum at least partially preserved); 1 – low damage (<20% of the shell area display chalky appearance); 2 – moderate damage (20%–70% of the shell area display chalky appearance); and 3 – severe damage (more than 70% of the shell display chalky appearance). Hinge fine scale alteration was ranked similarly: 0 – no hinge alteration; 1 – hinge worn with reduction of the hinge area; and 2 – hinge lost. The degree of corrosion was scored in the following way: 0 – corrosion absent; 1 – shell with small pits; 2 – shell with large pits (craters); 3 – shell with small and large pits; 4 – shell with holes; 5 – shell with large pits and holes. Oxidation was scored based on the percentage of color alteration: 0 – shell surface with no oxidation; 1 – shell surface with low oxidation (<50% of the valve oxidized); and 2 – shell surface with high oxidation (>50% of the valve oxidized).

Taphonomic signature	Damage states	Illustration
Fragmentation	0 = no fragmentation	Fig. 3A and B
	1 = low fragmentation	Fig. 4C
	2 = moderate fragmentation	Fig. 4D
	3 = severe fragmentation	Fig. 4E
Edge modification Commissure	0 = none	Fig. 3A and B
	1 = rounded	Fig. 3F
	2 = chipped	Fig. 3G
Broken margin	1 = rounded	Fig. 3L
	2 = chipped	Fig. 3H
Dissolution Surface alteration	1 = up to 20%	Fig. 3I
	2 = 20–70%	Fig. 3J
	2 = more than 70%	Fig. 3K
Fine-scale hinge alteration	0 = none	Fig. 3A and B
	1 = worn	Fig. 3F and L
	2 = lost	Fig. 3M
Corrosion Degree of corrosion	0 = none	Fig. 3A and B
	1 = small pits	Fig. 3D
	2 = large pits	Fig. 3K
	3 = small and large pits	–
	4 = holes	Fig. 3K
Corrosion extent	5 = large pits and holes	Fig. 3K
	1 = up to 20%	Fig. 3D
	2 = 20–70%	Fig. 3C
Oxidation	3 = more than 70%	Fig. 3K
	0 = none	Fig. 3A and B
	1 = up to 50%	Fig. 3L
	2 = more than 50%	Fig. 3N

The alteration in the outer shell surface was divided into two categories: surface alteration and corrosion. The first category is related to the chalky appearance of the shells, and a high percentage of the shell surfaces displayed this feature. The second category consisted of several alteration types, caused either by biological or physical damage, which can only be distinguished by analyzing the SEM images (e.g., Best and Kidwell, 2000a). From the latter category, tallies included (from minor to major alteration degree) the occurrences of minor pits, major etches (large pits) and holes (perforations). The detailed taphonomic protocol is listed in Table 1. The significant differences observed in the mean taphonomic damage between the outcrops were assessed using the non-parametric test, Mann–Whitney U, in the SPSS statistical package.

### 3.4. $^{14}\text{C}$ AMS dating

Three shell samples were dated with Accelerated Mass Spectrometry (AMS)  $^{14}\text{C}$ . One *Erodona mactroides* valve from outcrop 1 (sample label MVd-01-Em) and two shells from outcrop 2 (one valve of *Amiantis purpurata*, sample label Pal-03-Amp, and another of *E. mactroides*, sample label Pal-01-Em) were dated. The  $^{14}\text{C}$ -AMS dating were conducted at Beta Analytic© laboratories (Miami, Florida, USA).

## 4. Results

Based on the  $^{14}\text{C}$ -AMS analysis performed on the shells, both outcrop 1 and 2 show similar age range (from 1060 to 1490 cal yrs BP; Table 2). Most taphonomic variables and states indicated significant differences between the two outcrops (Tables 3 and 4). The fragmentation degree was significantly different; shells from outcrop 1 exhibited a predominantly low to moderate fragmentation (less than 20% of shell loss), whereas shells from outcrop 2 exhibited mostly 50% of shell surface loss (Table 3). Shell margins were predominantly rounded in outcrop 2 and chipped in outcrop 1 (Table 3). However, the fragmented margin is mostly rounded in both the outcrops with no significant difference between the two (Fig. 4C; Table 4). Although the taphonomic feature disarticulation was not included in the taphonomic protocol, all bivalve shells from both outcrops were disarticulated.

**Table 2**  
Conventional and calibrated  $^{14}\text{C}$  ages obtained for shell samples.

Outcrop	Lab sample name	Beta sample number	Species	Conventional $^{14}\text{C}$ age	Calibrated $^{14}\text{C}$ age
1	MVd-01-Em	Beta -296447	<i>Erodona mactroides</i>	1580 ± 30	1220–1060
2	Pal-01-Em	Beta -296448	<i>Erodona mactroides</i>	1540 ± 30	1170–1040
2	Pal-03-Amp	Beta -296449	<i>Amiantis purpurata</i>	1870 ± 30	1490–1340

With regard to dissolution, shells from both outcrops display the same taphonomic profile (Table 3; Fig. 4D). The chalkiness texture varies from 20% to 70% (Table 3). However, the absolute frequency of this taphonomic signature was significantly different between the two outcrops (Fig. 4D; Table 4). The proportion of fine-scale hinge alteration varies among outcrops (Fig. 4E; Table 4). However, in both outcrops a high proportion of worn out fine-scale hinge alteration is evident (Table 3).

Corrosion is mostly present as pitting in outcrop 1 and as major etchings (large pits) in outcrop 2 (Table 3). However, the

**Table 3**

Percentages of damage states (with 95% confidence intervals) for each taphonomic signatures analyzed, in both outcrops.

Taphonomic signature	Outcrop 1	Outcrop 2
<b>Fragmentation</b>		
Up to 20%	47.0 (±4.4)	39.2 (±4.3)
±50%	38.8 (±4.3)	41.8 (±4.3)
More than 80%	14.2 (±3.1)	19.0 (±3.4)
<b>Edge modification</b>		
<b>Commissure</b>		
None	0	0
Rounded	26.2 (±3.9)	51.8 (±4.4)
Chipped	73.8 (±3.9)	48.2 (±4.4)
<b>Broken margin</b>		
Rounded	90.2 (±2.6)	77.6 (±3.6)
Chipped	9.8 (±2.6)	22.4 (±3.6)
<b>Dissolution</b>		
<b>Surface alteration</b>		
Up to 20%	5.0 (±1.9)	31.3 (±4.1)
20–70%	91.0 (±2.5)	68.2 (±4.0)
More than 70%	4.0 (±1.7)	0.2 (±0.4)
<b>Fine-scale hinge alteration</b>		
None	0.6 (±0.6)	0.6 (±0.6)
Worn	77.6 (±3.7)	72.0 (±3.9)
Lost	21.8 (±3.6)	27.4 (±3.9)
<b>Corrosion</b>		
<b>Degree of corrosion</b>		
None	2.8 (±1.4)	1.2 (±0.9)
Small pits	47.4 (±4.4)	41.2 (±4.3)
Large pits	30.4 (±4.0)	50.4 (±4.4)
Small and large pits	13.6 (±3.0)	4.2 (±1.8)
Holes	2.0 (±1.2)	1.8 (±1.2)
Large pits and holes	3.8 (±1.7)	1.2 (±0.9)
<b>Corrosion extent</b>		
Up to 20%	52.4 (±4.4)	74.2 (±3.8)
20–70%	45.8 (±4.3)	24.5 (±3.7)
More than 70%	1.8 (±1.2)	1.2 (±0.9)
<b>Oxidation</b>		
None	1.8 (±1.2)	3.6 (±1.6)
Up to 50%	78.6 (±3.6)	58.6 (±4.2)
More than 50%	19.6 (±3.5)	37.8 (±4.3)

**Table 4**

Differences in the mean damage score between shells from the two outcrops. Significances were assessed using the Mann–Whitney U test.

Taphonomic variable	Mann–Whitney statistics
Fragmentation	$Z = -2.742, p = 0.006$
<b>Edge modification</b>	
Commissure	$Z = -8.295, p < 0.0001$
Broken margin	$Z = -1.353, p = 0.176$
<b>Dissolution</b>	
Surface alteration	$Z = -11.490, p < 0.0001$
Fine-scale hinge alteration	$Z = -2.024, p = 0.043$
<b>Corrosion</b>	
Degree of corrosion	$Z = -0.538, p = 0.591$
Corrosion extent	$Z = -7.153, p < 0.0001$
Oxidation	$Z = -5.562, p < 0.0001$

degree of corrosion is not significantly different between outcrops (Fig. 4F; Table 4). The corrosion extent is small (up to 20%) in both outcrops (Table 3) but with varying absolute frequencies (Fig. 4G; Table 4).

Less than 50% of the shell surface is covered by oxidation signs in the majority of shells from both outcrops (Table 3). Although both outcrops exhibit similar oxidation profiles, significant differences exist between them (Fig. 4H; Table 4).

