UNIVERSIDADE FEDERAL DE SANTA MARIA
CENTRO DE CIÊNCIAS NATURAIS E EXATAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BIODIVERSIDADE ANIMAL

ASSINATURAS TAFONÔMICAS E FIDELIDADE QUANTITATIVA DE MOLUSCOS DA FORMAÇÃO TOURO PASSO (PLEISTO-HOLOCENO), BRASIL

DISSERTAÇÃO DE MESTRADO

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Santa Maria, RS, Brasil
2007

ASSINATURAS TAFONÔMICAS E FIDELIDADE QUANTITATIVA DE MOLUSCOS DA FORMAÇÃO TOURO PASSO (PLEISTO-HOLOCENO), BRASIL

por

Fernando Erthal

Dissertação apresentada ao Programa de Pós-Graduação em Biodiversidade Animal, Área de Concentração em Bioecologia de Moluscos, da Universidade Federal de Santa Maria (UFSM, RS), como requisito parcial para obtenção do grau de **Mestre em Biodiversidade Animal**

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Santa Maria, RS, Brasil

2007

Universidade Federal de Santa Maria

Centro de Ciências Naturais e Exatas
Programa de Pós-Graduação em Ciências Biológicas

A Comissão Examinadora, abaixo assinada,
aprova a Dissertação de Mestrado

ASSINATURAS TAFONÔMICAS E FIDELIDADE QUANTITATIVA DE MOLUSCOS DA FORMAÇÃO TOURO PASSO (PLEISTO-HOLOCENO), BRASIL

elaborada por
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como requisito parcial para obtenção do grau de
Mestre em Biodiversidade Animal

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Dedico

À minha mãe e à minha avó Maria Paulina Erthal (*in memorian*), meus grandes exemplos de Doação.

AGRADECIMENTOS

Não quero ser injusto, mas sei que esquecerei pessoas importantes, que de uma forma ou de outra estiveram presentes durante todo meu trabalho. Dentre as que me recordo, minha mais sincera gratidão:

À professora e orientadora Carla Bender Kotzian, pela confiança em mim depositada, pela orientação, pela empatia, pelo exemplo de profissional e pessoal, pela compreensão, pela paciência e disponibilidade incondicional de tempo para meus questionamentos, mesmo os mais absurdos.

Ao colega dos moluscos Alcemar Martello por, no meu primeiro dia no Laboratório de Malacologia, ainda no final da graduação, me deixar ficar com os fósseis.

Ao professor Átila Augusto Stock da Rosa (Universidade Federal de Santa Maria), pelo empréstimo de material, bibliografia e mapas, e aos professores Sergio Martinez (Universidad de La Republica - Montevideo) e Marcello Guimarães Simões (Universidade Estadual Paulista Júlio Mesquita Filho – UNESP - Botucatu), por comentários significativos e extremamente úteis no projeto inicial desta Dissertação.

A todos meus colegas do mestrado, em especial Camila e Paloma, pelo carinho.

Ao pessoal da primeira turma do Mestrado em Biodiversidade Animal, em especial à Rafaele e Simone pelo carinho, acolhida e pelo estímulo constante.

À Leocádia Indrusiak, pelas oportunas palavras de estímulo, pela amizade e pelo onipresente cafezinho.

Aos meus pais e minha irmã, pelo apoio.

A todos meus amigos, em especial à Carol Henn, pelas palavras certas nas horas certas, à Circe Dietz, pelas palavras certas em todas as horas, e ao Anderson Fiori, pelo apoio e estímulo constante.

Ao pessoal que passou e ficou no Laboratório de Malacologia: Fernanda, Gabriela, João Henrique, Michele, Paula, Fernanda, Thamise e Vanessa, todos me ajudando a triar, medir, contar os 2.879 fragmentos de conchas maiores de 1 mm, que foram utilizados no meu trabalho.

“Não entendo. Isso é tão vasto que ultrapassa qualquer entender. Entender é sempre limitado. Mas não entender pode não ter fronteiras. Sinto que sou muito mais completa quando não entendo. Não entender, do modo como falo, é um dom. Não entender, mas não como um simples de espírito. O bom é ser inteligente e não entender. É uma bênção estranha, como ter loucura sem ser doida. É um desinteresse manso, é uma doçura de burrice. Só que de vez em quando vem a inquietação: quero entender um pouco. Não demais: mas pelo menos entender que não entendo.”

Clarice Lyspector

“...when you have eliminated the impossible, whatever remains, however improbable, must be the truth.”

Sherlock Holmes

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1. INTRODUÇÃO

1.1 Apresentação

Assinaturas tafonômicas são simplesmente danos ao material biogênico morto, como: fragmentação, desarticulação, incrustação. São facilmente quantificáveis, e muito úteis para interpretar ambientes sedimentares de deposição. No ambiente marinho o dano é mais relacionado a processos específicos atuando na interface água-sedimento, do que a tipos de ambientes e seus gradientes, principalmente devido à influência de características intrínsecas dos moluscos. No ambiente de água doce, assinaturas tafonômicas são pouco conhecidas, mas parecem ser afetadas pelos mesmos fatores que no ambiente marinho.

A fidelidade quantitativa de assembléias de moluscos representa uma importante ferramenta para maior confiabilidade de dados paleobiológicos e paleoecológicos, pois permite o acesso direto à biodiversidade antiga, contribuindo diretamente para estudos de Biologia da Conservação. Com esse propósito, são efetuadas comparações entre assembléias para acessar o potencial de preservação, para responder efetivamente: O quanto da assembléia viva (biocenose) original é preservado? Estudos com moluscos marinhos têm gerado resultados bons (acima de 85% de fidelidade). Entretanto, para ambientes de água doce, são raros os trabalhos.

A fidelidade quantitativa permite responder questões a respeito de produtividade, biomassa e estrutura de comunidades antigas, assim como ecologia de alterações antropogênicas. Porém, assembléias mortas (tanatocenoses) de moluscos raramente são utilizadas para testar o registro fóssil Quaternário (quantitativamente). Existem poucos trabalhos, embora com enfoque quase qualitativo, comparando assembléias fósseis com assembléias de moluscos atuais. Valentine *et al*. (2006) encontrou 76% de representação das espécies encontradas vivas no registro sedimentar. Alin & Cohen (2004), trabalhando com ostracodes, econtraram índices de fidelidade altos.

O Rio Touro Passo é um tributário do Rio Uruguai, localizado no extremo Oeste do Rio Grande do Sul. Drena uma bacia de aproximadamente 800 km^2, sendo um rio de 4ª ordem. Apresenta morfologia meandrante, tendendo a anastomosada, com setores retilíneos. O substrato é principalmente arenoso. Possui um regime hidrológico intermitente, com o nível de base controlado pelo rio Uruguai, e existem intervalos periódicos de seca, onde o leito é praticamente exposto.

A Formação Touro Passo é uma unidade sedimentar Pleistocênica depositada em discordância erosiva sobre a Formação Serra Geral, e foi descrita por Bombin (1976). Apresenta dois membros (Fig. 1). O membro inferior (rudáceo) é um ortoconglomerado polimíctico, onde são encontrados fósseis de mamíferos. O membro superior (lamítico) é composto de silte argiloso e areia síltico-argilosa, e são encontrados fósseis de moluscos. Um perfil da seção-tipo é apresentado na figura 1. Os moluscos da Formação Touro Passo, que compreendem 5 gêneros de bivalves e 3 de gastrópodes, correspondem taxonomicamente à fauna atual, o que permite o estudo do potencial de preservação dos moluscos do Rio Touro Passo.

1.2 Objetivos

O objetivo do presente trabalho é avaliar se o potencial de preservação das tanatocenoses de moluscos do Rio Touro Passo, no que se refere à fidelidade quantitativa e assinaturas tafonômicas (KOTZIAN & SIMÕES, 2006; MARTELLO et al. 2006), foi mantido na tafocenose da Formação Touro Passo (antigo Rio Touro Passo, Pleistoceno Superior). Dentro desse objetivo, também se pretende identificar os moluscos da Formação Touro Passo, complementando os dados previamente apresentados por Bombin, (1976), Oliveira (1989), Oliveira & Milder (1990) e Oliveira (1996).

Especificamente, pretende-se obter um escore quantitativo das assinaturas tafonômicas dos moluscos da Formação Touro Passo fornecendo, assim o primeiro perfil tafonômico para moluscos fósseis de água doce, e comparar tal escore com o obtido por Kotzian & Simões (2006) para os moluscos recentes do Rio Touro Passo. Serão, também, verificadas a abundância de espécies da Formação Touro Passo e a riqueza e a ordem de dominância das mesmas, as quais serão contrastadas com os dados obtidos por Martello et al. (2006), i.e., comparadas utilizando-se os índices de fidelidade propostas por Kidwell e Bosence (1991).

1.3 Referencial Teórico

1.3.1 Tafonomia

Tafonomia é o estudo dos processos de fossilização (ou destruição) de restos animais e vegetais, e de como esses processos incluem tendenciamentos no registro fóssil (BEHRENSMEYER et al., 2000). A tafonomia lida com aspectos como a determinação de taxas de destruição de restos mortos (e.g. HARPER, 2000; NEVES et al., 2007), compreensão dos tendenciamentos de preservação envolvidos na conversão de assembléias vivas em assembléias mortas (= assembléias fósseis em potencial) (ALIN & COHEN, 2004; LOCKWOOK & CHASTANT, 2006), definição de associações modernas de propriedades tafonômicas e suas relações com processos ambientais (i.e. tafofácies; PARSONS-HUBBARD, 2005; YESARES-GARCIA & AGUIRRE, 2004) e, especialmente, relação entre propriedades tafonômicas e contextos deposicionais (BEST et al., 2007).

Processos de destruição podem ser inferidos observando-se restos acumulados (mortos ou fósseis) com base em processos físicos e biológicos atuais (PARSONS & BRETT, 1991). Isso significa que, baseado no tipo de dano que um esqueleto (e.g., ossos, conchas) apresenta, determinam-se os processos que causaram tal injúria. Portanto, é possível interpretar, com base em informações atualísticas, como foi o ambiente onde um determinado esqueleto foi soterrado (BRETT & BAIRD, 1986; PARSONS & BRETT, 1991).

Inúmeros estudos sobre fontes de tendenciamentos como resolução temporal e fidelidade espacial e composicional têm sido realizados (BEHRENSMEYER et al., 2000; KIDWELL, 2002b; CARROL et al., 2003; KIDWELL et al., 2005). A fidelidade quantitativa de associações de moluscos tem sido muito estudada, principalmente em ambientes costeiros/plataformais (KIDWELL & BOSENCE, 1991; ZUSCHIN et al., 2000; ZUSCHIN & OLIVER, 2003; KOWALEWSKI et al., 2003). Um bom exemplo é a Província da Califórnia, onde hoje se sabe que pelo menos 76 % das espécies vivas (atuais) também ocorrem no registro fóssil (VALENTINE et al., 2006). Embora não se trate de amostragem rigorosamente quantitativa, esse estudo representa um bom modelo de perspectiva para o estudo do potencial de preservação de assembléias de moluscos atuais (ou seja, quantitativamente, “quantas espécies deixam, ou podem deixar, um registro fóssil local”?).

Mesmo com o crescente número de estudos, seguindo metodologias rigorosas (KIDWELL, 2000a; SIMÕES & GHILARDI, 2000; KOWALEWSKI et al., 2003; KOWALEWSKI & HOFFMEISTER, 2003), ainda são necessárias medidas mais confiáveis para a determinação do potencial de preservação (a probabilidade de uma espécie, gênero, assembléia etc. ser preservada em um registro sedimentar local) para diferentes tipos de organismos e ambientes, mais especificamente para análises de assembléias Plio-Pleistocênicas, com táxons análogos modernos (i.e., Fidelidade Vivo/Fóssil). Scholz e Hartman (2007) conduziram estudo com esse tipo de objetivo, considerando dados de presença/ausência de moluscos em uma unidade sedimentar cretácea, atribuindo analogias entre os moluscos fósseis cretáceos e espécies atuais, estabelecendo equivalentes ecológicos.

1.3.2 Assinaturas tafonômicas de moluscos

Os variáveis tipos de dano às conchas constituem o que se chama de assinaturas tafonômicas (BRETT & BAIRD, 1986; DAVIES et al., 1989; PARSONS & BRETT, 1991; KIDWELL et al., 2001). As características mais comuns utilizadas como assinaturas tafonômicas (em moluscos) são: orientação, seleção por tamanho, desarticulação, fragmentação, abrasão, corrosão (estes dois últimos não são distinguíveis a olho nu ou estereomicroscópio, sendo necessária a utilização de microscópio eletrônico para tanto), bioerosão, incrustação (mais comum em ambiente marinho raso), arredondamento de margem e degradação de superfície. Cada assinatura em particular pode ter uma origem própria, dependendo do contexto deposicional (Tabela 1; PARSONS & BRETT, 1991). Entretanto, sabe-se que, enquanto no ambiente marinho a incrustação e bioerosão (modificações biogênicas) costumam predominar (BEST & KIDWELL, 2000a,b), em ambiente de água doce alterações químicas (principalmente dissolução) são majoritárias (PIP, 1987; BROWN et al., 2005; KOTZIAN & SIMÕES, 2006; NEWELL et al., 2007).