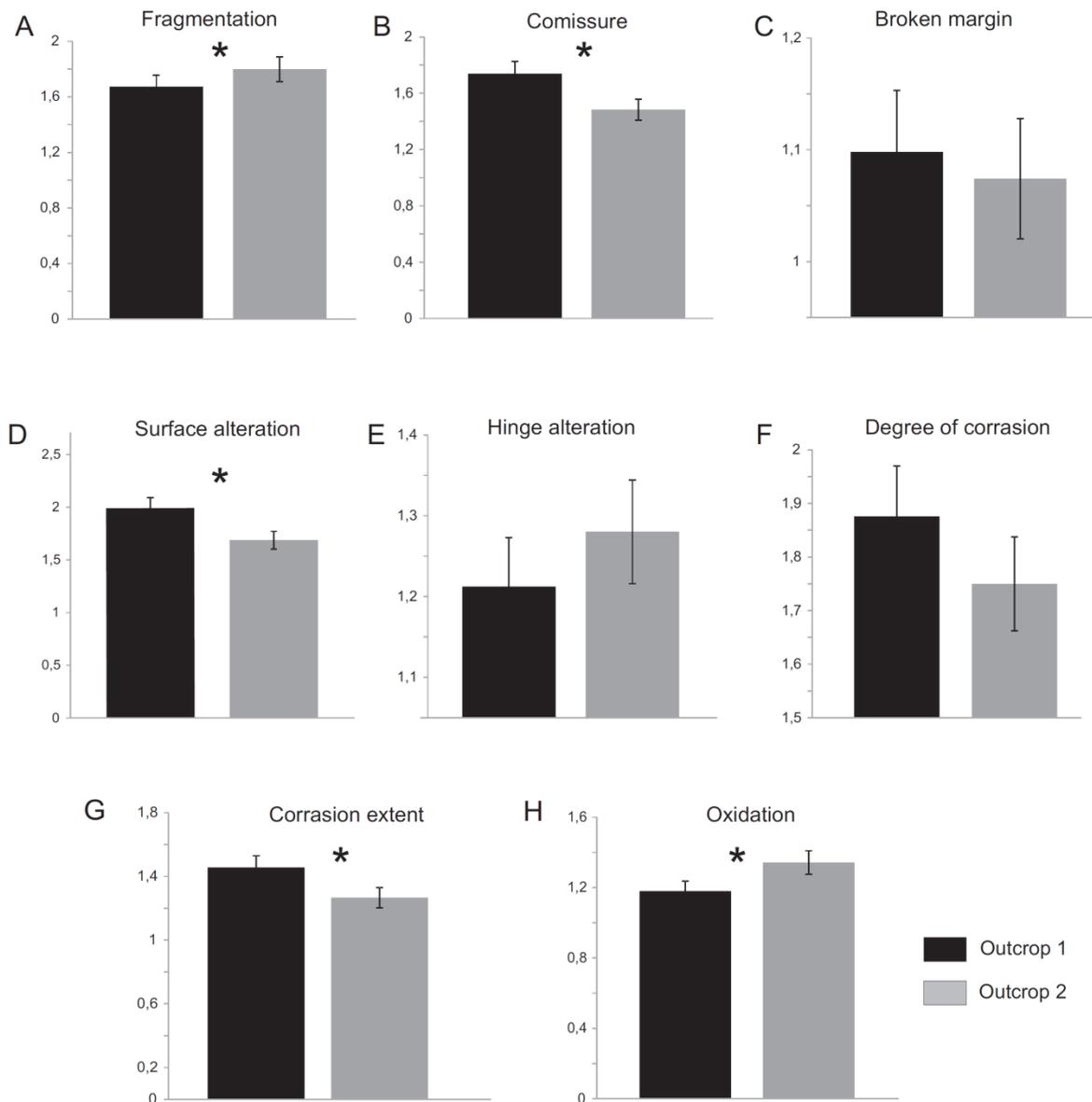


Fig. 4. Mean taphonomic damage (whiskers are 95% confidence intervals for mean). Asterisk denotes significant differences.

## 5. Discussion

*Erodona mactroides* is one of the most common (top-ranked) species among those found in the euryhaline habitats of river mouths, lagoons and bays from southern South America, and thrives in sandy substrates (Costa, 1971; Jorcin, 1996). This species is also found in several Quaternary deposits along the coast of Argentina (e.g., Aguirre and Whatley, 1995; Aguirre and Farinati, 1999) and Uruguay (e.g., Martínez et al., 2006), as well as in estuaries along the Uruguayan coast (Jorcin, 1996; Muniz and Venturini, 2001). Along the coast of the State of Rio Grande do Sul in southern Brazil, the species is found abundantly in the Patos Lagoon estuary (Bemvenuti and Netto, 1998; Colling et al., 2007, 2010).

It is likely that the fossil assemblages found near the Tramandaí Lagoon may have been mainly deposited in an ancient environment that encompassed a larger lagoon in the northern part of CPRS, which might have even reached the Itapeva Lagoon (Tomazelli and

Villwock, 1991; Dillenburg, 1996). Nevertheless, the obtained ages indicate that this putative lagoon occupied this larger area until very recently. Currently, the Tramandaí 'prodelta' has high sedimentation rates (Dillenburg and Burnett, 1995; Dillenburg et al., 2009), which may be related to the siltation and more recent sedimentation of the lagoon.

This is the first taphonomic assessment for the entire region, and more stratigraphic evidence is needed to assure that this larger lagoon in fact existed. In this study, outcrops 1 and 2 are treated as replicates for assessing past variability of a single paleoenvironment. When more outcrops are discovered or become available, it will become easy to determine any taphonomic variability for this environment.

The available paleoclimatic studies that correlate with the paleoenvironment for the northern part of the CPRS are scattered and controversial, which complicates any correlation with these data. According to Ybert et al. (2001), a dry phase predominated

from 2500 to 1500 yrs BP in Southern Brazil. From this phase onwards, the region experienced a moister and colder climate (Behling, 1998; Ybert et al., 2001).

Martinho et al. (2008) evaluated the evolution of transgressive dunes in the CPRS during the middle to late Holocene and identified phases of eolian activity and soil formation. This phase is in agreement with the date for the shells of *E. mactroides*.

Disarticulation is a good estimator for the time-since-death, environmental energy, exposition in the sediment–water interface and bioturbation (Brett and Baird, 1986; Davies et al., 1989; Parsons and Brett, 1991; Fürsich and Oschmann, 1993). Following Parsons–Hubbard (2005) and Lockwood and Work (2006), the high disarticulation levels observed in this study are attributed to microbially-induced degradation, with the contribution of a small, but important, amount of environmental energy, although the overall taphonomic features do not support high-energy mediated disarticulation.

Dissolution appears to be pervasive in the estuarine settings (Marshall et al., 2008), and this may be partially responsible for the fragmentation observed in the shells from the Tramandaí Lagoon outcrops, as well as some crab-induced breakage (as also seen by De Francesco and Hassan, 2008). In addition to differentially affecting dissolution, intrinsic features such as microcrystalline and microarchitectural arrangement and shell organic content may strongly influence the skeletal remains resistance to fragmentation (Glover and Kidwell, 1993; Harper, 2000).

In marine settings, fragmentation is associated with not only high environmental energy but also with biological interactions, such as bioerosion, which weakens the shells in low energy environments (Zuschin and Stanton, 2001; Zuschin et al., 2003). De Francesco and Hassan (2008) did not find significant differences in the fragmentation degree between the fossil assemblages from environments with tide energy variation in an Argentinean coastal lagoon. Best and Kidwell (2000a) assigned fragmentation to pre-dation processes rather than to any physical mechanism.

Both outcrops present significant differences regarding the extent of oxidation (Fig. 4H; Table 4). In the marine environment, the origin of oxidation is mainly related to bioturbation, which induces alteration in the upper sediment redox conditions (Aller, 1982, 1994; Canfield, 1989; Ku and Walter, 2003; Best et al., 2007). However, in this study, the origin of oxidation may be related to the presence of organic matter and iron precipitation, and possibly to the presence of grass roots (Emerson et al., 1999; Tanner and Khalifa, 2010).

The corrosion degree did not display any difference between the outcrops, although the extent of corrosion differed significantly between them (Fig. 4F–G; Table 4). Nevertheless, a damage gradient exists, from small to large pits and holes. Arguably, dissolution is the leading taphonomic process that caused shell damage in this study. Lockwood and Work (2006), for example, considered that small and large pits, as well as the chalky appearance, have a common origin when those conditions are considered within a single taphonomic variable (fine-scale alteration). In marine environments, algae and fungi microbioeroders are an important source for biological alteration of the shell surface, producing the small pits and chalky appearance, and also causing the chemical dissolution (Best and Kidwell, 2000a).

The extent of encrustation and bioerosion were not studied in this paper. The only sign of biological activity that was noted, although rare, was the rhyzoconcretion, a characteristically fluvial taphonomic signature (Kotzian and Simões, 2006). This feature was found only in outcrop 2. Encrustation and bioerosion degrees are usually rare in lagoonal environments because the main encrusting taxa are typically marine (Tevesz and McCall, 1983; Parsons–Hubbard, 2005; De Francesco and Hassan, 2008). Additionally, the low or absent

bioerosion may be due to the little exposure time within the taphonomically active zone (TAZ) (Farinati et al., 2008), i.e., no exposure of the bioclasts to the sediment–water interface. In present-day estuarine/lagoonal environments, bioeroded or encrusted shells may accumulate as a consequence of past conditions, or from reworking of marine shells (De Francesco and Hassan, 2008).

Surface alteration is pervasive in both outcrops (Fig. 4D). In the marine setting, the taphonomic processes related to the dissolution are mostly unimportant, despite the constant CaCO<sub>3</sub> nonsaturation being an important taphonomic factor while the shells are within the TAZ (Sanders, 2004; Cherns et al., 2011). In the marine environment, bioerosion and bioturbation are the main causes that are responsible for fostering dissolution (Canfield and Raiswell, 1991; Canfield et al., 1993; Best, 2008). Outer shell surface alteration (small pitting and chalky appearance) can occur with higher frequency in the estuaries as a consequence of the slightly acidic nature of brackish water (Trewin and Welsk, 1976; Alexandersson, 1979). In the coastal environments in Argentina, the weathering caused by the high precipitation, sun exposure, temperature fluctuations and increasing groundwater level are regarded as the main dissolution agents for the shell remains found in the Quaternary marine terraces (Farinati et al., 2008).

Variations in the sedimentation dynamics can serve as the primary control over paleobiologic and taphonomic processes (Kidwell, 1986). Much surface dulling and shell loss that is informally referred to as dissolution is attributable to the leaching of organic matrix, microboring, and biological processes rather than to the dissolution of mineral phases alone (Kidwell and Bosence, 1991). In this study, however, the data suggest that the dissolution bias may be entirely of a chemical nature, with little contribution from any biological factor.

## 6. Concluding remarks

Although it has been indirectly indicated in the existing literature, this study reaffirms that dissolution seems to be a leading taphonomic agent in lagoonal environments. The shells from the two outcrops are within the TAZ and, because of the intense dissolution, they will most likely leave no geological record.

Several taphonomic features, such as small and large pits and/or holes, are indirectly influenced or sometimes even caused by dissolution. The taphonomic signatures, which are commonly caused by biological agents in the marine environment, are produced by dissolution in the estuarine/lagoonal environment. Nevertheless, the taphonomic patterns that constitute the destructive processes in the estuarine (and lagoonal) environment are more similar to fluvial than the marine environment, at least in subtropical lagoons such as the Tramandaí Lagoon. The consensus is that the putative lagoon that is thought to have existed in the northern CPRS coastal area became segmented immediately after the Post-Glacial Marine Transgression after which the regressive phase began. However, the overwhelmingly high abundance of the mixohaline species in outcrop 2 seems to indicate the opposite: considering the present lagoon position, there might have existed, until recently, a large lagoon towards outcrop 2. In this larger lagoon, higher salinity water could have existed in the north, which might have ensured favorable environmental conditions for the *E. mactroides* to flourish. This species is common in other lagoons from the northern part of the CPRS but has few living representatives in the Tramandaí Lagoon.

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## CAPÍTULO 3

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## FIDELITY BIAS IN MOLLUSK ASSEMBLAGES FROM COASTAL LAGOONS OF SOUTHERN BRAZIL

MATIAS DO NASCIMENTO RITTER

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**ABSTRACT** – The South America southern coast exhibits many outcrops with abundant shell beds, from the Pleistocene through the Recent. How much biological information is preserved within these shell beds? Or, what is the actual probability a living community has to leave a fossil record corresponding to these shell deposits? Although ecological and biogeographical aspects might had been pointed, considering these temporal scales, up to the moment there is no taphonomically-oriented studies available. Quantitative comparisons between living (LAs), death (DAs) and fossil assemblages (FAs) are important not only in strictly taphonomic studies, but have grown a leading tool for conservation paleobiology analysis. Comparing LAs, DAs and FAs from estuaries and lagoons in the Rio Grande do Sul Coastal Plain makes possible to quantitatively understand the nature and quantity of biological information preserved in fossil associations in Holocene lagoon facies. As already noted by several authors, spatial scale parts the analysis, but we detected that the FAs reflects live ones, rather than dead ones, as previously not realized. The results herein obtained illustrates that species present in DA are not as good preserved in recent (Holocene) fossil record as originally thought. Strictly lagoon species are most prone to leave fossil record. The authors consider that the fidelity pattern here observed for estuarine mollusks to be driven by (i) high temporal and spatial variability in the LAs, (ii) spatial mixing in the DA and (iii) differential preservation of shells, due to long residence times in the taphonomically active zone.

**Key words:** death assemblages, spatial mixing, time-averaging, estuaries, lagoons.

**RESUMO** – A costa sul da América do Sul apresenta diversos afloramentos com concentrações conchíferas, desde pleistocênicas até recentes. Quanta informação biológica está preservada nestas concentrações? Ou, qual a probabilidade de uma associação viva deixar um registro fóssil análogo a estas? Embora diferenças ecológicas e biogeográficas já tenham sido apontadas entre estas escalas temporais, até o presente momento nenhum trabalho analisou diferenças sob o ponto de vista tafonômico. A possibilidade de se comparar quantitativamente associações vivas, mortas e fósseis é importante não somente em estudos tafonômicos, como também tem se tornado uma ferramenta poderosa na paleobiologia da conservação. Este trabalho compara quantitativamente associações vivas, mortas e fósseis de lagunas e estuários da Planície Costeira do Rio Grande do Sul. Os resultados reforçam trabalhos anteriores, demonstrando que a escala espacial interfere na análise. Este trabalho também constatou que a associação fóssil reflete a associação viva. Além disso, as espécies estritamente lagunares têm maior probabilidade de deixar registro fóssil. Os resultados obtidos neste trabalho ilustram que as espécies presentes nas associações mortas não são tão bem incorporadas no registro fóssil recente. As espécies estritamente lagunares têm maior probabilidade de deixar registro fóssil. Foi aqui considerado que o padrão observado na fidelidade de moluscos estuarinos é ocasionado pela (i) alta variabilidade temporal e espacial nas associações vivas, (ii) mistura espacial na associação morta e (iii) preservação diferencial, devido à destruição por um longo tempo na zona tafonomicamente ativa.

**Palavras-chave:** associações mortas, mistura espacial, condensação temporal, estuários, lagunas.

### INTRODUCTION

The resemblance between DAs and FAs to the original living community is a valuable appraisal of taphonomic bias (Behrensmeier *et al.*, 2000; Lockwood & Chastant, 2006), and also provides data on broad temporal scales, which is important in conservation biology (see review by Kidwell, 2013). The comparison between assemblages (*i.e.* live-dead studies), called compositional fidelity or quantitative fidelity,

estimates how much of the original community (measured by its richness, abundance, structure and evenness) is preserved in a local fossil record (Kidwell & Bosence, 1991; Behrensmeier *et al.*, 2000).

Despite most live-dead studies focuses on marine organisms that leave refractory remains (see generalization for the term “shell”, by Kidwell, 2013), recent works have been done with different taxonomic groups and environments: estuarine diatoms (Hassan *et al.*, 2008), ostracodes (Allin &

Cohen, 2004; Michelson & Park, 2013), freshwater mollusks (Martello *et al.*, 2006; Erthal *et al.*, 2011; Tietze & De Francesco, 2012), terrestrial gastropods (Yanes *et al.*, 2008, 2011; Yanes, 2012), fruits and seeds (Vassio & Martinetto, 2012), small-mammals (Terry, 2010a,b) and stranding cetaceans (Pyenson, 2010, 2011).

The richness of DAs, for example, can differ from the corresponding LAs due to processes such as differential preservation, postmortem transport, differential turnover, natural temporal variability in the LAs and environmental change within the window of time-averaging (Olszewski & Kidwell, 2007; Olszewski, 2012; Kidwell, 2013). As has long been recognized, DAs are the complex product of the LAs (Johnson, 1965; Walker & Bambach, 1971).

In marine environments, death assemblages are richer than the local living community, due time-averaging, reaching up to 25% more species than the later (Kidwell, 2001, 2002a). In lagoon and estuarine environments, some authors have pointed out that the DAs virtually mirror the LAs. For example, a comparison between empty shells (DA) and living mollusk species from intertidal settings (Magu Lagoon), have indicated that shell mixing between habitats is not typical in these environments (Warne, 1969). Another study, conducted in Tomales Bay, California, shows that the DA is mostly composed of shells from mollusks living nearby, and within habitat transport is negligible (Johnson, 1965). However, more studies are needed to fully develop scenery of processes that affect the fossil preservation in lagoon environments, which need to be refined under the viewpoint of quantitative fidelity between live and death assemblages.

The aim of this paper is to determine fidelity of molluscan assemblages fossilization in coastal lagoons, illustrating how much information can actually be preserved in death and fossil assemblages originated during the Holocene in an estuarine-lagoon (E-L) system (Rio Grande do Sul Coastal Plain, CPRS), at two different spatial scales, local and regional.

#### Quaternary shell beds in South America

The southern South America coasts present high potential for taphonomic studies with mollusks, owing to the expressive presence of Quaternary shell concentrations (marine and E-L) from southern Brazil as far as Patagonia (Argentina) (Martínez *et al.*, 2013 and references therein). In Brazil, works conducted in the late 1960s and early 1970s dealt specifically with some of those shell assemblages in Rio Grande do Sul State (RS), regardless their taphonomy. Bianchi (1969), for example, described Pleistocene oyster beds in Pelotas municipality and surroundings, which are now lost due to mining activities. Closs & Forti (1971) listed mollusk species found in Holocene sediments. Studies in outcrops from the Chui region are still in early phases, addressing mainly taxonomic features (Lopes & Simone, 2012).

In addition, several sandy biotrititic deposits are present in the southern Brazilian continental shelf, informally named “bioclastic provinces” (Erthal, 2012). They are morphologically linear, distributed parallel to the present coastline (associated to ancient coastlines), and are mostly composed of molluscan

shells, derived from inner shelf environments. These features have been mapped on shelf at water depths such as 20-25 m, 32-45 m, 60-70 m, 80-90 m and 120-130 m, but can be found even in present-day beaches (Corrêa *et al.*, 1996; Calliari *et al.*, 1999).

Shells from these “provinces” are commonly reworked, and along with biologic/bioclastic material, transported to the present shores during meteorological tides, mainly in the southern part of the CPRS (Calliari *et al.*, 1999). These reworking events, which happen since at least the late Pleistocene, mix temporally the molluscan shells, making it very difficult to attribute a reliable age.

Albeit the whole region shows potential for taphonomic studies, questions such as “what percentage of species living today in a province have also a Pleistocene record somewhere within it?” are still little addressed (see Kidwell, 2013). For example, from complementary data made available by Martínez *et al.* (2013) it is possible to state that nearly 90% of Holocene species are also recorded in the Pleistocene for the Uruguayan coast.

#### STUDY AREA

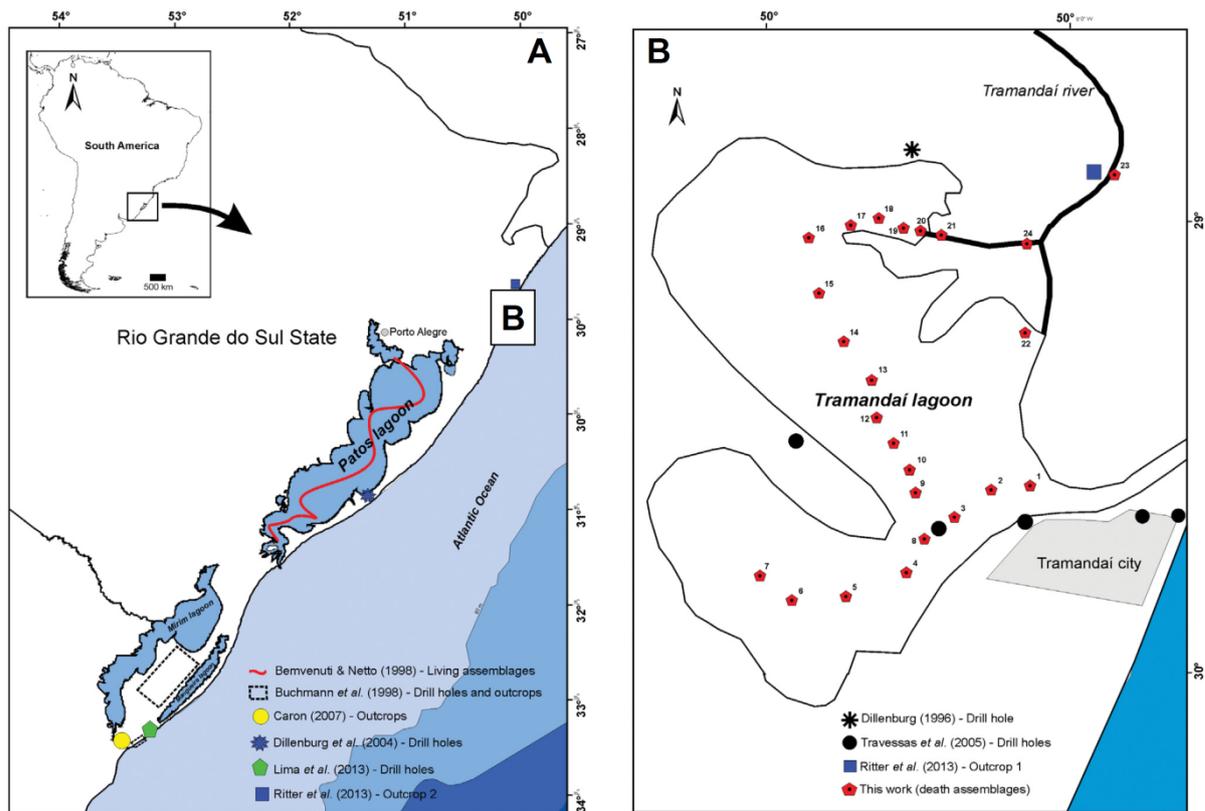
The study area encompasses lagoon systems of the Coastal Plain of Rio Grande do Sul State (CPRS; Figure 1). The CPRS was formed during the Quaternary by the juxtaposition of sedimentary deposits from four barrier-lagoon systems designated as I (oldest) to IV (youngest) by Villwock *et al.* (1986). The first three are Pleistocene (Villwock *et al.*, 1986) while the younger barrier-lagoon system (Barrier-Lagoon IV) was formed during the Holocene (Villwock *et al.*, 1986; Tomazelli & Villwock, 2000).