Cabe lembrar que as decisões metodológicas na análise tafonômica quantitativa são importantes fatores que influenciam os resultados. Frações de tamanho pequenas (menor que 4 mm) podem resultar em um perfil de dano quantitativamente mais baixo que o real. Por exemplo, incrustação certamente será menos freqüente em exemplares pequenos (KIDWELL et al., 2001; KOWALEWSKI & HOFFMEISTER, 2003). É necessária a inclusão dos fragmentos na análise para a obtenção de resultados mais confiáveis (KIDWELL et al., 2001). De fato, Lockwood e Chastant (2006), verificando os padrões de danos em conchas da baía de Chesapeake (nordeste dos Estados Unidos), encontraram maiores freqüências de incrustação em exemplares de tamanho maior (i.e., incrustação mais freqüênte em exemplares maiores de 2 mm que em exemplares menores de 2 mm).

De acordo com o estudo de Best e Kidwell (2000b), a origem das assinaturas pode ser relacionada a fatores intrínsecos aos moluscos, como mineralogia e microestrutura da concha, modo de vida (epifauna ou infauna; vida livre ou fixos; bissados/cimentados) e a fatores extrínsecos (controlados pelo ambiente) como química e granulometria do substrato, energia da água, tempo decorrido entre a morte e o soterramento. Os padrões de incrustação, perfuração biológica, fragmentação e alteração geral de superfície também variam conforme o tipo de concha (alto conteúdo orgânico; calcítica ou aragonítica) e a espessura da concha, em ambientes siliciclásticos/carbonáticos tropicais (BEST & KIDWELL, 2000b). A origem em vida de certos atributos tafonômicos, como incrustação, abrasão de umbo (em moluscos de água doce; KOTZIAN & SIMÕES, 2006) também tornam a análise de assinaturas tafonômicas um estudo complexo. Uma estratégia para evitar esse tipo de tendenciamento é efetuar a análise dos atributos do interior das conchas, uma área não suscetível a modificações em vida, como a área externa à linha palial (BEST & KIDWELL, 2000a).

Os processos que modificam o material conchífero, deixando uma impressão tafonômica geral, podem ser usados para interpretar paleoambinentes onde os indivíduos viveram ou algum fator ecológico antigo, já que há variação significativa entre séries de ambientes (BRETT & BAIRD, 1986). Davies e colaboradores (1989), utilizando material conchífero proveniente de testemunhos de sondagem na costa do Texas (Estados Unidos), produziram um perfil de dano tafonômico relacionado ao ambiente deposicional. Nesse local, foi sugerido que assinaturas como abrasão, dissolução, fragmentação e arredondamento da margem estariam associadas ao habitat de origem, enquanto que freqüências de tamanho e orientação da concha indicariam processos de deposição (DAVIES et al., 1989). Adicionalmente, esses autores argumentaram que a análise tafonômica em fragmentos é mais eficiente, por estes permanecerem mais tempo na Zona Tafonomicamente Ativa (DAVIES et al., 1989; veja também PARSONS & BRETT, 1991).

Nessa mesma linha, estudos visando à determinação de tafofacies (facies sedimentares que possuem atributos tafonômicos em conchas com origens similares) são comuns. Yesares-Garcia e Aguirre (2004), trabalhando em depósitos de plataforma do Plioceno do Sudeste da Espanha argumentaram que quanto maior o número de atributos tafonômicos utilizados, melhor é a resolução em análises de agrupamento (*cluster analyses*) e, portanto, melhor a resolução da análise paleoambiental envolvida. Parsons-Hubbard (2005) utilizou conchas coletadas em superfície nas Ilhas Virgens (Estados Unidos) e na Ilha de Mona (Porto Rico), e testemunhos de sondagens em recifes próximos à Ilha Buck (Porto Rico). Foram produzidas ordenações de ambientes de deposição com base nos atributos tafonômicos das respectivas conchas (seguindo um protocolo tafonômico quantitativo rigoroso), as quais demonstraram que a assinatura tafonômica composta é um indicador confiável do ambiente de deposição (PARSONS-HUBBARD, 2005).

Best e Kidwell (2000a), considerando cinco ambientes com base na granulometria, determinaram que: A) a fragmentação não depende de profundidade, energia da água ou espessura da concha, sendo sua origem possivelmente biogênica; e B) a incrustação e a perfuração biogênica são proporcionais à disponibilidade de substrato duro, assim como o arredondamento de margem e a alteração de fina escala (veja Tabela 1). O perfil de dano às conchas é basicamente diferente entre substrato duro e substrato lamoso. Além disso, é sugerida a análise de assinaturas tafonômicas na superfície interna da concha, apenas onde o dano é exclusivamente post-mortem (i.e., na área externa à linha palial). A análise de outras regiões da concha possuiriam efeitos apenas quantitativos (i.e. aditivos) no perfil de dano então obtido (BEST & KIDWELL, 2000a).

Em estudo realizado em três ambientes sedimentares (siliciclástico, carbonático e misto), no arquipélago de San Blas, no Panamá, Kidwell e colaboradores (2005) e Best e colaboradores (2007) verificaram que, considerando o estado tafonômico das conchas de moluscos, os maiores graus de dano às conchas ocorrem em ambientes predominantemente carbonáticos, enquanto que a variação de idade é muito maior (2-3 ordens de magnitude) em ambientes siliciclásticos. As conchas mais antigas tendem a estar bem preservadas em siliciclastos, e as conchas relativamente recentes são pobremente preservadas em sedimentos carbonáticos (KIDWELL et al., 2005). Isso significa que as conchas de sedimentos carbonáticos possuem menor potencial de preservação (menor fidelidade composicional), ao mesmo tempo em que, nos sedimentos siliciclásticos, a resolução temporal (veja CARROL et al., 2003) é muito menor, devido ao menor dano tafonômico (BEST et al., 2007).

Em análise de assinaturas tafonômicas de moluscos da baía de Chesapeake (Nordeste dos Estados Unidos), Lockwook e Work (2006) avaliaram o efeito de atributos intrínsecos (modo de vida, mineralogia e conteúdo orgânico da concha) das conchas no perfil de dano, de maneira similar a Best e Kidwell (2000b). Organismos da epifauna, com mineralogia calcítica e alto conteúdo orgânico, apresentaram maior freqüência de incrustação e fragmentação, enquanto que organismos da infauna, de mineralogia não calcítica e baixo conteúdo orgânico, estavam mais sujeitos aos danos de origem química, tal como alteração de fina escala e perda de perióstraco (LOCKWOOD & WORK, 2006). Essas observações são notadamente diferentes do que foi observado por Best e Kidwell (2000b), que argumentam que a natureza do suprimento de conchas modula a intensidade do dano, não o seu padrão fundamental.

Considerando a ampla variedade de ambientes deposicionais existentes e que o tipo de assinatura tafonômica impressa nas conchas de moluscos pode variar conforme o ambiente, e ainda que a grande quantidade de informação disponível, no que tange a ambientes marinhos, as assinaturas tafonômicas de moluscos de água doce são pobremente conhecidas. Os estudos existentes apresentam resultados não quantitativos (presença/ausência), como os trabalhos de Hanley e Flores (1987) para moluscos do Eoceno/EUA, onde o tipo de sedimentação foi interpretado com base em características tafonômicas gerais; de Good (1987) para moluscos do intervalo Cretáceo-Eoceno/EUA, com interpretação de agrupamentos de espécies; e de Martinez e Rojas (2004), que revisaram a riqueza de moluscos pleistocênicos do Noroeste do Uruguai. Embora tenham tido o objetivo de determinar a distribuição de moluscos em uma planície de inundação moderna (Rio Lech, norte da Áustria), Briggs e colaboradores (1990) encontraram padrões de fragmentação que variam conforme a espécie. Entretanto, essa fragmentação foi interpretada como tendo origem biogênica (predação).

Em análise de assinaturas tafonômicas relacionadas á áreas contaminadas por mercúrio (Virginia, Estados Unidos), Brown e colaboradores (2005) verificaram que os maiores índices de danos (baseado em assinaturas tafonômicas quantitativas) estavam diretamente relacionados ao grau de contaminação por mercúrio. À medida que aumentava a distância do ponto de contaminação, diminuía o escore tafonômico das conchas dos moluscos (BROWN et al., 2005). Nesse estudo foi mostrada a utilidade das assinaturas tafonômicas para prognósticos de extinção de espécies.

Newell e colaboradores (2007), com o objetivo de determinar os mecanismos de fragmentação no bivalve *Unio* sp. (mexilhão de água doce) no Rio Sakmara (fronteira Rússia-Casaquistão) encontraram resultados particulares. Em mais de 1000 exemplares analisados, a abrasão foi o dano mais comum. Além disso, foi sugerido que a fragmentação das conchas seria resultado da abrasão exagerada, e a maior freqüência de perfurações (conseqüente de abrasão física) foi encontrada nas regiões naturalmente mais finas da concha (NEWELL et al., 2007). Portanto, para ambientes de água doce de energia variável, a fragmentação não, necessariamente, significa transporte.

Em análise paleoambiental de moluscos unionóides do Cretáceo Superior em Montana, Estados Unidos, Scholz e Hartman (2007) definiram três tipos de depósitos, cujas conchas de moluscos apresentam aspectos tafonômicos distintos: A) depósito de transbordamento: 80% de desarticulação, pouca abrasão, ausência de seleção de tamanho ou orientação preferencial; B) depósito de canal: desarticulação e fragmentação muito alta, próximas de 100%, conchas muito abradidas ou foliadas, preservadas na base do preenchimento do canal e; C) depósito lacustre: alta desarticulação, baixa fragmentação, abrasão moderada, conchas geralmente foliadas, muito dispersas (SCHOLZ &HARTMAN, 2007). No entanto, não foi estabelecido um protocolo de assinaturas rigoroso, com escalas quantitativas (veja PARSONS-HUBBARD, 2005).

No Rio Touro Passo (Sul do Brasil), Kotzian e Simões (2006), utilizando assembléias mortas de moluscos para análise de assinaturas tafonômicas, determinaram que a condição ácida da água (pH 5,5 a 6,4) pudesse ser responsável por grande parte dos danos às conchas. Além disso, de modo geral, os moluscos de setor retilíneo (mais energético) apresentaram maior freqüência de características como alteração (erosão) de extremidades (ápice e umbo) e perda parcial de perióstraco. No entanto, conforme os autores constataram, o retrabalhamento (mistura) de conchas fósseis ocorrentes em alguns locais e a complexa origem das assinaturas observadas no Rio Touro Passo, indicam que as interpretações paleoambientais de depósitos de águas continentais são análises bastante incompletas, sendo necessárias observações sedimentológicas e estratigráficas.

Além disso, e apesar da bem conhecida ação da mistura temporal em meio marinho (veja CARROL et al., 2003), para ambientes de água doce são raras as informações sobre mistura temporal de assembléias conchíferas. Um bom exemplo é fornecido por Alin e Cohen (2004), no qual assembléias sub-fósseis de ostracodes do Lago Tanganyika (leste da África, em território tanzaniano) foram datadas, alcançando mais de 300 anos. Para moluscos de água doce, a mistura temporal pode variar de 287 a 57.530 anos, de acordo com dados obtidos com moluscos do Rio Touro Passo, sul do Brasil (SIMÕES et al., 2007). Em assembléias de gastrópodes terrestres de depósitos quaternários das Ilhas Canárias, Yanes e Kowalewski (2007) também encontraram uma sensível variação temporal, alcançando cerca de 6.000 anos variacão.

Não foi encontrado nenhum trabalho de potencial de preservação no que concerne à assinaturas tafonômicas de tafocenoses, em comparação a tanatocenoses, para moluscos de água doce.

1.3.3 Fidelidade quantitativa de moluscos

Fidelidade quantitativa, de acordo com Kidwell e Bosence (1991) e Behrensmeyer et al. (2000), é a semelhança quantitativa entre uma comunidade viva (biocenose) e a sua assembléia morta potencial (tanatocenose) correspondente. Mais precisamente, é a fidelidade quantitativa do registro de formas, classes de idades, riqueza em espécies, abundância de espécies etc., aos sinais biológicos originais (BEHRENSMEYER et al., 2000). Uma boa forma de padronizar esse tipo de medida é através dos assim chamados índices de fidelidade", originalmente propostos por Kidwell e Bosence (1991), que são: (a) F1, percentual de espécies encontradas vivas que também são encontradas mortas no mesmo local (fidelidade vivo/morto) [(nº de espécies encontradas tanto vivas quanto mortas x 100)/(nº total de espécies encontradas vivas)]; (b) F2, percentual de espécies encontradas mortas que também são encontradas vivas (fidelidade morto/vivo) [(nº de espécies encontradas tanto vivas quanto mortas x 100)/(nº total de espécies encontradas mortas)] e; (c) F3, percentual de indivíduos da assembléia morta que são de espécies encontradas vivas [(nº de indivíduos das espécies tanto vivas quanto mortas x 100)/(nº total de indivíduos da assembléia morta)].

Os moluscos, especialmente os bivalves (KOWALEWSKI et al., 2003), são um dos táxons mais estudados no que se refere à fidelidade quantitativa. Trabalhos de revisão mostram uma forte concordância entre assembléias vivas e mortas de moluscos marinhos, com a maioria (80-95%) dos indivíduos mortos pertencendo a espécies documentadas vivas no mesmo lugar (KIDWELL & BOSENCE, 1991; KIDWELL & FLESSA, 1996; KIDWELL, 2001). Comparando a ordem de dominância de espécies de assembléias vivas e mortas, no meio marinho, também são encontradas altas percentagens (cerca de 92%) de correlação na ordem de dominância (KIDWELL, 2001).