The most recent lagoon-barrier depositional system of CPRS is represented by a suite of coastal lakes and lagoons, which were fully developed by the maximum Holocene transgression, such as the Tramandaí Lagoon (Tomazelli & Villwock, 2000; Dillenburg *et al.*, 2009). Then, most of the lowlands, presently constituting the Holocene lagoon plain, were flooded and formed large lagoon bodies that were connected to the ocean (Tomazelli & Villwock, 1991).

The Tramandaí Lagoon has an area of 12.86 km<sup>2</sup> and an average depth of 1.10 m (Schwarzbold & Schäfer, 1984); it receives, through the Tramandaí river, water inflow and fine sediments (silt and clay) originated in the rivers and lagoons situated northwards of the system. The Tramandaí estuary is linked to the Atlantic Ocean by a 1.5 km long channel with average depth of 3.0 m (Tabajara & Dillenburg, 1997).

#### MATERIAL AND METHODS

Here, living assemblage – **LA** – refers to specimens collected alive; some original authors included empty shells with adhering flesh and even still-articulated empty shells in this category, but this is difficult to standardize post hoc. **DAs** refers to dead shells; herein are included fragments in their counts of dead individuals if unique (*e.g.* bivalve fragments that included the hinge, gastropods that included the apex).



**Figure 1.** Location of the study area. **A**, general overview of the study area, highlighting those sites where fossil mollusks have been found in E-L sedimentary facies, as well as living molluscan data for Patos Lagoon; **B**, DA data recovered in Tramandai Lagoon by the authors (see Table 1), plus published work here used for FA.

**FAs** refers to specimens found in sedimentary deposits, at Holocene E-L facies, within the youngest barrier-lagoon system (Barrier-Lagoon IV).

#### Living assemblages

Data for LA were compiled from only two lagoons from which data were available (or were of best quality): Tramandai Lagoon (Pedroso & Girardi, 2003; Kapusta *et al.*, 2009) and Patos Lagoon (Bemvenuti & Neto, 1998). These three works surveyed benthic invertebrates in general. Growing human-induced alteration during the past few decades prevented the present LA data to be pristine (see Kidwell, 2007), mainly due to high estuaries alteration (Lötze *et al.*, 2006). Nevertheless, not every polluted areas show low live-dead agreement (Kidwell, 2008).

#### Death assemblages

In this study were sampled 24 sites (= replicates) in the Tramandai Lagoon. These sites were selected to represent a variety of environments (differing according to salinity regime) and to maximize the amount of sediments types and taphonomic bias (Figure 1B; Table 1). DA data for the Patos Lagoon are still not available in the bibliography. However, it is assumed that whenever such kind of data becomes available,

it will change the outcomes of our discussion only in side details, due to possible addition of rarer species to the DA. The effects of this sampling strategy will be justified in the Discussion section.

Samples were collected by the authors, with field logistic assistance provided by CECLIMAR/UFRGS and the site location was established using GPS (accurate to within 10 m). One sample was collected at each site (in autumn 2010) using Eckamm (recovering a volume of 4.6 L, with mesh sieve 1 mm). Whole specimens and identifiable fragments (DAs) were sorted under a dissecting microscope and identified to genus using a variety of general and specific shell guides (Abbott, 1974; Forti-Esteves, 1974; Rios, 2009; Mikkelsen & Bieler, 2008).

#### Fossil assemblages

Data for fossil assemblages were compiled from publications concerning Holocene geological evolution of CPRS. We considered only species found at muddy facies, classified by the authors as E-L sedimentary deposits (Dillenburg, 1996; Buchmann *et al.*, 1998; Dillenburg *et al.*, 2004; Travessas *et al.*, 2005; Caron, 2007; Lima *et al.*, 2013) (Figures 1A, B). The authors also included data from previous taphonomic studies conducted in the area (Ritter *et al.*, 2013; Tramandai

**Table 1.** Details of the sites sampled (DAs) in the Tramandaí Lagoon.

Site	Sediment	Depth (m)	Composition
1	sand	0.90	absent
2	fine sand	1.30	rare fragments of <i>Tagelus plebeius</i>
3	fine sand	1.30	absent
4	sand	1.30	rare fragments of <i>T. plebeius</i>
5	sand	1.15	rare fragments of <i>T. plebeius</i>
6	sand	0.75	absent
7	sand	0.85	absent
8	fine sand	1.05	absent
9	sand	1.05	absent
10	sand	0.95	absent
11	sand	1.20	absent
12	fine sand	1.40	absent
13	fine sand	1.20	few shells of <i>Erodona mactroides</i>
14	fine sand	1.10	rare fragments of <i>T. plebeius</i>
15	sand	0.70	few shells of <i>Heleobia</i> sp. and <i>E. mactroides</i>
16	sand	0.95	few shells of <i>Heleobia</i> sp. and <i>E. mactroides</i>
17	sand	0.65	absent
18	sand	1.60	absent
19	silt	4.50	several shells
20	silt	5.50	several shells
21	silt	5.80	several shells
22	silt	3.80	several shells
23	silt	2.00	absent
24	silt	2.50	absent

Lagoon). Some classic publications (e.g. Closs & Forti, 1971; Forti-Esteves, 1974) were not included because they do not specify whether mollusks were found in E-L facies.

#### Fidelity analysis

The fidelity analyses focused on the two indices proposed by Kidwell & Bosence (1991), including the so-called F1, the percentage of shelly species found alive that were also found dead  $[(NS \times 100)/(NS + NL)]$  (a measure of the preservation potential of species in their natural habitat); and F2, the percentage of species found dead that were also found alive  $[(NS \times 100)/(NS + ND)]$  (a measure of the spatial fidelity of skeletal remains to their original community); where NS = number of species shared by the two assemblages; ND = number of species found only in DA; and NL = number of species found only in LA. These indices were adapted to compare the fidelity of the FA in relation to the LA and DA (see also Erthal *et al.*, 2011), as follows: F1, the percentage of species found alive that were also found in the FA, and the percentage of species found dead that were also found in the FA; F2, the percentage of species found in the FA that were also found live, and the percentage of species found in the FA that were also found in the DA.

The fidelity measures were conducted at the genus level, in order to avoid biases arising from possible misidentification of fossil species (Valentine, 1989), especially among species from geological studies. Two spatial levels were considered

for the fidelity analysis: (i) local scale, considering only LA, DA and FA data from Tramandaí Lagoon; and (ii) regional scale, where LA data from Patos Lagoon were included as well as all FA data of all known fossil deposits from Holocene E-L facies in the CPRS. It is herein recognized that DA information is the same in both assessments, and any limitations are discussed. Species listed on only a single paper was excluded from de LA in the regional approach because they are punctual register and could be equivocates.

The Mann-Whitney-U test was used to test if live-dead-fossil differed in median values. Statistical significance is considered at  $\alpha = 0,05$ . We performed a Non Metric Multidimensional Scaling (NMDS), using the Jaccard similarity index, which is appropriate for the available presence-absence data (Legendre & Legendre, 1998). In order to test whether groups of assemblages differed, was used the Multivariate Analysis of Variance with Permutation (PERMANOVA; Anderson, 2001). Statistical analyses were performed using PAST v2.17 software (Hammer *et al.*, 2001).

## RESULTS

Bottom samples from Tramandaí Lagoon (Figure 1B) yielded a few shell remains (Table 1). A total of 15 bivalves and 11 gastropods species were recorded across all modern (LA and DA) and fossil assemblages (Table 2). Of these, one bivalve genus (*Anomalocardia*) and one gastropod genus

(*Crepidula*) occurred only as fossils; one bivalve genus (*Macoma*) and one gastropod genus (*Melampus*) occurred only in modern assemblages (Tramandaí Lagoon; Table 2).

Regardless molluscan class, the presence of living species found also in death assemblages, at local scale, is slightly lower than at regional scale, while the spatial fidelity is low for both spatial scales here considered, reaching less than 20% (Figure 2A). Dead species are represented far well in fossil assemblages at regional scale than at local scale, with more than 80% of spatial fidelity (F2), at both spatial scales (Figure 2B). Living species are fully represented in fossil layers at regional scale (100%), but reach less than 60% at local scale. Their spatial fidelity is very low at regional scale, becoming higher at local scale (up to 80%; Figure 2C).

Accordingly to the Mann-Whitney U test, the LAs differ significantly from DA at both spatial scales (local:  $Z=-3.937$ ,  $p<0.001$ ; regional:  $Z=-3.574$ ,  $p<0.001$ ) and FAs at regional scale ( $Z=-3.64$ ,  $p<0.01$ ), but not at local scale ( $Z=-0.6425$ ,

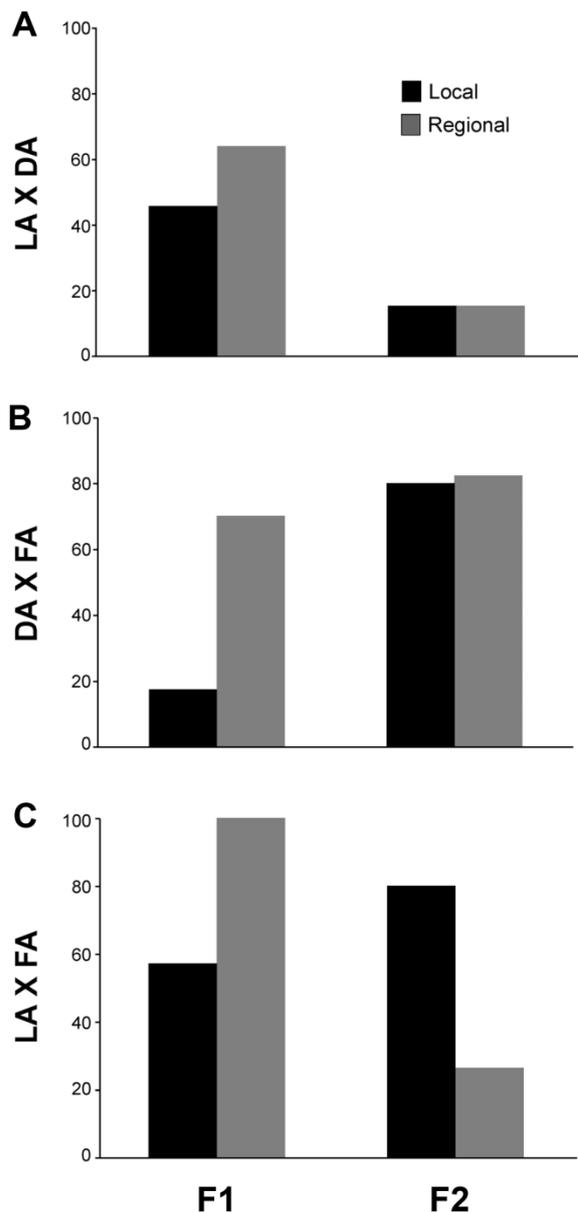
$p>0.05$ ). DA showed significant difference from FA at local scale ( $Z=-4.472$ ,  $p<0.001$ ), but not at regional scale ( $Z=-1$ ,  $p>0.05$ ).

NMDS shows that the FAs are scattered regarding the mollusk composition (Figure 3). The two LAs here considered are within the space encompassed by the group formed by FAs, while the DA is considerably different from the first two assemblages. The PERMANOVA showed no significant difference between living, death and fossil assemblages ( $F=1.401$ ,  $p=0.1009$ ).

In the DA, richness is considerably higher than in LA and FA at both scales (Table 2). Considering the data only from Tramandaí Lagoon (local scale), living gastropods are better preserved in the DA than bivalves, which present more resemblance (living x dead) at regional scale (Figure 4A). The preservation of spatial fidelity (F2) is very low for bivalves and gastropods at both scales (Figure 4B). The preservation of species found dead into FA, for both gastropods and bivalves is remarkably low at local scale, and overall high at regional,

**Table 2.** Presence/absence data compiled from coastal lagoons of Rio Grande do Sul State. **Fossil**<sup>1</sup>, data only from Tramandaí Lagoon; **Fossil**<sup>2</sup>, species found across all Holocene lagoon deposits. **Abbreviations:** **E**, estuarine; **M**, marine.

Classification	Genus	Live	Dead	Fossil <sup>1</sup>	Fossil <sup>2</sup>	Environmental preference
<b>Gastropoda</b>						
Calyptraeidae	<i>Calyptraea</i>		x		x	M
	<i>Crepidula</i>				x	M
Cochliopidae	<i>Heleobia</i>	x	x	x	x	E
Columbellidae	<i>Costoanachis</i>		x			M
	<i>Olivella</i>		x		x	M
Pyramidellidae	<i>Turbonilla</i>		x			M
	<i>Parodizia</i>	x			x	E
Bullidae	<i>Bulla</i>		x		x	M
Cylichnidae	<i>Cylichnella</i>		x			M
	<i>Acteocina</i>		x		x	M
Ellobiidae	<i>Melampus</i>	x				E
Gastropoda total		3	8	1	7	
<b>Bivalvia</b>						
Nuculidae	<i>Nucula</i>		x	x	x	M
Mytilidae	<i>Mytilus</i>		x			M
Ostreidae	<i>Ostrea</i>		x		x	M
Lucinidae	<i>Ctena</i>		x			M
Carditidae	<i>Carditamera</i>		x		x	M
Cardiidae	<i>Laevicardium</i>		x			M
Tellinidae	<i>Tellina</i>	x		x	x	E
	<i>Macoma</i>					E
Veneridae	<i>Anomalocardia</i>		x		x	M
	<i>Pitar</i>		x		x	M
	<i>Transennella</i>		x			M
Mactridae	<i>Mactra</i>		x		x	M
Corbulidae	<i>Corbula</i>		x		x	M
	<i>Erodona</i>	x	x	x	x	E
Solecurtidae	<i>Tagelus</i>	x	x	x	x	E
Bivalvia total		3	13	4	10	
TOTAL		6	21	5	17	



**Figure 2.** Fidelity indices (F1 and F2) comparing living, death, and fossil assemblages at local and regional scales pooled data for gastropods and bivalves.

larger scale, where data from Patos Lagoon were included (Figure 4C). However, the spatial fidelity for preservation of dead species in FA is quite high, being slightly lower for bivalves at local scale (Figure 4D).

Although the preservation of living species in FA is higher at regional scale (with 100% of preservation for both gastropods and bivalves) than at local scale (Figure 4E), the spatial fidelity is much lower in regional scale than in local scale (where gastropods present 100% of preservation), when LA and FAs are compared (Figure 4F).

## DISCUSSION

The lack of surveys of living communities through broader time spans, enough to capture all its natural variability, is one of the leading problems in live-dead comparisons (Kidwell, 2001, 2008; Olszewski & Kidwell, 2007). Moreover, DAs present some degree of time-averaging (that may reach up to tens of thousands of years; see Flessa & Kowalewski, 1994; Kidwell, 2002a, 2013) and within-habitat spatial condensation, which naturally produces some departing in live-dead similarities (Kidwell & Bosence, 1991; Tomašových & Kidwell, 2009a, 2011).

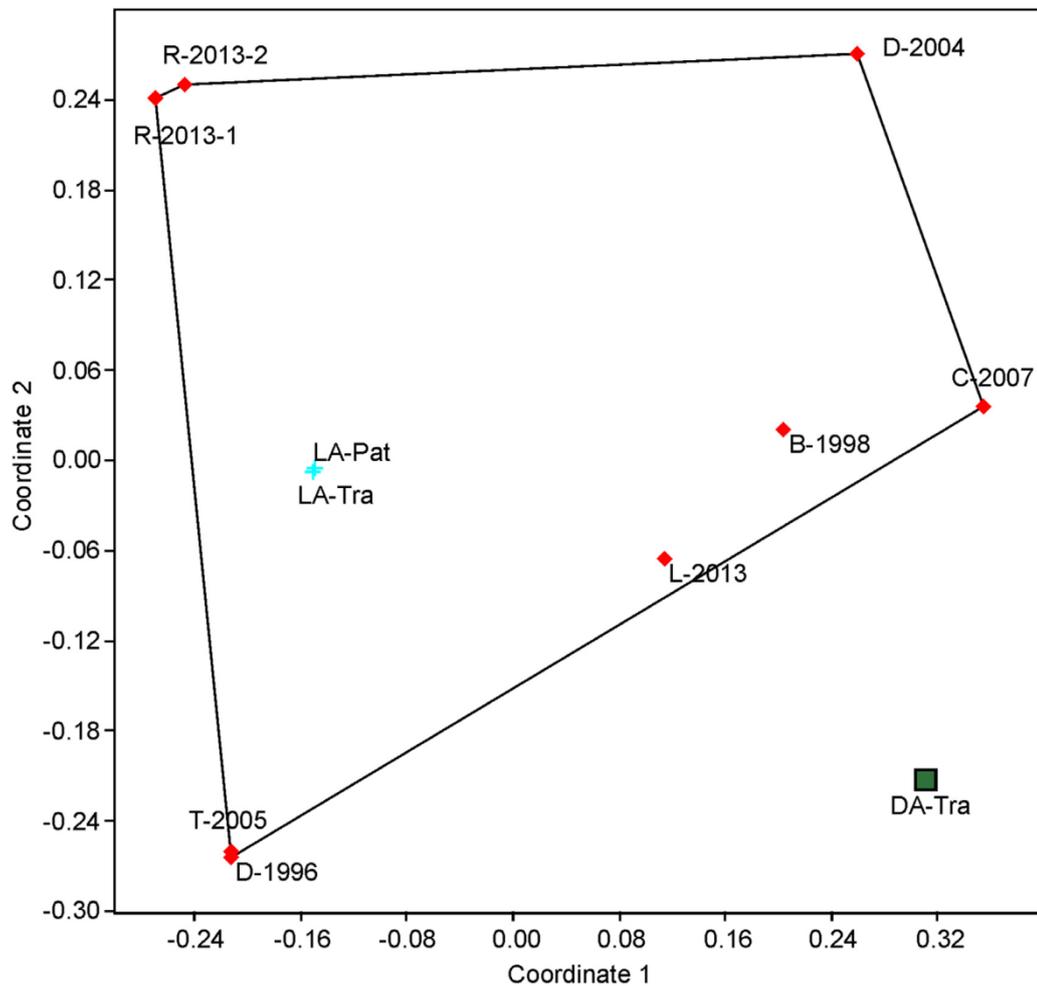
Here is assumed that the living community data came from patchy samples and may not represent a wide sample (see Lockwood & Chastant, 2006 for a temporal series over 20 years of LA sampling). This sampling bias would matter in studies evaluating relative species abundance, since the numerical dominance influence live-dead comparisons (Tomašových & Kidwell, 2009a).