É importante enfatizar que grande parte das diferenças entre estudos, nos resultados de fidelidade quantitativa, é gerada por métodos de amostragem diferentes. Por exemplo, em uma meta-análise de 45 estudos de fidelidade vivo-morto (num total de 85 bases de dados de habitats) de moluscos marinhos, Kidwell (2002a) verificou que à medida que o tamanho da malha de peneira aumenta, também aumenta a significância da comparação vivo-morto (Tabela 3). Bases de dados com mais de 100 indivíduos vivos produzem índices de fidelidade mais altos (Tabela 3). Outro fator importante é o tipo de amostragem da assembléia viva: amostragens longas (20 anos), multi-estação, ou de várias áreas de pequena escala tendem a gerar índices de fidelidade maiores (KIDWELL, 2002a; porém veja LOCKWOOD & CHASTANT, 2006 para resultados diferentes). Kowalewski e colaboradores (2003) encontraram índices razoáveis de fidelidade composicional em assembléias mistas moluscos-braquiópodes (F1 = 77,2% e F2 = 69,8%) considerando gêneros, com todas as frações de tamanho, e incluindo fragmentos.

Todavia, há poucos dados no que diz respeito à fidelidade quantitativa de moluscos de água doce. Cummins (1994), em reservatórios e rios no estado de Ohio/EUA, registrou índices de fidelidade altos, e comparáveis aos obtidos em estudos conduzidos em meio marinho: F1 = 94% (dados agrupados, variação de 50 a 100% entre diferentes locais); F2 = 60% (variação de 40 a 100% entre locais); F3 = 80% (variação de 58 a 100% entre locais) (Tabela 4). Martello et al. (2006) encontraram, no Rio Touro Passo, Rio Grande do Sul, Brasil, valores mais baixos de fidelidade: F1 = 60% (60% para o setor retilíneo e 66,6% para o setor meandrante); F2 = 47,3% (30% para o setor retilíneo e 61,5% para o setor meandrante); e F3 = 72,3% (67,7% para o setor retilíneo e 86,9% para o setor meandrante).

Informaçãoções sobre fidelidade quantitativa de assembléias fósseis (tafocenoses) também são escassas. Na ilha de San Nicolas, costa da Califórnia, Russel (1991) encontrou baixos índices de correspondência entre assembléias mortas e fósseis (pleistocênicas) de moluscos: 57,35% das espécies mortas também foram encontradas no registro fóssil, quase 61% das espécies fósseis também foram encontradas nas tanatocenoses, sendo que 85% dos indivíduos encontrados fósseis foram de espécies encontradas nas assembléias mortas. Comparando os moluscos marinhos atuais da Província da Califórnia com os moluscos de afloramentos do Pleistoceno da Califórnia, Valentine (1989) encontrou fidelidade vivo/fóssil relativamente alta (aproximadamente 77% das espécies fossilizadas também foram registradas vivas). Cabe ressaltar, que este último estudo baseia-se em um conhecimento da fauna atual (viva) de mais de um século, não sendo baseado, portanto, em coletas e amostragens utilizando a metodologia sugerida em estudos mais modernos (veja KIDWELL & BOSENCE, 1991; KIDWELL 2002a).

Quanto ao potencial de preservação de assembléias vivas e mortas em relação aos moluscos fósseis de água doce, não há informações na literatura. Para ostracodes, Alin e Cohen (2004) observaram que 89% das espécies vivas também são encontradas mortas; 66% das espécies mortas também são encontradas vivas, e 90% das espécies fósseis (subfósseis) são encontradas mortas.

1.3.4 Biologia da Conservação e Potencial Fossilífero

A confiabilidade de assembléias mortas acumuladas naturalmente, em relação às biocenoses, é importante do ponto de vista ecológico, onde são necessárias perspectivas temporais longas na composição de comunidades para a discriminação de fatores naturais e antropogênicos na mudança de ecossistemas (KIDWELL, 2001). O registro fóssil (principalmente do Pleistoceno e Holoceno) é, portanto, indispensável e pode servir para demonstrar efeitos deletérios da invasão de espécies alienígenas, como modificações induzidas por alterações em fluxos de rios (KOWALEWSKI et al., 2000) e extinção local de espécies de moluscos de água doce por contaminantes como o mercúrio (BROWN et al., 2005).

Os moluscos, principalmente os bivalves, por serem organismos filtradores, registram as alterações químicas ambientais com grande confiabilidade (MARKICH et al., 2002; BROWN et al., 2005), e, havendo um registro sedimentar correlacionado, pode-se facilmente acessar a história de alterações sofridas por malacofaunas atuais. Dado o grande impacto de espécies invasoras de moluscos de água doce, principalmente *Corbicula fluminea* (MANSUR & GARCES, 1988), espécies da malacofauna nativa podem estar sendo eliminadas sem mesmo terem sido noticiadas (DARRIGRAN, 2002), e a tafonomia de moluscos pode auxiliar na quantificação de impactos aos ecossistemas naturais (KOWALEWSKI et al., 2000; BROWN et al., 2005).

1.4 Área de Estudo

1.4.1 O Rio Touro Passo

O Rio Touro Passo é um tributário do Rio Uruguai, situado no oeste do estado do Rio Grande do Sul, e representa um bom lugar para a realização de estudos quali e quantitativos de: A) assinaturas tafonômicas de moluscos de água doce (KOTZIAN & SIMÕES, 2006), B) fidelidade quantitativa de assembléias vivas e mortas de moluscos (MARTELLO et al., 2006) e C) potencial de preservação (em termos de assinaturas tafonômicas e fidelidade quantitativa) das assembléias de moluscos atuais. O Rio Touro Passo possui um regime hidrológico intermitente, controlado pelo nível de base do Rio Uruguai. Existem intervalos periódicos de seca, quando o leito do rio é exposto (pelo menos parcialmente; BOMBIN, 1976), o que permite uma boa amostragem das biocenoses e tanatocenoses de moluscos. Enchentes também são freqüentes, como conseqüência de enchentes do Rio Uruguai, ou chuvas torrenciais, que são comuns na região, e também devido à baixa capacidade de retenção hidrológica do sistema como um todo (BOMBIN, 1976). O curso do Rio Touro Passo possui morfologias variadas, predominantemente meandrantes ou retilíneas, mas com setores tendendo a anastomosados (BOMBIN, 1976). As margens são predominantemente dominadas por vegatação ripária, e o substrato é basicamente arenoso (BOMBIN, 1976; MARTELLO et al., 2006).

A identidade dos moluscos do Rio Touro Passo é relativamente bem conhecida (BOMBIN, 1976; OLIVEIRA, 1989; OLIVEIRA & MILDER, 1990; KOTZIAN & SIMÕES, 2006; MARTELLO et al., 2006), tendo sido apontados gêneros de bivalves como *Anodontites* Bruguière 1792, *Cyanocyclas* Blainville 1811, *Castalia* Lamark 1819, *Eupera* Bourguignat 1854, *Diplodon* Spix 1827, *Leila* Gray 1840, *Monocondylaea* Orbigny 1835, *Mycetopoda* Orbigny 1835, *Pisidium* Pfeiffer 1821 e o gênero invasor *Corbicula* Megerle 1811; e de gastrópodes como *Biomphalaria* Preston 1910, *Gundlachia* Pfeiffer 1849, *Heleobia* Stimpson 1865, *Pomacea* Lamark 1819 e *Potamolithus* Pilsbry & Rush 1896.

As margens do Rio Touro Passo exibem afloramentos da Formação homônima, a Formação Touro Passo (Pleistoceno-Holoceno) onde foram registrados 11 táxons de moluscos (BOMBIN, 1976; OLIVEIRA & MILDER, 1990; OLIVEIRA, 1996). A presença de tal malacofauna, que corresponde claramente (em termos taxonômicos) aos moluscos modernos encontrados no Rio Touro Passo (KOTZIAN & SIMÕS, 2006; MARTELLO et al., 2006) permite a testar o potencial de preservação da tanatocenose do rio.

1.4.2 A Formação Touro Passo

A Formação Touro Passo é uma unidade sedimentar correlacionável em idade com a Formação Sopas (Norte do Uruguai) e com a Formação Luján (Argentina); (BOMBIN, 1976; MARTINEZ & ROJAS, 2004; UBILLA et al., 2004). Os afloramentos aparecem a partir de aproximadamente 35 km de distância da foz do Rio Touro Passo, e apresentam depósitos originados na antiga planície de inundação do mesmo. A unidade encontra-se depositada em discordância erosiva sobre a Formação Serra Geral (Jurássico-Cretáceo), e apresenta dois membros com litologias distintas (BOMBIN, 1976). O membro inferior, rudáceo, é um ortoconglomerado polimíctico, que ocasionalmente apresenta cimentação calcárea (BOMBIN, 1976), e possui fósseis retrabalhados de mamíferos da megafauna pleistocênica. O membro superior, lamítico, possui maior possança, é basicamente composto por silte argiloso, e areia síltica ou areia síltica-argilosa, apresentando subfósseis de moluscos, assim como material arqueológico (BOMBIN, 1976).

Os fósseis de moluscos (assim como também de vertebrados) ocorrem no membro lamítico. As camadas fossilíferas apresentam pequena espessura, não ultrapassando 20 cm, e também não são extensas lateralmente (BOMBIN, 1976), uma característica também observada em unidades coevas, como a Formação Sopas (MARTINEZ & ROJAS, 2004). Nos afloramentos mais acessíveis, os fósseis de moluscos estão dispersos de modo caótico, podendo-se classificar tais camadas como de empacotamento disperso (segundo classificação proposta por KIDWELL, 1991). Raros bivalves soterrados em posição de vida também são encontrados (BOMBIN, 1976).

Levantamentos da malacofauna fóssil indicam a existência de bivalves dos gêneros *Anodontites*, *Leila*, *Diplodon* e *Cyanocyclas*, e de gastrópodes *Gundlachia*, *Heleobia* e *Potamolithus* (BOMBIN, 1976; OLIVEIRA, 1989; OLIVEIRA & MILDER, 1990; OLIVEIRA, 1996). Datações com ^{14}C (em dois exemplares de *Diplodon delodontus wymani* Lea 1860) geraram idades entre 18.570 anos A.P. e 20.690 A.P. (KOTZIAN et al., 2005). Resultados preliminares de um estudo utilizando datação por Ressonância de Spin Eletrônico mostraram uma variação de idade entre 692 e 25.059 anos nas conchas de um afloramento. Porém conchas retrabalhadas encontradas no leito do rio, atingiram idades entre 287 e 57.530 anos A.P. (SIMÕES et al., 2007).

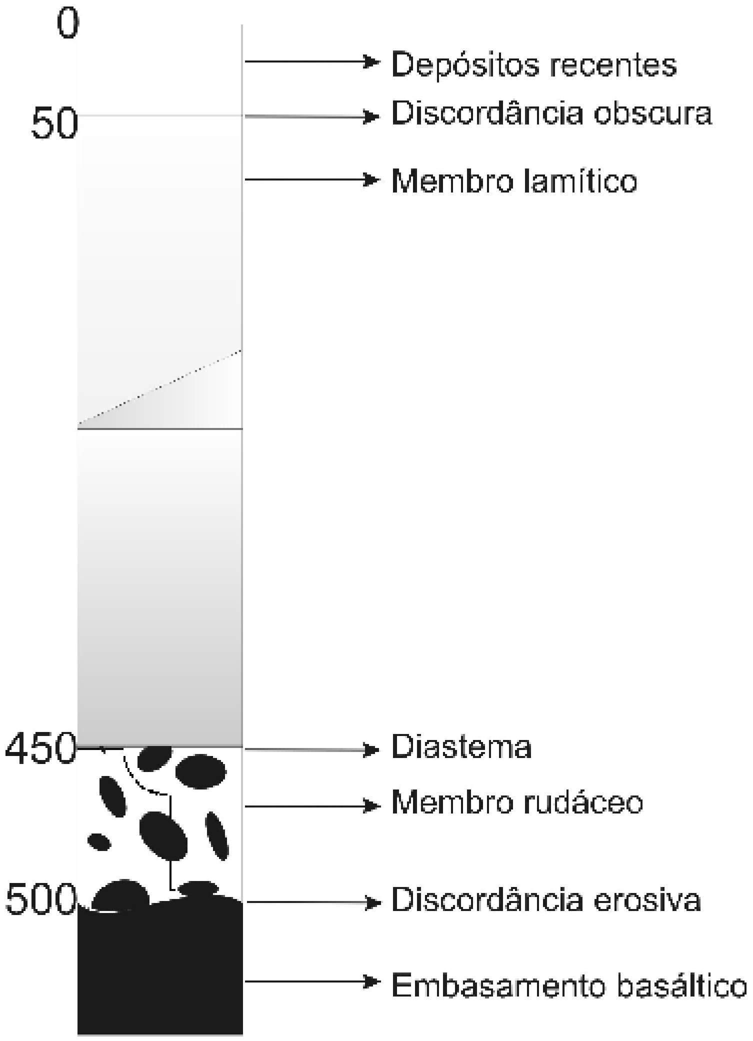

Figura 1 - Perfil estratigráfico da seção-tipo da Formação Touro Passo (Pleistoceno-Holoceno), modificado de Bombin (1976).