In addition, E-L environment is known to be poorer in species than marine environments, due to limiting factors such as salinity variation, low depths, restricted water circulation, etc. However, the fidelity data herein presented are not of poorer quality, since the live-dead-fossil comparison here performed was done considering a wide spatial scale. Though some species might be absent from DA, and either LA or FA, due to limited sampling effort, some studies suggest the contrary (Tomašových & Kidwell, 2009a, 2010b). The magnitude of the diversity excess in DAs, relative to LAs, will decrease with decreasing spatial resolution from alpha to beta scales, because each local assemblage is increasingly likely to (i) be colonized by species from the shared species pool and (ii) experience habitat conditions that occur in adjacent communities, thus reducing spatial variation in species composition and abundance (Tomašových & Kidwell, 2009a, 2010b).

### Fidelity

Three main processes are probably responsible for fidelity pattern observed here: (i) high temporal and spatial variability of the living communities. Given many generations, and in consequence to time-averaging in the DA, the LA becomes very different (and rarefied in species) than the DA; (ii) spatial mixture in the DA, with the addition of (dead) shells from other environments, mainly strictly marine species (low spatial fidelity at regional scale in the live x dead comparison) (Figure 2A; Table 2); and (iii) differential preservation, since shells may reside for a long time after destruction in the surficial E-L sediment (Ritter & Erthal, 2011), determining the dissimilarity with the LA and the FA at local scale. DAs may acquire higher richness than the corresponding LAs by multiple factors (shell input more than shell destruction and sedimentation rate).

The low richness recorded in LAs may be consequence of undersampling (see Lockwood & Chastant, 2006). Estuaries and coastal lagoons may be aggressive environments, allowing poorer mollusc faunas to develop (Lerberg *et al.*,



**Figure 3.** Scatter plot showing the NMDS analysis conducted with living (crosses), death (square) and fossil assemblages (diamonds) of coastal lagoons from southern Brazil. Stress = 0.1568. **Abbreviations:** LA-Tra, living assemblage from Tramandaí Lagoon; LA-Pat, living assemblage from Patos Lagoon; DA-Tra, death assemblage from Tramandaí Lagoon. Fossil assemblages: R-2013-1, fossil data from Ritter *et al.* (2013), outcrop 1; R-2013-2, data from Ritter *et al.* (2013), outcrop 2; L-2013, Lima *et al.* (2013); C-2007, Caron (2007); T-2005, Travessas *et al.* (2005); D-2005, Dillenburg *et al.* (2004); B-1998, Buchmann *et al.* (1998); D-1996, Dillenburg (1996).

2000), mainly due to the high osmotic pressure this setting is subject (Shumway, 1977; Rhodes-Ondi & Turner, 2010). This may be true for the Patos and Tramandaí lagoons, as Coutinho & Seeliger (1984) found salinity varying from 3 to 36‰. Also, the low depths, typical of CPRS coastal lagoons (including Patos Lagoon to some degree; Möller & Castaing, 1999), may complicate the thriving of more marine species (Allen, 1978, 2008). E-L molluscan LAs may be highly variable, with little persistence of less abundant species in the community through time (Kidwell, 2002a; Zuschin & Oliver, 2003; Kidwell & Rothfus, 2010; Olszewski, 2012). DAs may, on the other way, acquire higher richness than corresponding LAs by multiple factors. Time-averaging, as a leading agent, results in accumulating ecologically persistent species (sometimes rare) over long-term time spans (Kidwell & Bosence, 1991; Flessa & Kowalewski, 1994; Kidwell & Flessa, 1995; Kowalewski *et al.*, 2000; Kidwell, 2002a;

Tomašových & Kidwell, 2009a, 2010a,b, 2011). It provides a window of opportunities for postmortem transportation to homogenize species composition, mixing skeletal remains from multiple generations of living populations and environmental randomness, and from ecological succession and environmental change occurrences in a spatial fashion (Tomašových & Kidwell, 2009a,b). Furthermore, these models are neutral in terms of preservation: they assume that all species have the same (stochastic) per-individual rate of shell destruction or removal from the DA (Tomašových & Kidwell, 2010a,b, 2011).

Although with a considerably time-averaging, and including long-lasting elements (with high durability), the E-L DA here recorded shows high preservation potential, mainly for bivalves at regional scale (Figures 4A,C). This may be a result of processes such as high input of marine shells from the inner shelf during meteorological tides, low biogenic

destruction (De Francesco & Hassan, 2008; Ritter *et al.*, 2013) and high sedimentation rates (the sedimentation rate at the mouth of Tramandaí River is 4.2-4.4 mm/yr.; Dillenburg & Burnett, 1995). Those processes may explain why DA is located far the LA and FA cloud in the NMDS (Figure 3).

E-L environments, being transitional sedimentary settings, also display a transitional preservation pattern, at least for mollusks, for several reasons. The LA is preserved in the FA (Figures 3, 4C), even though the DA may be 'polluted' by non-indigenous shells, raising the DA richness with species that will not further preserve in FA (Figure 4B), at least at local scale. The differential preservation of lagoon shells may be the reason for their persisting in the recent fossil record, whilst, as already examined by Ritter *et al.* (2013), the main destructive process in the E-L sedimentary column is dissolution, a typical fluvial agent (see also Pip, 1988; Kotzian & Simões, 2006; Erthal *et al.*, 2011), which could cause low preservation in lagoon environments. However, the high production of mollusk shells in E-L environments, observed for *Erodona mactroides* Bosc, 1802 both presently in the Patos Lagoon (Colling *et al.*, 2010) and in lagoon outcrops in CPRS (Ritter *et al.*, 2013) possibly mean constant input of shells through the taphonomically active zone (TAZ).

The live-dead agreement, for mollusks, is on average poorer on shelves than in estuaries and lagoons (Kidwell, 2001, 2002b), and taphonomic processes other than within-habitat time-averaging (probably environmental condensation) are more important there (Tomašových & Kidwell, 2011). Indeed, the present results indicate that both LA and FA in E-L environments are basically constituted by indigenous species, though FA may be somehow enriched with marine species which resisted differential destruction in E-L TAZ (Ritter *et al.*, 2013; Figures 4D,F). In addition, marine species found in FA (at estuarine facies) might have not been transported, but are instead relicts of earlier populations which lived at approximate locations during sea-level variations (see Flessa, 1998 for a close example).

Despite transport of non-indigenous species may be an important factor for the discordance, the leading process is time-averaging. Kidwell (2013) found that richness and composition of molluscan DAs overwhelmingly reflect the effects of time-averaging rather than postmortem bias, due time averaged nature of the DAs, which captures rare and patchy species not sampled alive during a one-time survey, and by lateral shifting in habitats within the window of time-averaging.

#### Spatial scale issues

The question 'What percentage of species sampled alive is also encountered dead?' can be asked for any spatial scale: at a site, in a habitat, in a region and across scales (*e.g.* 'What percentage of species in a regional checklist can be found among the dead at a single site?'). Presence-absence tests of live-dead agreement can be applied to a broad array of groups and settings and thus allow cross-scale comparisons (Kidwell, 2013), although they may be significantly homogenized by time-averaging (whilst spatial

mixture may mask relative abundance; Olszewski & West, 1997). These approaches provide a relatively simple means of quantifying per-taxon 'fossilization rates', although none are true rates (Kidwell, 2013).

Several censuses and/or sampling many sites of LAs are necessary to obtain meaningful relationships among LAs and DAs. In marine settings, this procedure has yielded values around 62%-88% for F1, and 63%-94% for F2, (Kidwell & Bosence, 1991; Zuschin *et al.*, 2000; Kidwell, 2002a; Kowalewski *et al.*, 2003; Zuschin & Oliver, 2003; Lockwood & Chastant, 2006). In fluvial settings, Erthal *et al.* (2011) found lower values for F1 and F2, ranging from 30% to 58% at the species level and from 66% to 75% at the genus level. In the present study, the values range from 75-100% for F1 and from 12.5-100% for F2.

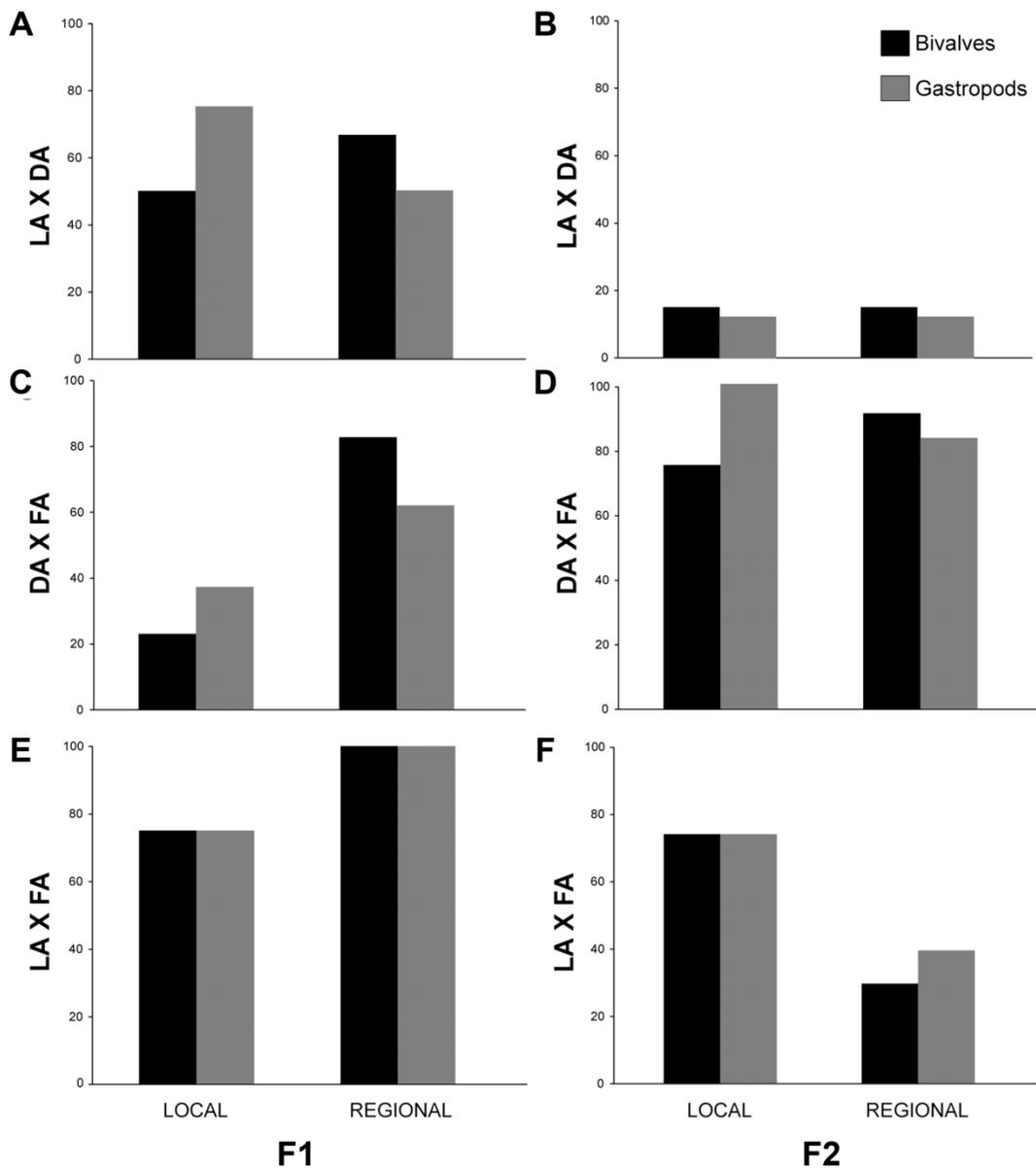
It is conceivable that spatial scale of sampling influences the fidelity outcomes. In small scales, sometimes, the proximity between sampling sites may alone explain the resemblance between LAs and DAs (spatial autocorrelation; Tomašových & Kidwell, 2009a). In the present study, the difference between scales (local x regional) is observed in the living x fossil comparison (Figure 2C). Despite lagoon species, in both scales, display high relative probability of preservation, F2 values at regional scale show that FA actually reflects the DA. In other words, lagoonal species are in fact preserved, but owing to time-averaging (*e.g.* Olszewski & Kidwell, 2007) and spatial mixing (*e.g.* Fürsich, 1978) processes the richness is increased and then incorporated to the recent fossil record.

The degree of transport is basically determined by the habitat spatial scale, *i.e.*, whether there is within- of multi- habitat spatial mixing (Kidwell & Bosence, 1991; Kidwell, 1998). The basic premise is that DAs suffer a natural increase in the richness due to time-averaging, but also as a consequence of transport between contiguous areas (spatial mixing), transferring diversity from  $\beta$  (beta levels, between sites) to  $\alpha$  (local, at facies level) (Kidwell & Bosence, 1991; Olszewski & Kidwell, 2007; Tomašových & Kidwell, 2009a,b). For example, local DAs on average capture 80% of regional richness whereas LAs capture only 60% (Tomašových & Kidwell, 2009a).

It is still not all clear how taphonomic, and even ecological factors, may influence the resemblance of living, death and fossil assemblages in estuaries and lagoons. Dissolution is the main taphonomic process altering biological information in those environments (Ritter *et al.*, 2013), but differential preservation may be, perhaps, the responsible for introducing bias from living to fossil assemblages. It may considerably dilute the increase in DA richness, accounted by the time-averaging and within- and multi-habitat and spatial mixing.

#### CONCLUDING REMARKS

The results above indicate that DAs and FAs in E-L environments present significant spatial multi-habitat mixing, by the addition of inner shelf species and considerable time-averaging, since most of DA richness is captured by local



**Figure 4.** Fidelity indices (F1 and F2) comparing living, death, and fossil assemblages at regional scales, separately for bivalves and gastropods.

FA. Fossil mollusk assemblages found in strictly lagoon sedimentary environments in the CPRS present multi-habitat spatial condensation, probably with significant time-averaging, and are not a strong reflection of lagoon DA species. Therefore, these assemblages represent more than a single depositional environment, with several mollusk generations. As a consequence, the age of a supposedly life-positioned shell do not temporally reflect the facies as a whole, but a single episode instead, probably from a late depositional event.

Several taphonomic factors (both intrinsic and extrinsic to the mollusks) may operate in the formation of the assemblages here studied, such as preferential preservation of infaunal

elements. Nevertheless, more knowledge about LAs and DAs (*e.g.* abundance) are still needed, since long-term fidelity studies with mollusks are absent in the CPRS.

Additionally, the inclusion of live-dead-fossil information from adjacent areas (such as the coast of the State of Santa Catarina, in Brazil, and the coasts of Uruguay and Argentina) would improve our understanding of fidelity in a wider spatial scale, as well as temporal, with data from the Pleistocene. Yet, intersecting information from quantitative fidelity and paleobiogeography can, in concert, lead to new insights into the faunistic change in South America coastal area all along the Quaternary.

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## CAPÍTULO 4

## 4. CONSIDERAÇÕES FINAIS

### 4.1 CONCLUSÕES

Em estuários e lagunas, os processos de sedimentação dominam sobre processos erosivos. Além disto, ambientes transicionais comumente apresentam alta abundância e baixa riqueza relativa de espécies. Portanto, devido a estes fatores, é esperada uma adição expressiva de conchas à zona tafonomicamente ativa (ZTA), formando depósitos com alta concentração de conchas, mas de poucas espécies (como por exemplo, Figura 1, Capítulo 1).

O ambiente estuarino-lagunar, por sua vez, é semelhante ao ambiente fluvial, como apontavam indiretamente alguns trabalhos, confirmando a hipótese inicialmente proposta. A dissolução atua como o principal processo tafonômico, destruindo os remanescentes biológicos que são adicionados sistematicamente à ZTA. Embora tais ambientes sejam propícios a formar amplo registro fóssil, a dissolução oblitera a alta produção de conchas, tornando difuso ou raro o registro biológico nestes ambientes.

Contudo, a dissolução não é um viés que reduz a fidelidade, devido provavelmente ao um *input* de conchas superior à taxa de destruição na ZTA. Não obstante, o registro fóssil de fácies lagunares é composto majoritariamente por espécies marinhas, decorrente do transporte e do *time-averaging* presente na associação morta e parcialmente preservada no registro fóssil.

A interpolação dos trabalhos permite algumas generalizações finais: (i) a dissolução atua como o principal fator tafonômico que oblitera negativamente a preservação das espécies (pelo menos para moluscos) adicionada à ZTA e de forma seletiva (conchas marinhas podem ser mais propensas à dissolução do que conchas estuarinas/lagunares); (ii) a alta produção de conchas (devido à alta produtividade destes ambientes) equilibra a perda de material bioclástico por dissolução, possibilitando a formação de registro fóssil com alta fidelidade, no caso das espécies lagunares; (iii) a presença de espécies marinhas na associação morta e fóssil é decorrente de dois processos naturais: transporte entre habitats e *time averaging*.

## 4.2 PERSPECTIVAS

Fica evidente, com este estudo, a importância de se ampliar a amostragem a outras lagunas da costa do Rio Grande do Sul. Ainda inexplorada sob o ponto de vista tafonômico, a Laguna dos Patos, por exemplo, permitirá estudos tafonômicos de ampla escala geográfica e abordagens de fidelidade quantitativa relacionada à partição da diversidade. Um grande obstáculo a ser superado, entretanto, é a carência de estudos atuais (associação viva), o que dificulta a expansão dos resultados tafonômicos a outros atributos ecológicos, como abundância, equitabilidade, estrutura populacional e variação temporal natural da comunidade, embora dados de presença/ausência possam ser também robustos.

## **APÊNDICE**

## GLOSSÁRIO

**Associação viva:** um conjunto de indivíduos vivos de uma ou mais espécies. Por exemplo, o conjunto de invertebrados coletados vivos durante um levantamento biótico. Inglês: *living assemblage*.

**Associação fóssil:** um conjunto de organismos soterrados permanentemente recuperados do registro sedimentar, ocorrendo abaixo da camada superficial de mistura de uma moderna superfície tanto terrestre quanto marinha. Inglês: *fossil assemblage*.

**Associação morta:** é um conjunto taxonomicamente identificável de remanescentes orgânicos mortos ou descartados presente na camada superficial do fundo do mar, de uma laguna ou de uma paisagem terrestre. Por exemplo, remanescentes de conchas na beira da praia ou folhas no solo de uma floresta. Inglês: *death assemblage*.

**Diversidade alfa ( $\alpha$ ):** diversidade local. Atributo ecológico de uma única amostra. Por exemplo, a riqueza de um ponto amostral em uma laguna.

**Diversidade Beta ( $\beta$ ):** Alteração da composição de espécies entre amostras (estimado pela riqueza, diversidade etc.), ou entre habitats.

**Espécie não indígena:** espécie que foi transportada, naturalmente não encontrada viva num habitat. Sinônimo de alóctone, ao expressar conchas transportadas do ambiente marinho ao ambiente estuarino-lagunar. Inglês: *nonindigenous*.

**Metacomunidade:** uma rede de comunidades locais interligada por dispersão. Também pode ser definida, de forma geral, como o conjunto de espécies regional.

**Metapopulação:** conjunto de populações locais interligadas por migração.

**Taphonomic bias:** distorção pós-morte da informação biológica, devido tanto a diferenças interespecies dentro de uma população que se altera no tempo e no espaço, como na durabilidade de partes moles e o transporte para fora do habitat.

***Time-averaging***: termo em inglês que significa o processo natural no qual indivíduos não contemporâneos estão em uma única camada sedimentar (fóssil) ou associação (mortos). Ocorre porque as taxas de soterramento são relativamente baixas em relação ao tempo de geração dos organismos vivos. Termo geralmente utilizado em português: mistura temporal.

**Zona tafonomicamente ativa**: é o intervalo físico abaixo, mas também incluindo a interface sedimento-água em ambiente marinho (lagunar ou fluvial) ou a interface ar-solo incluindo o último, onde ocorrem os processos de alteração da informação biológica. Inglês: *taphonomically active zone*.

**ATA Nº 665**

A comissão abaixo assinada tendo examinado a Dissertação de Mestrado do aluno **MATIAS DO NASCIMENTO RITTER**, intitulada “**TAFONOMIA DE MOLUSCOS COM ÊNFASE EM SISTEMAS ESTUARINO-LAGUNARES DA PLANÍCIE COSTEIRA DO RIO GRANDE DO SUL, BRASIL**”, atribui os seguintes conceitos:

Prof. Dr. Sérgio Martínez (Universidad de La Republica)  
**CONCEITO: “A” (EXCELENTE)**

Prof. Dr. Claudio G. de Francesco (Universidad Nacional de Mar del Plata)  
**CONCEITO: “A” (EXCELENTE)**

Profa. Dra. Carla Bender Kotzian (UFSM)  
**CONCEITO: “A” (EXCELENTE)**

Porto Alegre, de de 2013.