Tabela 1 - Principais características tafonômicas e suas interpretações gerais com relação a processos de origem (modificado de PARSONS & BRETT, 1991; KIDWELL & BOSENCE, 1991).

Assinatura	Interpretação
Fragmentação	Indica alta energia ambiental, transporte, ou ainda quebra biogênica originada por bioturbadores e/ou predadores (Best e Kidwell, 2000a). Pode indicar compactação após o soterramento final; pode ser conseqüência de abrasão extensiva (NEWELL et al., 2007).
Desarticulação	Presença de articulação indica soterramento rápido; do contrário, pode indicar retrabalhamento, bioturbação. Freqüentemente possui origem coordenada com a fragmentação. Perda de tecidos conectivos orgânicos por decomposição microbiana.
Corrasion	Termo que une a definição de corrosão (origem química) e abrasão (origem mecânica) de superfície, já que ambas não podem ser distinguidas sem auxílio de Microscópio Eletrônico (BRETT & BAIRD, 1986). Significa alta energia ambiental, combinada ou não com sedimento de mineralogia grosseira (areia). Uma definição mais apropriada seria alteração de fina-escala (*FSA alteration*) de superfície, que pode possuir origem combinada (biogênica e abiótica; BEST & KIDWELL, 2000a).
Dissolução	É mais um processo que assinatura, mas normalmente a dissolução deixa as conchas com aspecto gredoso (*chalky*), facilmente identificável. A dissolução é produzida em ambientes (ou microambientes) insaturados com relação ao mineral constituinte do esqueleto/concha, muitas vezes promovida por água percolante (CAI et al., 2006).
Arredondamento da margem	Provável combinação de corrasão e dissolução, o arredondamento de margem fragmentada fornece uma estimativa de tempo desde a quebra.
Incrustação	É um fenômeno muito comum em ambiente marinho raso. Qualquer superfície relativamente estática é suscetível à acomodação de uma variedade de organismos epifaunísticos.
Seleção de tamanho	É um indicador confiável da capacidade de fluxo em sistemas aquáticos, já que depois da morte o indivíduo se comporta como uma partícula sedimentar. Também pode indicar perda seletiva de diferentes estágios ontogenéticos, introduzindo tendenciamentos.

Tabela 2 – Exemplos de percentagens obtidas em estudos de revisão ou de áreas particulares sobre fidelidade quantitativa em assembléias vivas, mortas e fósseis (V, M e F, respectivamente), em vários ambientes marinhos transicionais e plataformais.

Ambiente	Assembléia	F1	F2	F3	Referência
Vários ambientes na região da costa da Califórnia (EUA)	V/F	77	-	-	Valentine (1989)
Intertidal	V/M	83	54	90	Kidwell & Bosence (1991)
Costeiro subtidal	V/M	95	33	89	Kidwell & Bosence (1991)
Mar aberto	V/M	84	45	70	Kidwell & Bosence (1991)
Subtidal	M/F	57	60	85	Russel (1991)
Baía, subtidal, substrato duro	V/M	68	62	78	Zuschin et al. (2000)
Subtidal, substrato duro	V/M	85	94	94	Zuschin & Oliver (2003)
Onshore-offshore	V/M	62	64	-	Kowalewski et al., (2003)
Baía, subtidal	V/M	77	71	99	Lockwood & Chastant (2006)

Tabela 3 – Porcentagens de fidelidade quantitativa para dados agrupados (± Intervalo de Confiança de 95%), em relação ao tamanho de malha e tamanho da amostragem da comunidade viva, referente à meta-análise de Kidwell (2002a). São mostrados apenas os dados agrupados. Números entre colchetes referem-se à quantidade de bases de dados utilizadas (compilado de KIDWELL, 2002a).

Bases de dados	F1	F2
a) Total	88 ± 6 [85]	73 ± 3 [85]
Malha ≤ 1 mm	83 ± 9 [43]	67 ± 5 [43]
Malha ≥1,5 mm	94 ± 8 [42]	76 ± 4 [42]
b) Bases com mais de 100 indivíduos vivos (total)	88 ± 6 [62]	76 ± 3 [62]
Malha ≤ 1 mm	84 ± 9 [38]	68 ± 6 [38]
Malha ≥ 1,5 mm	93 ± 9 [24]	81 ± 5 [24]

Tabela 4 – Exemplos de estudos de fidelidade quantitativa de assembléias vivas, mortas e fósseis (V, M, F respectivamente) em ambiente fluvial-lacustre.

Ambiente	Assembléia	F1	F2	F3	Referência
Rio meandrante-retilíneo	V/M	100	50	78	Warren (1991)
Represas	V/M	83	70	93	Cummins (1994)
Rio meandrante	V/M	91	55	76	Cummins (1994)
Lacustre	V/M	89	66	94	Alin & Cohen (2004)
Lacustre	M/F	83	90	-	Alin & Cohen (2004)
Lacustre	V/F	89	71	-	Alin & Cohen (2004)
Rio meandrante/retilíneo	V/M	60	47	72	Martello et al. (2006)

2. ARTIGO I: QUANTITATIVE FIDELITY OF MOLLUSKS FROM THE TOURO PASSO FORMATION (PLEISTOCENE-HOLOCENE), SOUTHERN BRAZIL: GAINING AND LOSING DATA ON THE BIODIVERSITY OF THE PRESENT DAY FRESHWATER MOLLUSCAN ASSEMBLAGES

QUANTITATIVE FIDELITY OF MOLLUSKS FROM THE TOURO PASSO FORMATION (PLEISTOCENE-HOLOCENE), SOUTHERN BRAZIL: GAINING AND LOSING DATA ON THE BIODIVERSITY OF THE PRESENT DAY FRESHWATER MOLLUSCAN ASSEMBLAGES

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RRH: QUANTITATIVE FIDELITY OF FRESHWATER FOSSIL MOLLUSCAN ASSEMBLAGES
LRH: ERTHAL AND KOTZIAN
Keywords: taphonomy, preservation potential, live assemblages, dead assemblages.

ABSTRACT

This study shows the first ~~rigorous~~ quantitative assessment on the fidelity of mollusk fossil assemblages. Additionally, it also shows that the sedimentary record can provide more than simply answers to fidelity questions. Rather, information on the original, i.e., non human-impacted, freshwater malacofauna biodiversity can be rescued based on Pleistocene shells. The freshwater molluscan taphocoenosis from the Touro Passo Formation (Pleistocene-Holocene) was compared to live and dead assemblages of the Touro Passo River, Southern Brazil. Contrary to the expected results, the fossil assemblage showed poor resemblance to the live/dead species composition. About 45% of the species of the biocoenoses and 58% of the species of the tanatocoenoses were also found fossilized. Although 72% of the fossil specimens were from species also found dead, only 11% belong to species found alive. No correlation was observed, concerning the rank order of the dominant species, between the fossil and the present day assemblages. The former was dominated by two species, the declining bivalve *Cyanocyclas limosa* and the gastropod *Heleobia* aff. *bertoniana*, both rare in biocoenoses and only found in dead assemblages. The modern literature suggest that the invasion of freshwater environments by exotic molluscan species, as well as other contemporary environmental problems, rather than taphonomic processes, are the main factors

avoiding to acquire satisfactory results on the fidelity of the fossil assemblages. Hence, the Pleistocene-Holocene mollusks from the Touro Passo Formation should reflect the original biodiversity of the Touro Passo River, prior to the river alterations caused by human activities.

INTRODUCTION

The efforts to produce paleontological studies adopting quantitative and standardized methods (e.g., Kidwell, 2002a) have revealed itself very useful. Many lines of taphonomic investigation are yielding quantitative data, conferring the desirable and expected more reliable and “scientific” trait to Paleontology (Beherensmeyer et al., 2000). Quantitative fidelity, defined by Behrensmeyer et al. (2000) as the “quantitative faithfulness of the record of morphs, age classes, species richness, species abundances, trophic structure etc. to the original biological signal”, is one of the approaches that have provided some valuable information. Thanks to such kind of study, questions as “how much of the original biocoenoses was lost during their transference to the lithosphere?” or “to what reliability degree is it possible to interpret and old assemblage?” are now being understood. Quantitative fidelity is also yielding important and useful data for evolutionary and Conservation Biology purposes (e.g. Kowalewski et al., 2000; Brown et al., 2005; Valentine et al., 2006)

The fossil record is mostly constituted by fossilized dead assemblages (Brett and Baird, 1986; Kidwell and Bosence, 1991; Flessa and Kowalewski, 1994; Kidwell and Flessa, 1996). Thus, most studies on quantitative fidelity deals with comparisons between live and dead assemblages, in order to assess, in numbers, the preservation potential of the former, i.e., how much of the original biocoenoses is preserved in the fossil record. The majority of the live/dead analyzes have been conducted with marine bivalves, proceeding of a wide range of depositional settings (see revisions in Kidwell and Bosence, 1991 and Kidwell and Flessa 1995; see also Zuschin et al., 2000 and Zuschin and Oliver, 2003 for hard substrata). In general, these studies show reasonable high values of live/dead fidelity, ca. 88% for live species also found dead, at large scale (pooled data) approaches (e.g., Kidwell, 2002a; Lockwood and Chastant, 2006). For freshwater environments the data are scarce and controversial. For rivers, Cummins (1994) found relatively high percentages regarding live species also found dead (94%), but Martello et al. (2006) assigned poor results (60%). Anyway, the dominant species’ rank order is generally maintained in both marine and freshwater environments, when large scale analyzes are adopted (Kidwell and Bosence, 1991; Cummins, 1994; Kidwell, 2002b; Martello et al., 2006).

In spite of the numerous studies on the quantitative fidelity of tanatocoenoses, their data are rarely used for comparing or testing the Quaternary fossiliferous record (taphocoenoses), using similar quantitative approaches. Certainly, many molluscan marine dead assemblages contain Pleistocene shells (Kowalewski, 1996; Best and Kidwell, 2000a; Carrol et al., 2003; Kidwell et al., 2005). However, the time averaging detected in marine shelly concentrations clearly demonstrate that the majority of the specimens are Recent, i.e., they are usually scattered around young ages (less than 1,000 years; e.g., Carrol et al., 2003). In other words, the biases that could be introduced by burial or diagenesis processes in these tanatocoenoses are probably underestimated. Problems related to identification, at specific level, of Pleistocenic mollusks and to the availability of sedimentary bodies containing fossil species, corresponding to the local and modern live/dead assemblages, undoubtedly raise difficulties to conduct such kind of investigation. Valentine et al. (2006; see also Valentine, 1989) provide us the few, but important, information on the fidelity of live/fossil assemblages. Their study shows that about 76% (simple percentage comparison) of the living genera and subgenera are also found as fossils in the Californian Province. An interesting study was conducted by Alin and Cohen (2004), which investigates the quantitative fidelity of freshwater live/dead/subfossil ostracod assemblages. They pointed out that the taphocoenosis reflected with high reliability the original live community.

Quantitative fidelity of fossil assemblages not only allows to answer questions such as ancient species richness and numerical abundance, but also comprehending questions concerning ancient productivities, biomasses, community structure, and also some ecological features of the modern and human impacted malacofauna (Kowalewski et al, 2000; Markich et al., 2002; see also Alin and Cohen, 2004). The Touro Passo River (southernmost Brazil) is particularly well suited to test some of the above issues. Outcrops of the Touro Passo Formation, containing Pleistocenic (Kotzian et al., 2005; Simões et al., 2007) rich-shell beds, with mollusks clearly corresponding, at specific level, to the modern species of the region (Oliveira and Milder, 1990; Martinez and Rojas, 2004; Kotzian and Simões, 2006; Martello et al., 2006), are found in the margins of the homonymous river. Data on the quantitative fidelity of its live/dead molluscan assemblages are also available (Martello et al. 2006), and show that the biocoenoses is poorly preserved (ca. 60% of live species also found dead), probably due to intense dissolution processes (Kotzian and Simões, 2006), but the rank order of dominance is good (Spearman r = 0.56, $p<0.05$, Martello et al., 2006). Some modern environmental problems, such as the presence of the invasive Asiatic clams (*Corbicula fluminea* and *C.*

largillierti), are also recorded for the Touro Passo River (Kotzian and Simões, 2006; Martello et al., 2006).

Taking hand of such information, we are able to investigate the fossil assemblage from the Touro Passo Formation, in order to understand some interesting but poorly known questions in taphonomic studies. Would be the taphocoenosis in question, quantitatively more similar to the dead assemblages than to the live assemblages, as predicted by Kidwell and Flessa (1996)? Or, should it present a particular and different profile? How much of information was lost, after the live and/or dead assemblages were incorporated into the sedimentary record? We could also ask, in an optimist, but inverse expectative, how much information on the original malacofauna, i.e., non human impacted biocoenoses and tanatocoenoses, was lost by the present day freshwater molluscan assemblages?

STUDY AREA

The Touro Passo River is located in western Rio Grande do Sul state, southern Brazil, and it is a tributary of the Uruguay River, an important tributary of the Paraná River basin (Fig. 1). The course of the Touro Passo River shows a great range of depths and a variety of channel morphologies, including straight and meandering channels. (Fig. 1A). The margins are predominantly dominated by low riparian vegetation (Fig. 1B, C) and scattered sandy bottoms. The river has a variable flow regime, mostly controlled by the base level of the Uruguay River, and sometimes by the torrential rain characteristic of the region (Bombin, 1976; Instituto Nacional de Meteorologia, 2007). Flooding is very frequent, due to the floods in the Uruguay River and the low hydrological retention capability of the system (Bombin, 1976). On the other hand, dry periods are also common, when many secondary channels change into temporary abandoned channels and ponds.

Live species of mollusks are represented by *Pomacea canaliculata* (Lamarck, 1822), *Potamolithus* spp., *Biomphalaria* sp., *Diplodon delodontus wymani* (Lea, 1860), *Anodontites trapesialis forbesianus* (Lamarck, 1819), *Eupera klapenbachii* (Mansur and Veitenheimer, 1975), *Pisidium punctiferum* (Guppy, 1867) and *P. sterkianum* (Pilsbry, 1897), including the invasive Asiatic bivalves, *Corbicula largillierti* (Philippi, 1844) and *Corbicula fluminea* (Müller, 1774) (Martello et al., 2006). Shells of species such as *Heleobia* aff. *bertoniana* (Pilsbry, 1911), *Cyanocyclas limosa* (Maton, 1811) [=*Neocorbicula limosa*], *Mycetopoda siliquosa* (Spix, 1827), and *Diplodon parallelopipedon* (Lea, 1834) were also found in the riverbed (Martello et al., 2006).

TOURO PASSO FORMATION

The Touro Passo Formation is a Pleistocene-Holocene sedimentary unit, correlating in age to the Uruguayan Sopas Formation and the Argentinean Luján Formation (Bombin, 1976; Martinez and Rojas, 2004; Ubilla et al., 2004). It begins to crop out about 35 km distant from the mouth of the homonymous river, and was probably originated by the ancient floodplain of the Touro Passo River (Bombin, 1976). According to Bombin (1976), the unit is constituted by two members. The lower member lies in discordance on extrusive basalt rocks from the Serra Geral Formation (Jurassic-Cretaceous). It is rudaceous, sometimes showing carbonate cementation, and encloses reworked sub-fossil mammal material (13,000 to 12,000 years BP; Bombin, 1976). The upper member is muddy and constituted essentially by clayed siltstone and siltic to siltic-clayed sandstone, locally showing one level of volcanic ash. It also presents the majority of fossils from the Touro Passo Formation, as well as archaeological material of recent traditions (12,000 to 3,500 years BP; Bombin, 1976). There is no evident sedimentary structure in the upper member, and carbonate concretions are very common (Bombin, 1976).

The mollusks from the Touro Passo Formation were previously studied by Bombin (1976), who assigned the species *Anodontites trapesialis forbesianus* (Lamarck, 1819), *Leila blainvilleana* (Lea, 1834), *Diplodon delodontus wymanii* (Lea, 1860), *D. variabilis* (Maton, 1809) and *Cyanocyclas* [= *Neocorbicula*] *limosa* (Maton, 1811). *Heleobia piscium* (Orbigny, 1835), *H. parchappei* (Orbigny, 1835), *H. australis* (Orbigny, 1835), *Potamolithus lapidum* (Orbigny, 1835), *P. petitianus* (Orbigny, 1840) and *Gundlachia* sp. are also registered (E.V. Oliveira, personal communication, 2005).

MATERIALS AND METHODS

The two outcrops studied are located in the meandering sector (Fig. 1A) of the river, where part of the molluscan live/dead assemblages here analyzed, was previously investigated by Martello et al. (2006). This locality was also selected for the study, since the outcrops are usually well exposed, even in periods of no extreme dryness, and allow sampling the fossils in different seasons of the year. The meandering sector is situated in the middle course of the Touro Passo River, where an intermittent secondary channel delimitates a vegetated alluvial island (point bar), during the dry periods (Fig. 1A).

The outcrop 1 is located in the left margin of the Touro Passo River main channel, where its rich-fossil bed is located right below a dark layer of soil, which is commonly intersected by roots of the island vegetation (Fig. 1B, D). The fossil layer has, approximately, 4-5 m of extension and is 20 cm thick. It is loosely-packed (according to Kidwell, 1991), showing chaotic biofabric (Fig. 1D). Calibrated ^{14}C dating of two bivalve specimens of this outcrop yields ages varying from 18,570 to 20,690 ca. years (Kotzian et al., 2005). However, ongoing studies, using Electron Spin Resonance (ESR), suggest a longer time averaging, from 12,885 to 25,059 ca. years (Simões et al., 2007).

The outcrop 2 is situated in the left margin of the secondary channel (Fig. 1C), which in dryness periods delimits the alluvial island here considered. It is poorer in fossils than the outcrop 1, and the fossiliferous "bed" is not well defined, for its extension is not traceable along the channel margin. The fossil layer is located near the channel bed, far bellow the soil layer, and it is approximately 20 cm thick.

A rigorous "bed-by-bed" sampling of mollusks was undertaken, as suggested elsewhere (Simões and Ghilardi, 2000). In the fossil-rich outcrop 1, samplings were conducted in two sites. In a vegetated area, where the fossil bed is root-intersected (Fig. 1B), we selected four 2D blocks (=sampling units) for analyses, three of 20 cm x 20 cm and one of 160 x 20 cm (length x height respectively). Additionally, in a vegetation-bare place, we selected four 3D blocks, three of 20 cm x 20 cm x 10 cm and one 60 cm x 80 cm x 20 cm (lenght x width x height respectively). In site 2, poor in fossils, we selected four 20 cm x 20 cm x 10 cm (length x height x width) blocks. In both outcrops, the "bed by bed" sampling was conducted using four 5 cm thick levels (1, 2, 3, 4, from the top to the base). In all outcrops, molluscan remains greater than 1 mm were removed by hand, according to four levels of 5 cm thick.

Jaccard similarity index was adopted in order to compare species relative abundances between collection levels. The index obtained (0.91) showed that there was no important difference in species composition between such levels, thus data obtained were pooled in all the analyses.

The small and unidentified mollusk-like remains were stored in plastic bag and examined in the laboratory in order to avoid biases regarding the small body size (e.g. Valentine et al., 2006). Whenever possible, each specimen was identified to species level, based on extensive regional malacofauna descriptions (see references in Veitenheimer-Mendes et al., 1992; Mansur and Pereira, 2006; Martello et al., 2006; Silva, 2003). The voucher specimens are deposited in the Coleção de Moluscos Fósseis, Departamento de Biologia, Universidade Federal de Santa Maria (UFSM).

In general, the analyses of the fossil assemblages were conducted using the same methodology adopted by Martello el al. (2006), in order to allow comparisons between the quantitative fidelity of the fossil and present day (live/dead) assemblages. Only the identifiable mollusks were considered (=restrictive approach, see Kowalewski et al., 2003), and the species were analyzed regarding their relative frequency (%) and dominance (numerically dominant species). To avoid overestimation of bivalve richness, we applied a correction factor of 0.5 for unmatching valves, because a single valve does not represent a whole individual, and have two times probability of being collected than the gastropods unique shell (Kowalewski, et al., 2003).

For the study of quantitative fidelity of the fossil assemblage, we compare the data here obtained for the fossil mollusks with the live/dead assemblages data originally obtained by Martello et al. (2006). The comparisons were conducted using two approaches, according the spatial scale. In the small scale approach, the fossil assemblage was compared with the live/dead assemblages of the meandering sector (MS) of the Touro Passo River, and for the large scale approach, the taphocoenosis was compared with the live/dead assemblages of the river as a whole (RS) (see further information in Martello et al., 2006).

The Sorensen index of similarity was used to compare the species composition of live, dead and fossil assemblages, according to the formula: $S = 2C/(A + B)$ where S = index of similarity, A = number of species in one assemblage, B = number of species in the other assemblage and C = number of species common to both assemblages in consideration. The Spearman Rank correlation (rs) test was adopted to compare the ranking order of the most abundant species of the bio-, tanato- and taphocoenoses.

The quantitative fidelity analyses used the three questions of Kidwell and Bosence (1991): "F1= what percentage of shelly species found live are also found dead? [(NS x 100)/(NS + NL)]; F2= what percentage of species found dead are also found live? [(NS x 100)/(NS + ND)] and; F3= what percentage of dead individuals are from species found alive? [(dead individuals of NS x 100)/(dead individuals from (NS + ND))], where NS= number of species shared by the two assemblages; ND= number of species found only in dead assemblage and; NL= number of species found only in live assemblage". Each question was used two times; once for constructing the live/fossil (percent of live species also found as fossils) and fossil/live (percent of fossil species which are from live species) fidelity; and again for comparing the dead/fossil (percent of dead species found in fossil assemblage) and fossil/dead (percent of fossil species which are from dead species) fidelity. We also determined the percentages of live individuals from fossil species (and vice-versa) and the percent of dead individuals from fossil species (and vice-versa). We also recalculated the live/dead and dead/live fidelities, based on abundance data provided in Martello et al. (2006).

Further and complementary analysis using mollusks classified at generic level was conducted, in order to avoid biases regarding misidentification of the fossil species (see Valentine, 1989), especially those with high levels of morphological variation, such as *Heleobia* (see Gaillard, 1973; Silva, 1993; Darrigran, 1995) and *Potamolithus* (Lopez-Armengol and Darrigran, 1998).

RESULTS

A total of 22 species of mollusks were registered in the live/dead/fossil assemblages studied (Table 1). *Heleobia* aff. *piscium, H*. aff. *parchappei*, *Potamolithus* aff. *lapidum*, *P*. aff. *callosus* (Fig. 2) were found only as fossils; *Mycetopoda siliquosa* (Spix, 1827), only as “dead shell”; and *Diplodon* sp. and *Pisidium punctiferum* (Guppy, 1867), only alive. *Monocondylaea minuana* (Orbigny, 1835) and *Diplodon rhuacoicus* (Orbigny, 1835) were also found as “dead shell” in the Touro Passo River by Kotzian and Simões (2006).

The Sorensen similarity index shows relatively high similarities between live and dead assemblages species composition at large (RS) and small (MS) scales (Table 2). However, lower values are found when the present-day assemblages are compared to the fossil assemblage. This index never exceeds 51% of similarity at large and small scales approach (Table 2). At generic level, the Sorensen index increases regarding the fossil assemblage (Table 2), reaching levels similar to those obtained in live/dead comparisons. Notably, at river scale, the value was higher for live/fossil comparison than for dead/fossil comparison (Table 2).

In the live-dead assemblages, the taxocoenoses are dominated by specimens of the genus *Potamolithus* (Tables 3 and 4). At small scale (MS), *Potamolithus* sp. is the most frequent species (45%) in the biocoenosis, followed by *P*. aff. *orbignyi* (41%, Table 3). At large scale (RS), the latter is dominant (50%), followed by the former (38%, Table 4). In the dead assemblages, *Potamolithus* sp. and *P*. aff. *orbignyi* are the dominant species at both scales (Tables 3 and 4). However, in the fossil assemblage, the dominant mollusks are represented by two different taxa. *Cyanocyclas limosa* is the most frequent species (43%), followed by *Heleobia* aff. *bertoniana* (Pilsbry, 1911) (19%, Tables 3 and 4). This result determines the differences observed in the rank order of dominance between taphocoenosis and tanatocoenoses (and biocoenoses): *C. limosa* is registered in the 9th position, only at large scale (Table 4), and *H*. aff. *bertoniana*, is in the 5th (MS) or 6th (RS) rank order in tanatocoenoses (Tables 3 and 4).

Regarding the Spearman correlation index, the biocoenoses and tanatocoenoses correlates well and positively in terms of rank order of dominance, at any spatial scale (MS = 0.59, RS = 0.56, $p<0.01$, Martello et al., 2006). However, when the present day assemblages are compared to the fossil assemblage, the live species abundance correlates negatively (i.e. inversely) to the fossil species rank order (MS = -0.550, RS = -0.565, $p<0.01$), and the dead assemblage does not correlate in any way with the fossil assemblage (MS = -0.239, RS = -0.395 Spearman rank; *p* value >0.05 in all cases). The indices obtained at genus-level category were similar (Tables 5 and 6), but no correlation (positive or negative) was observed between the fossil and present-day assemblages ($p>0.05$ in all cases).

In general, the quantitative fidelity of the fossil assemblage was far from the expected results (Fig. 3). Regarding the F1 questions (the percentage of live/dead species also found fossil), the results were ordinary for the dead assemblages (MS = 50%, RS = 58%) and poorer for the live assemblages (MS = 44%, RS = 45%). The percentages obtained for the F2 questions were also very low, and the percentage of fossil species found alive (MS = 30%, RS = 35%) was lower than the percentage found dead (MS = 35%, RS = 50%). The F3 question showed the unique good result, as it were, for the quantitative fidelity analyses. The percentage of fossil individuals that represent dead species is 72 % at river scale (but only 27% at meandering sector scale; Fig. 3). However, when the same question was addressed to the live species, the frequency obtained the lowest values, 11 % at both spatial scales (Fig. 3).

The quantitative fidelity results improve when the analysis is conducted at genus-level (Fig. 3 D to F). The F1 question (live or dead genus found also fossil) reaches high values, with the live genera being better represented in the fossil assemblage (MS = 71%, RS = 75%) than the dead genera (66% for both spatial scales; Fig. 3D). The F2 index also becomes higher, with the fossil genera representing 75% of the dead assemblage (for both spatial scales), and the fossil genera reflecting 62% (MS) and 75% (RS) of the live assemblage (Fig. 3E). The F3 index, as well, shows a notable high index for fossil individuals from dead genera (96% for both spatial scales), and a lower value for fossil individuals from live genera (63% and 66% for MS and RS respectively, Fig. 3F).

DISCUSSION

This is the first time that molluscan live/dead assemblages are tested regarding their preservation potential. Or, paraphrasing Kidwell and Bosence (1991), we provide the initial answer to the question “how much of the richness, abundance, and rank-order dominance of a life (or dead) assemblage is actually preserved in a local sedimentary record?” Our data show that the quantitative fidelity of the fossil assemblage is far from that we could desire. However, as will be discussed below, our results were determined not only by the loss of original information during the passage of live/dead assemblages to the fossil record, i.e., by taphonomic biases, but also for other factors.

It is well known that the dominant, taphonomically resistant (e.g. thick-shelled) and big body sized (> 1 cm) mollusks species of original biocoenoses are generally dominant and well preserved in their corresponding dead and/or fossil (Pleistocenic) assemblages (Valentine, 1989; Russell, 1991; Best and Kidwell 2000a,b; Kidwell, 2002a; Vermeij and Herbert, 2004; Valentine et al. 2006). A previous study (Martello et al. 2006) shows that in the dead assemblages of the Touro Passo River, only the abundance affected the data obtained. In other words, the rank order of the dominant species of the biocoenoses was maintained in the tanatocoenoses, in spite of some of the frequent species be represented by thin shelled or small mollusks (e.g. *P. canaliculata*, *Biomphalaria* sp. and *Potamolithus* species; Tables 3 and 4). However, in the fossil assemblage from the Touro Passo Formation, only the required “taphonomic resistance” played an important role in the compositional fidelity found. The majority of the missing species, regarding the present-day assemblages, are thin-shelled mollusks, such as *Pomacea, Biomphalaria, Pisidium* and *Eupera* species (Tables 1, 3 and 4). On the other hand, the taphocoenosis was well represented by a diversified and numerous assemblages of minute, but thick-shelled, species of *Potamolithus* and *Heleobia* (Tables 1, 3 and 4). Hence, the intrinsic factor “thickness” could have promoted their preservation and the high numbers of such mollusks in the Touro Passo Formation. However, the high frequency of these species certainly contributed to their presence in the fossil assemblage studied.

As mentioned above, the rank order of the dominant species of the taphocoenosis does not show the expected profile. The most frequent fossil species, *Cyanocyclas limosa* and *Heleobia* aff. *bertoniana*, were not registered in the biocoenoses, and occupied the 9th and 6th or 7th ranking in the dead assemblages respectively (Tables 3 and 4). The low Sorensen similarity indexes (Table 2) and the low, and sometimes negative, values obtained in Spearmann correlation test, when the fossil species assemblage was compared to the present day species assemblages, clearly show complete lack of correspondence, regarding the taxonomic composition and dominance of the assemblages.

Cyanocyclas limosa is a native and endemic Corbiculidae bivalve from Eastern South America (Parodiz and Hennings, 1965; Garces et al., 1989; see also revision in Mansur and Pereira, 2006), which was very common in rivers, lakes and wetlands of the State of Rio Grande do Sul, until the 80`s (Mansur and Garces, 1988). The well known decline of this species in many regions (Mansur et al., 2003; Mock et al., 2004) coincide with the arrival of the related Asiatic species *Corbicula fluminea*, which was recorded for the first time in the state by Veitenheimer-Mendes (1981). Recent studies (e.g., Callil and Mansur, 2002) show that *C. fluminea* is now being substituted by its conspecific, and also exotic, *Corbicula largillierti*, which was one of the most frequent species in the Touro Passo River (Martello et al., 2006; Table 4). Hence, the discrepancy between the rank order of *C. limosa* in the fossil and live/dead assemblages was not determined by the abundance of the species in the ancient Touro Passo River, but rather by the modern declining process that is affecting many freshwater bivalves (Ricciardi and Rasmussen, 1999; Darrigran, 2002). Additionally, the mean-size of the fossil specimens (15.79 ± 7.28 mm and 18.01 ± 7.99 mm) shows that the *C. limosa* from the Touro Passo Formation was an medium-sized species, probably resistant to pore water dissolution, as proved by its abundance in the sedimentary record. Consequently, the species can be considered taphonomically resistant, and its abundance in the fossil assemblage reflects its frequency in the past, or at least in a non human-disturbed Touro Passo River. In other words, the fossil record was not incomplete concerning this species. Actually, the present day river malacofauna is “incomplete”, i.e., impoverished regarding their original, non-impacted taxocoenosis.

The genus *Heleobia* comprises numerous species with highly variable shell morphologies (Gaillard, 1973; Silva, 1993; Darrigran, 1995; Silva, 2003). About five species are described or assigned to the State of Rio Grande do Sul, but the real status of each species is poorly known (Silva, 2003). Consequently, studies on the ecology and life habits of the species of *Heleobia* are also rare. One of the best known species, *Heleobia piscium* (Orbigny, 1835), is euryhaline, and is thought to be a good indicator of salinity in estuarine water bodies (Darrigran, 1995), but studies on other species are lacking. The few information on *Heleobia bertoniana* reveals that the species occurs in rivers, mainly at *Eichornea azurea* (Sw.) Kunth roots (Pfeifer and Pitoni, 2003; Silva, 2003). Apparently, the Touro Passo River sustains suitable settings for the life of *Heleobia* species, and the question regarding the scarcity of *H.*

aff. *bertoniana* (and other species of this genus) in the bio and tanatocoenoses of the Touro Passo River (Tables 1, 3 and 4) still needs answer.

It is important to emphasize that the differences regarding the taxonomic composition of the fossil *versus* live/dead assemblages were not determined by a snapshot effect of the sedimentary process(es) that originated the fossiliferous bed studied. Preliminary studies indicate that the molluscan shells from the outcrop here investigated probably show considerable time averaging (12,885 to 25,059 years BP, Simões et al. 2007). Additionally, its loosely packing and chaotic biofabric (see Materials and Methods) also suggest that the shells were reworked.

The differences concerning the taxonomic composition and the rank order of dominance, between the fossil and the present day assemblages, clearly affect the unexpected results on the quantitative fidelity of the taphocoenosis from the Touro Passo Formation. The measures adopted shows that, regarding the questions F1 and F2, the fidelity of the fossil assemblages is poor, and far from being similar to that was reached by the tanatacoenoses (Martello et al. 2006, Fig. 3). This result is farther and far worse, when the data of the taphocoenosis are compared to those of the biocoenoses (Fig. 3). The percentage of fossil individuals that are from species found dead (F3), at river scale, was the only question that showed a good result (about 72%), and was determined by the two dominant fossil species, which also occurs in the dead assemblage, but not in the live assemblage (Table 1). In other words, we could say that our results are contrasting, concerning the classical study of live/fossil fidelity (Valentine, 1989), which found high live/fossil agreement, and comparable to most live/dead studies.

We must consider that some species here studied could be misidentified, as alerted above, and consequently our results could be slightly biased. Many authors (e.g., Mansur, 1970; Mansur and Anflor, 1981) have shown that the systematic of the freshwater mollusks species is a complex and difficult task. Whereas destitute of soft parts, which are very important to specific-level classification, the shell of gastropods such as *Potamolithus* and *Heleobia* is highly variable in present day environments, (Gaillard, 1973, Silva, 1993, Darrigran, 1995). The shell form of the *Potamolithus* species may also suffer influence of factors such as age, sex, and presence of parasites (Lopez-Armengol and Martorelli, 1997). Notable morphological variation is well documented for freshwater mussels (e.g., Mansur, 1970; Mansur and Anflor, 1981). Besides, the specimens of some species of the fossil assemblage here studied commonly show bigger shells than the same species found in the present day assemblages. The fossil specimens of *Cyanocyclas limosa* are bigger than the *C.*

limosa specimens found in the tanatocoenoses. The fossil shells of *Diplodon delodontus wymani* are also bigger than the present day species ($p<0.05$ for height and length, ANOVA).

The complementary analyses conducted at generic level, in order to avoid the biases introduced by the possible misidentification of the species, provide the only remarkable "successful" results for the taphocoenosis. The Sorensen similarity indices yielded slightly better and higher similarity for live/fossil comparison than dead/live comparison (Table 2). Regarding the quantitative fidelity, the potential of preservation of the dead assemblages becomes very similar or equal to the one of the live assemblages, concerning the taphocoenosis and the tanatocoenoses respectively, for the F2 and F3 questions, and the values increase for F1 (Fig. 3). The F1 is rather better when live assemblages are compared with the fossil assemblage (Fig 3).

Apparently, our study suggests that the biocoenoses and/or the tanatocoenoses of the Touro Passo River lost their original diversity during the transition to the taphocoenosis, whilst many species were not found as fossils. However, we emphatically argue that the important differences, regarding the taxonomic composition and species dominance, observed in the fossil assemblage, are not taphonomically related, such as the abundance of *C. limosa* and the diversity of the species of *Heleobia* and *Potamolithus*. The discrepancies concerning the species level analyzes were probably originated by the modern environmental problems, which are causing the decline and the local extinction of many freshwater mollusks (Ricciardi and Rasmussen, 1999; Darrigran 2002). Alien mollusks, some of them introduced by foreign ship ballast water, are probably driving away many native species (Darrigran, 2002). As observed by Markich et al. (2002) and Brown et al. (2005), the anthropogenic alteration of the freshwater environments can affect the benthic communities, to such a degree that much of the information of the original community structure may be permanently lost. Hence, by the time, we can not ensure that the bio/tanatocoenoses were poorly preserved in the fossil record. Perhaps, the taphocoenosis may reflect the "original" assemblages prior to the anthropogenic influence, but the information on the undisturbed assemblages that lived in the Touro Passo River, in the preceding four or five decades is lost. In the other hand, "releasing the data locked in the fossil record" (Allison and Briggs, 1991), via quantitative fidelity analysis, showed to be useful for mollusks conservation. It could be used, such as demonstrated by Kowalewski et al. (2000), for confirming the decline of some species and/or for rescuing the original biodiversity data, contributing to the policy of programs in Conservation Biology.

Finally, we suggest that for paleoenvironmental purposes, using fossil genera certainly will retrieve more secure results than employing specific level classification. However, some aspects related to paleoecology, such as the original community structure, will be far from being reconstructed.

CONCLUSIONS

The quantitative fidelity of the fossil assemblage of the Touro Passo River does not reflect satisfactorily the original live and dead assemblages, even when the study is conducted in a large scale approach. Of course, many missing or rare species of the taphocoenosis represent mollusks affected by taphonomic processes, as also observed in the dead assemblages. However, the unexpected discrepancies, concerning the fidelity questions and specially the rank order of dominance, are apparently not taphonomic-related biases. Quite for the contrary, the answers for the differences must be searched in problems related to the present day biocoenoses. Some modern species are lacking or scarce in the Touro Passo River, probably due to the modern environmental problems, such as the invasion of exotic mollusk species. Moreover, some rare mollusks are members of the well-known declining freshwater species group.

The human-impacted condition of the live/dead assemblages hinders us to assess the real, or at least more precise, preservation potential of the live/dead assemblages of the Touro Passo River. Only studies conducted in the scarce undisturbed modern freshwater settings should give us the reliable information on the taphonomic filters, which act during the "passage" of shells from the live/dead to the fossil assemblage. Meanwhile, comparisons on the compositional fidelity between live, dead and Quaternary fossil assemblages have proved to be an useful tool in Conservation Biology studies, allowing us to assess some data lost by the modern malacofauna.

ACKNOWLEDGEMENTS

We are grateful to Átila da Rosa (UFSM, Brazil), Marcello G. Simões (UNESP, Botucatu, Brazil) and Sergio Martinez (Universidad de La Republica, Uruguay) for valuable comments in early stages of this study, and Édison V. de Oliveira (PUCRS, Brazil) for previous field trip assistance. Átila da Rosa and Saul Milder (UFSM, Brazil) kindly lent some photographs, maps and bibliography. We are also very thankful to the post-graduate students Camila K. Fagundes (UFSM) and Ana Emilia Siegloch (USP, Ribeirão Preto, Brazil) for field work helping, and Gabriela Soberón, João Henrique Franco and Fernanda Stüker for laboratory assistance. This paper is part of F.E. M.Sc. post-graduate dissertation.

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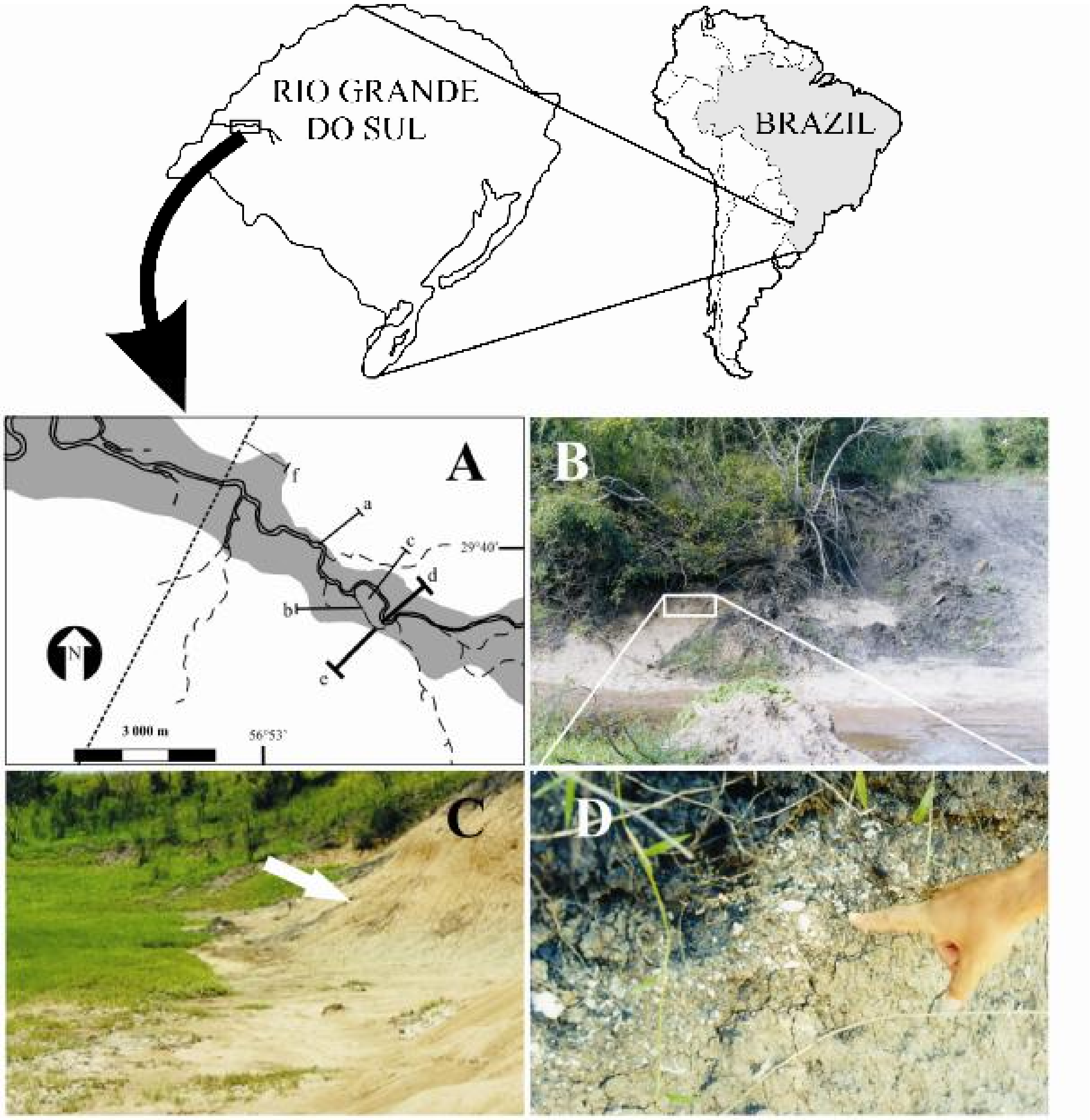

FIGURE 1—A) Location map of the studied area, showing the middle sector of the Touro Passo River, western Rio Grande do Sul State, southern Brazil. B) General view of the outcrop 1, showing the vegetation and the soil layer over the fossiliferous bed (white square). C) General view of the outcrop 2. The arrow shows the position of the fossiliferous “bed”. D) Detailed view of the outcrop 1, in the area delimited by the white square of the figure 1-B, showing the fossil-rich bed. Explanation: a) Main channel of the Touro Passo River; b) Secondary channel; c) vegetated alluvial island (point bar); d) location of the outcrop 1; e) location of the outcrop 2; f) Road BR 472.

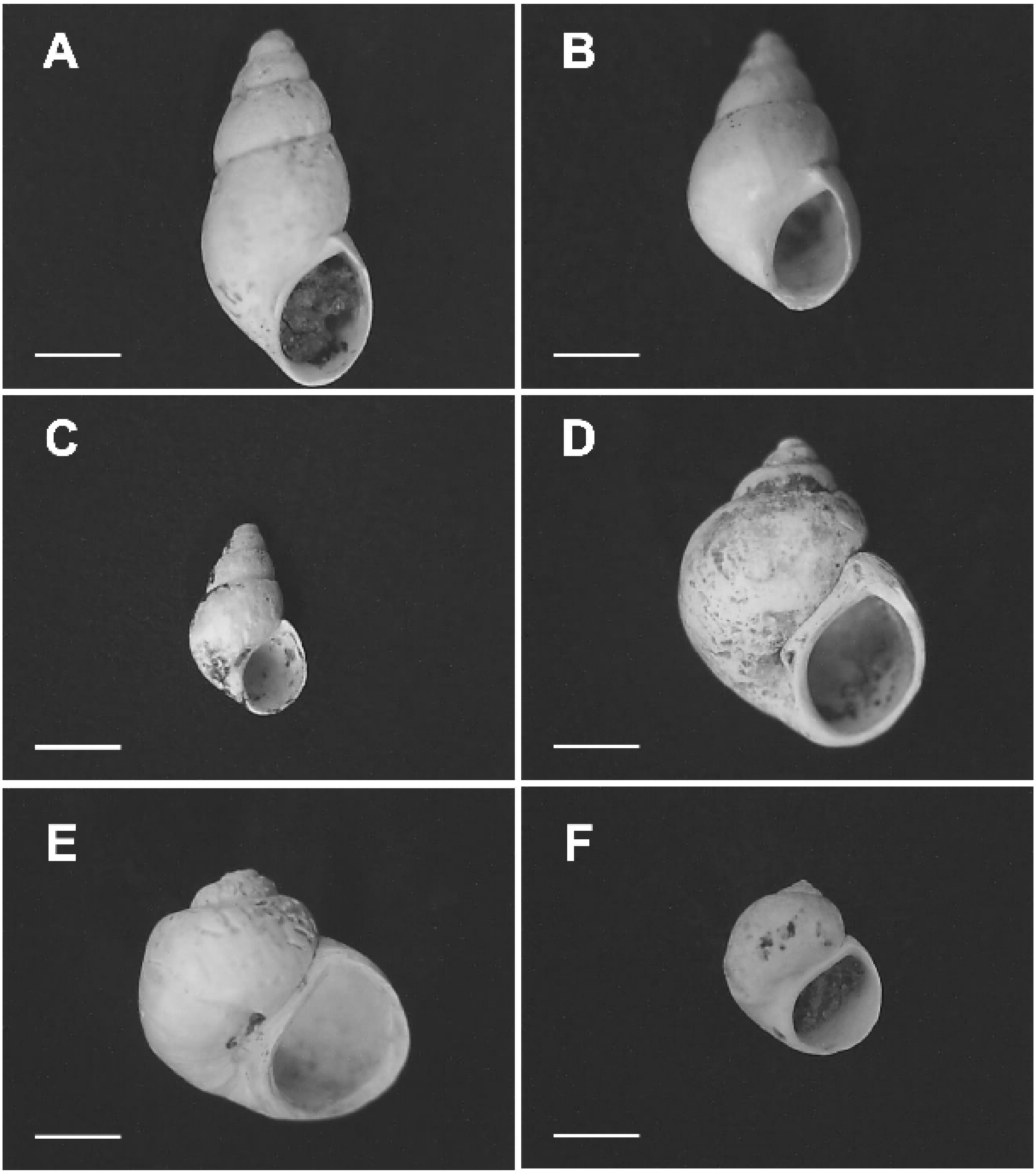

FIGURE 2—Gastropods from the Touro Passo Formation (collection number in parenthesis, after species name): A) *Heleobia* aff. *bertoniana* (E2-3D-4634). B) *H*. aff. *piscium* (BMbE-4635). C) *H*. aff. *parchappei* (E2-3D-4636). D) *Potamolithus* aff. *lapidum* (Cs-3D-4637). E) *P*. aff. *orbignyi* (BMtE-4638). F) *P*. aff. *callosus* (E2-3D-4639). Scale bar represents 1 mm in A and B, and 2 mm in C to F.

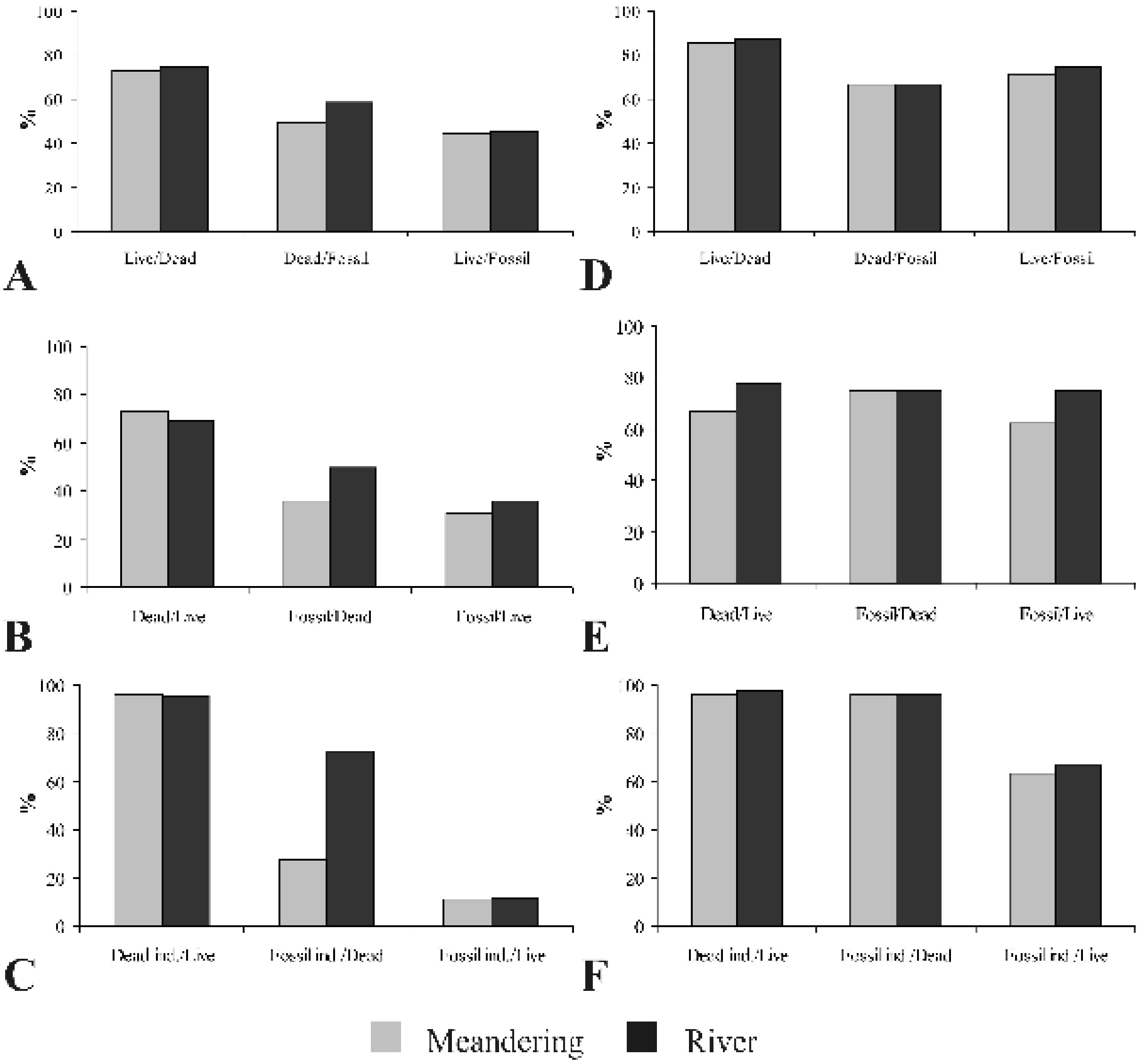

FIGURE 3—Fidelity indices for the species (A-C) and genera (D-F) of the live and dead assemblages of the Touro Passo River (raw data from Martello et al., 2006) and fossil assemblage from the Touro Passo Formation, Southern Brazil, at small (meandering sector) and large (River) scales. A/D – F1 = Percentage of: live species/genera found dead (Live/Dead), dead species/genera found fossil (Dead/Fossil) and live species/genera found fossil (Live/Fossil). B/E – F2 = Percentage of: dead species/genera found live (Dead/Live), fossil species/genera found dead (Fossil/Dead) and fossil species/genera found live (Fossil/Live). C/F – F3 = Percentage of: dead individuals from live species/genera (Dead ind./Live), fossil individuals from dead species/genera (Fossil ind./Dead) and fossil individuals from live/genera species (Fossil ind./Live).

TABLE 1—Number of specimens of the mollusk species found in the live/dead assemblages of the Touro Passo River (Martello et al., 2006) and in the fossil assemblage from the Touro Passo Formation, Southern Brazil. (N = number of individuals, S = richness, MS = Meandering Sector, RS = River). Asterisk denotes doubtful species, which were not included in the fidelity analyses (i.e., not included when calculating the fidelity measures for species).

	Live		Dead		Fossil
	MS	RS	MS	RS	
Pomacea canaliculata	0	5	1	11	1
Potamolithus aff. *orbigny*	431	615	57	86	17
Potamolithus sp.	467	467	89	89	0*
Potamolithus aff. *lapidum*	0	0	0	0	19
Potamolithus aff. *callosus*	0	0	0	0	16
Biomphalaria sp.	1	3	17	30	0
Heleobia aff. *bertoniana*	0	0	5	5	81
Heleobia aff. *piscium*	0	0	0	0	21
Heleobia aff. *parchappei*	0	0	0	0	12
Diplodon delodontus wymanii	4	4	2.5	3.5	14
Diplodon parallelopipedon	0	0	0	4	9
Diplodon rhuacoicus	0	0	0	0	25
Diplodon sp.	4	4	0	0	0*
Anodontites trapesialis forbesianus	1	1	0	0	15
Mycetopoda siliquosa	0	0	2	2	0
Monocondylaea minuana	0	0	0	0	6
Cyanocyclas limosa	0	0	0	4	180
Corbicula fluminea	12	12	5	11	0
Corbicula largilliertti	103	103	27.5	61.5	0
Eupera klappenbachii	1	2	1	1	1
Pisidium punctiferum	1	1	0	0	0
Pisidium sterkianum	1	9	3	3	0
N	1034	1226	210	311	417
S	11	12	11	13	14

TABLE 2—Sorensen similarity index between live, dead (Touro Passo River*) and fossil (Touro Passo Formation) assemblages, considering small (Meandering Sector) and large (River) scales, and species and genera levels of identification. *Obs. Data compiled from Martello et al. (2006).

	Species		Genera	
	Meandering Sector	River	Meandering Sector	River
Live/Dead	0.76	0.72	0.75	0.82
Dead/Fossil	0.41	0.51	0.70	0.70
Live/Fossil	0.32	0.38	0.66	0.75

TABLE 3—Relative frequency (%) of species of the live and dead molluscan assemblages of the Touro Passo River, at small (Meandering Sector) scale (after Martello et al., 2006); and of the fossil assemblage from the Touro Passo Formation, Southern Brazil. Numbers in parentheses after the live and death species rank represent species rank in the fossil assemblage. Asterisks indicate species not found in the fossil assemblage.

Live	%	Dead	%	Fossil	%
Potamolithus sp.	45.17(*)	*Potamolithus* sp.	42.38(*)	*Cyanocyclas limosa*	43.16
P. aff. *orbigny*	41.68(6)	*P.* aff. *orbigny*	27.14(6)	*H.* aff. *bertoniana*	19.42
C. largillierti	9.96(*)	*C. largillierti*	13.09(*)	*D. rhuacoicus*	5.99
C. fluminea	1.16(*)	*Biomphalaria* sp.	8.09(*)	*H.* aff. *piscium*	5.03
P. sterkiannun	0.87(*)	*C. fluminea*	2.38(*)	*P.* aff. *lapidum*	4.55
D. delodontus	0.38(9)	*H. bertoniana*	2.38(2)	*P.* aff. *orbignyi*	4.31
Diplodon sp.	0.38(*)	*P. sterkiannun*	1.42(*)	*P.* aff. *callosus*	3.83
Biomphalaria sp.	0.09(*)	*D. delodontus*	1.19(9)	*Anodontites* sp.	3.59
Anodontites sp.	0.09(8)	*M. siliquosa*	0.95(*)	*D. delodontus*	3.35
E. klappenbachi	0.09(13)	*E. klappenbachii*	0.47(13)	*H.* aff. *parchappei*	2.87
P. punctiferum	0.09(*)	*P. canaliculata*	0.47(13)	*D. parallelopipedon*	2.15
				M. minuana	1.43
				E. klappenbachi	0.23

TABLE 4—Same as Table 3, but at large (River) scale.

Live	%	Dead	%	Fóssil	%
P. aff. *orbigny*	50.16(6)	*Potamolithus* sp.	28.61(*)	*C. limosa*	43.16
Potamolithus sp.	38.09(*)	*P.* aff. *orbigny*	27.65(6)	*H.* aff. *bertoniana*	19.42
C. largiliertti	8.40(*)	*C. largiliertti*	19.77(*)	*D. rhuacoicus*	5.99
C. fluminea	0.97(*)	*Biomphalaria* sp.	9.64(*)	*H.* aff. *piscium*	5.03
P. sterkianum	0.73(*)	*P. canaliculata*	3.53(13)	*P.* aff. *lapidum*	4.55
P. canaliculata	0.40(13)	*C. fluminea*	3.53(*)	*P.* aff. *orbignyi*	4.31
D. delodontus	0.32(9)	*H.* aff. *bertoniana*	1.60(*)	*P.* aff. *callosus*	3.83
Diplodon sp.	0.32(*)	*D. parallelopipedon*	1.28(11)	*Anodontites* sp.	3.59
Biomphalaria sp.	0.24(*)	*C. limosa*	1.28(1)	*D. delodontus*	3.35
E. klappenbachi	0.16(13)	*D. delodontus*	1.12(9)	*H.* aff. *parchappei*	2.87
Anodontites sp.	0.08(8)	*P. sterkianum*	0.96(*)	*D. parallelopipedon*	2.15
P. punctiferum	0.08(*)	*M. siliquosa*	0.64(*)	*M. minuana*	1.43
		E. klappenbachi	0.32(13)	*E. klappenbachi*	0.23

TABLE 5—Relative frequency (%) of the genera of the live and dead assemblages of the Touro Passo River (after Martello et al., 2006) at small (Meandering Sector) scale, and of the fossil assemblage from the Touro Passo Formation, Southern Brazil.

Live	%	Dead	%	Fóssil	%
Potamolithus	86.84	*Potamolithus*	69.52	*Cyanocyclas*	34.09
Corbiculidae	11.12	Corbiculidae	15.47	*Heleobia*	32.38
Pisidium	0.96	*Biomphalaria*	8.09	*Potamolithus*	20.07
Diplodon	0.77	*Heleobia*	2.38	*Diplodon*	9.09
Biomphalaria	0.09	*Pisidium*	1.42	*Anodontites*	2.84
Anodontites	0.09	*Diplodon*	1.19	*Monocondylaea*	1.13
Eupera	0.09	*Mycetopoda*	0.95	*Pomacea*	0.18
		Pomacea	0.47	*Eupera*	0.18
		Eupera	0.47		

TABLE 6—Same as Table 5, but at large (River) scale.

Live	%	Dead	%	Fóssil	%
Potamolithus	88.25	*Potamolithus*	56.27	*Cyanocyclas*	34.09
Corbiculidae	9.38	Corbiculidae	24.59	*Heleobia*	32.38
Pisidium	0.81	*Biomphalaria*	9.64	*Potamolithus*	20.07
Diplodon	0.65	*Pomacea*	3.53	*Diplodon*	9.09
Pomacea	0.40	*Diplodon*	2.41	*Anodontites*	2.84
Biomphalaria	0.24	*Heleobia*	1.60	*Monocondylaea*	1.13
Eupera	0.16	*Pisidium*	0.96	*Pomacea*	0.18
Anodontites	0.08	*Mycetopoda*	0.64	*Eupera*	0.18
		Eupera	0.32		

SUPPLEMENTARY DATA

SUPLEMENTARY TABLE 1—Quantitative fidelity between molluscan assemblages of the Touro Passo River (compiled from Martello et al., 2006) and from the Touro Passo Formation, Southern Brazil, at species and genera levels of identification.

	Meandering	River
Species		
% live species found dead	72.72	75
% live species found fossil	44.44	45.45
% dead species found live	72.72	69.23
% dead species found fossil	50	58.33
% fossil species found live	30.76	35.71
% fossil species found dead	35.71	50
% dead individuals from live species	96.19	95.17
% fossil individuals from dead species	27.33	72.66
% fossil individuals from live species	11.27	11.51
Genera		
% live genera found dead	85.71	87.5
% live genera found fossil	71.42	75
% dead genera found live	66.66	77.77
% dead genera found fossil	66.66	66.66
% fossil genera found live	62.5	75
% fossil genera found dead	75	75
% dead individuals from live genera	96.19	97.74
% fossil individuals from dead genera	96.02	96.02
% fossil individuals from live genera	63.44	66.47

3. ARTIGO II: TAPHONOMIC SIGNATURES OF FRESHWATER MOLLUSKS FROM THE TOURO PASSO FORMATION (PLEISTOCENE-HOLOCENE), SOUTHERN BRAZIL: TESTING THE PRESERVATION POTENTIAL OF THE ORIGINAL DEAD ASSEMBLAGES

TAPHONOMIC SIGNATURES OF FRESHWATER MOLLUSKS FROM THE TOURO PASSO FORMATION (PLEISTOCENE-HOLOCENE), SOUTHERN BRAZIL: TESTING THE PRESERVATION POTENTIAL OF THE ORIGINAL DEAD ASSEMBLAGES

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RRH: TAPHONOMIC SIGNATURES OF FRESHWATER FOSSIL MOLLUSKS
LLR: ERTHAL AND KOTZIAN
Keywords: taphonomy, tanatocoenosis, taphocoenosis, Cenozoic

ABSTRACT

Several studies deals with paleoenvironmental interpretation using quantitative data, obtained in investigations on the relationships between taphonomic signatures of molluscan dead assemblages and some environmental factors. However, the injuries printed in shells due to post burial factors are poorly known. This study presents the first information on the preservation potential of taphonomic signatures of molluscan freshwater tanatocoenoses, comparing them to the co-occurring fossil assemblage from the Touro Passo Formation (Pleistocene-Holocene). It also provided the first taphonomic profile, regarding modern methodologies, to freshwater molluscan taphocoenosis. Some attributes were assigned exclusively in the fossil assemblage, such as the non organic spots, certainly constituted by oxides, and the rhyzoconcretions, a clear post burial damage. These features could also be registered in the dead assemblages, but only in specimens winnowed from the outcrops, i.e., fossil shells. In general, the shells from the taphocoenosis exhibited more severe injuries than the shells from the tanatocoenoses, as shown by the overwhelmingly higher frequencies of disarticulation, fragmentation, foliated condition of shell surface and margins, and loss of muscle scars. Such damages were probably yielded by porewater-induced dissolution, although the shell dissolution initiate early, during life or soon after the death, when the periostracum is lost. The

taphonomic signatures also showed differences, regarding the mollusk class. For the gastropods, cracks and oxide deposits were more frequent in the tanatacoenoses than in the taphocoenosis. The results suggest that Pleistocene taphocoenoses, although containing "well preserved" specimens and a specific-level taxocoenosis equal or very similar to the modern assemblages, do not show quantitative taphonomic profile similar to that observed in the tanatocoenoses. For the contrary, their damages could be strongly biased, not allowing direct interpretation of paleoenvironmental factors.

INTRODUCTION

Scarce information is available on the taphonomic signatures generated during the initial stages of molluscan shells fossilization. Some effects of post burial or diagenetic processes admittedly damage the shells previously to their complete destruction, such as porewater promoted dissolution, in the Taphonomic Active Zone (e.g., Davies et al., 1989; Cai et al., 2006; Best et al., 2007), but the matter is far from be well understood. Anyway, many studies have utilized taphonomic attributes observed in fossil molluscan assemblages to interpret some aspects of ancient environments, using information provided by investigations on tanatocoenoses (e.g., Nielsen and Funder, 2003; Yesares-Garcia and Aguirre, 2004).

Dead assemblages of marine bivalve mollusks have provided important quantitative data on the relationship between physical, chemical and biological factors and taphonomic signatures (e.g., Brett and Baird, 1986; Parsons and Brett, 1991). Previous studies have shown that shell damages are generally more related to processes (e.g., dissolution, abrasion, bioerosion; Best and Kidwell, 2000a; Parsons-Hubbard, 2005) than to specific environments and their gradients (e.g., granulometry and different depths) (e.g., Davies et al., 1989; Best and Kidwell, 2000a; Callender et al., 2002), and that mollusks intrinsic characteristics (e.g., life habits, shell microstructure and thickness) could also influence the injuries (see Best & Kidwell, 2000b, Lazo, 2004; Lockwood and Work, 2006 and Best et al. 2007 for further information). Taphonomic signatures of freshwater dead assemblages are poorly known (Pip, 1987, Kotzian and Simões, 2006, Newell et al., 2007), but seem to be affected by the same factors that determine the damages in marine assemblages.

Many shell accumulations previously analyzed contains specimens that were once included in sediment, and/or are Pleistocenic in age, as have been shown by time-averaging studies, on marine molluscan assemblages (e.g., Carrol et al., 2003). However, the majority of these specimens gravitate around young ages (e.g., Kidwell, 2001; Carrol et al., 2003). In other words, the injuries caused by diagenetic factors are underestimated and poorly represented.

Certainly, the long time span, which commonly separates the dead and fossil assemblages, is the most important factor hindering quantitative analyzes of the taphonomic signatures of taphocoenoses, in a similar way adopted by the studies on the former. The geological time, especially the Palaeozoic and Mesozoic eras, implicate the occurrence of very different molluscan taxocoenoses that constitutes an important source of bias, due to the influence of intrinsic factors on the taphonomy of the mollusk shells (Kidwell and Brenchley, 1996; Behrensmeyer et al., 2000). Other time-related sources of bias are the diagenetic processes, such as the porewater-promoted dissolution mentioned above, and the tectonic factors (Behrensmeyr et al., 2000).

The Touro Passo Formation (Southern Brazil) provides a rare opportunity to investigate, quantitatively, the “preservation potential” of the taphonomic signatures of the dead assemblages. Paraphrasing the