<b>Homologação pela Comissão de Pós-Graduação,</b>	
<b>Ata nº</b>	<b>Data:</b>
<b>Conceito Final:</b>	
<b>Rubrica:</b>	

ANEXO I
Título da Dissertação/Tese:
<b>TAFONOMIA DE MOLUSCOS COM ÊNFASE EM SISTEMAS ESTUARINO-LAGUNARES DA PLANÍCIE COSTEIRA DO RIO GRANDE DO SUL, BRASIL</b>
Área de Concentração: PALEONTOLOGIA
Autor: <b>MATIAS DO NASCIMENTO RITTER</b>
Orientador: João Carlos Coimbra
Examinador: Sergio Martinez
Data: 1-1-2014
Conceito: A- excelente
PARECER:
<p>La Disertación trata de un tema de mucho interés en la Paleontología y en las Ciencias de la Tierra en general, como lo es la Tafonomía, y en particular, la tafonomía de moluscos en sistemas estuarino-lagunares. Si bien por sus características de preservación las conchillas de moluscos son uno de los fósiles más utilizados en estos trabajos, quedan grandes campos aún prácticamente sin estudio. Uno de ellos son los ambientes estuarino-lagunares, el ambiente principal tratado en esta Disertación.</p> <p>Los objetivos de la Disertación - descripción de rasgos tafonómicos en las conchillas y evaluación de la fidelidad cuantitativa en las lagunas costeras de RS - son por lo tanto pertinentes y de sumo interés. Los resultados y conclusiones concernientes a cada objetivo han sido publicados en revistas internacionales arbitradas, lo que de por sí habla de la calidad de los trabajos realizados al haber sido sometidos a la evaluación por pares en forma rigurosa.</p> <p>En la Disertación, y lógicamente en forma más breve en los trabajos, hay una buena introducción al tema y se realiza una revisión bibliográfica completa y con sentido crítico.</p> <p>La metodología es en ambas publicaciones adecuada y rigurosa, tanto en los aspectos de muestreo, como en la descripción, clasificación de las observaciones y testeo de las hipótesis. Los métodos estadísticos y multivariados fueron empleados con buen criterio, adecuado a cada situación.</p>

Las conclusiones son originales y de suma utilidad, abarcando aspectos relativos a los sesgos de preservación, efecto de la escala, fidelidad asociación viva-muerta-fósil, entre otros, en un ambiente tan complejo como lo son las lagunas costeras de Rio Grande do Sul.

En resumen, creo que esta Disertación cumple con creces con los requisitos esperados, y los resultados de los trabajos que la componen representan un importante avance en los conocimientos tafonómicos, con proyección no solo en esta disciplina sino también en la Estratigrafía de la región y como base para futuros estudios de Paleobiología de la Conservación.

Assinatura:



Data: 1-1-2014

Ciente do Orientador:

Ciente do Aluno:

ANEXO I	
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Área de Concentração: PALEONTOLOGIA	
Autor: <b>MATIAS DO NASCIMENTO RITTER</b>	
Orientador: João Carlos Coimbra	
Examinador: Claudio Germán De Francesco	
Data: 30-12-2013	
Conceito: A-Excelente	
PARECER:	
<p>O trabalho está muito bem estruturado e apresentado, com um adequado desenho metodológico e análise dos dados. A redação é clara e apresenta uma excelente revisão bibliográfica, apropriada e atualizada. Os resultados têm sido claramente interpretados em função do marco teórico e os objetivos do trabalho. A introdução e o capítulo 1 brindam com um excelente resumo da relevância da tafonomia como disciplina e permite abordar a leitura dos demais capítulos com muito bom conhecimento dos conceitos envolvidos. Fui revisor dos dois artigos publicados (capítulos 2 e 3) e, portanto, não tenho nada novo para agregar aos comentários originalmente enviados às revistas, que já foram incorporados pelos autores nas respectivas publicações. Considero que os dois artigos têm nível internacional e são coerentes com os objetivos da tese. O capítulo 4 dá o acabamento a todo o trabalho da tese e apresenta as conclusões de forma clara e direta. Considero que o glossário é uma ferramenta acessória que facilita a leitura da tese para o pesquisador não versado em tafonomia. Acho que este trabalho de tese será uma referência obrigatória para futuros estudos de tafonomia em ambientes estuarinos. Somente tenho algumas mínimas sugestões (que são detalhadas abaixo). De qualquer maneira, considero que o trabalho deve ser APROVADO.</p>	
<div style="display: flex; justify-content: space-between;"> <div style="width: 40%;"> Assinatura:  </div> <div style="width: 40%; text-align: right;"> Data: 30-12-2013 </div> </div>	

Ciente do Orientador:

Ciente do Aluno:

### SUGESTÕES

1) Página 11, parágrafo 2: “Os processos tafonômicos são produzidos tanto por condições sedimentares (e.g. tipo de sedimento, geoquímica) e ambientais (e.g. temperatura, profundidade) quanto por fatores biológicos intrínsecos (e.g. hábito de vida, composição mineralógica da concha/osso)”

*Sugiro reescrever minimamente a parte final da oração. Os fatores biológicos podem ser também agentes tafonômicos independentemente de suas propriedades intrínsecas, por exemplo através da predação.*

2) Página 12, parágrafo 3: O artigo Tietze and De Francesco (2012) não foi realizado em ambientes estuarinos e, portanto, deveria ser eliminado aqui.

3) Página 13, Figura 1: Não entendo qual é a diferença entre os termos “Laguna” e “Lagoa” em português. Achava que o nome correto era “Lagoa dos Patos” mas vejo que na figura 1 foi referida como “Laguna dos Patos” e como “Lagoa Mirim” a outra. Agradeceria se podem checar isto aos fins de unificar critérios para todos os ambientes estudados na tese.

*Na figura 1, “Lagoa Mirim” não se lê. Faz favor, agrande o tamanho da letra.*

*Sugiro incluir no epígrafe da figura 1 uma referência à tese. Por exemplo, “Exemplos de diferentes concentrações conchíferas lagunares da Planície Costeira do Rio Grande do Sul estudadas na presente tese”.*

4) Página 14, Hipótese: Acho que a hipótese é válida mas sugiro incluir uma explicação à formulação. Você deveria incluir na hipótese a razão pela qual crê que os ambientes transicionais apresentam padrão de dano tafonômico mais semelhante ao ambiente fluvial. Em outras palavras, você deveria propor por que crê que a dissolução predomina em ambientes transicionais? Pode ser porque há dominância de água doce? Por o tipo de sedimento? hidrodinâmica? pH? etc? Acho que você tem uma ideia mas não foi expressada na hipótese.

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Área de Concentração: PALEONTOLOGIA
Autora: <b>MATIAS DO NASCIMENTO RITTER</b>
Orientadora: João Carlos Coimbra
Examinador: Carla Bender Kotzian
Data: 12.01.2014
Conceito: A - Excelente
PARECER:
A dissertação está muito boa, e os dois artigos apresentados refletem a vocação e a capacidade do aluno para atividades acadêmicas, as quais tenho acompanhado desde sua graduação. O assunto e a argumentação utilizada em ambos os artigos são complexos e mostram domínio de diversos conteúdos.
Minha principal crítica é quanto à parte pré-textual, por assim dizer. O texto, muitas vezes, é confuso, impreciso e não contém certas informações importantes, como as que seriam necessárias para a apresentação de uma hipótese de trabalho. Essas informações (sobre ambientes fluviais) só vão aparecer mais adiante, depois de a hipótese já ter sido apresentada. Também deveria ficar claro o que o autor considera como processos ambientais e biológicos. O estilo também narrativo muda em 'Estado da Arte' para indireto, onde aparecem 'objetivos' que, no meu entender, não deveriam estar neste tópico, ou melhor, não da maneira como foram apresentados.
Quanto à parte pós-textual, ou conclusões, senti falta de um parágrafo com conclusões práticas, ou seja: encontrando-se uma assembléia fóssil mais antiga, meso ou paleozóica, seria possível inferir uma região E-L pelas características tafonômicas?; ou pela composição taxonômica?
Artigo 1 - Um resultado importante não foi discutido: no afloramento 2, a presença de <i>A. purpuratus</i> , tipicamente marinha e com <i>time averaging</i> bem maior que a outra sp. datada, sugere condições ambientais e processos diferentes. No meu entender, este aspecto deveria ter sido discutido.
A discussão inicia e, portanto, dá ênfase a um assunto que não é objetivo do trabalho, qual seja, a interpretação paleoambiental da PCRS. Deveria iniciar discutindo os objetivos do trabalho. Por outro lado, parece-me que os resultados

tafonômicos obtidos não permitem fazer inferências sobre a extensão da laguna?
?Ou existe um conjunto de características indicativos de tamanho de área?
Nas conclusões, o leitor é informado de que existe uma grande abundância de spp. mixohalinas no afloramento 2. Mas esta informação não consta nos resultados. Ao contrário, parece que há mais spp marinhas ( <i>A. purpuratus</i> do que no afloramento 1).
Artigo 2
Em Material e Métodos, acho que poderia ser informado, logo no início, que a análise de fidelidade é feita exclusivamente com presença/ausência de táxons.
Também deveria ser explicado o que os autores consideram escala espacial e escala local. Escala local, em estudos ecológicos, costumam se referir a locais de amostragem e não a um conjunto de amostras, principalmente, porque se confunde com escalas de diversidade alfa e beta também usadas no trabalho.
Considero prematuro e, até certo ponto, sem sentido, justificar os resultados de fidelidade espacial e local com diversidades alfa e beta neste estudo.
Primeiramente, porque a escala local de 'amostragem' não tem a ver com escala alfa; segundo porque beta pode ser maior que alfa, e gama sempre é em vários estudos sobre diversidade de macroinvertebrados, e é muito influenciada pelo método de amostragem; e, terceiro, porque ambas, tanto fidelidade (com F1 e F2 fortemente embasadas em S) e diversidades alfa e beta são medidas diferentes, o que é particularmente verdadeiro para LAs e Das deste estudo.
Assinatura: <i>Carla Bender Kotzian</i> Data: 13 de janeiro de 2014
Ciente do Orientador:
Ciente do Aluno: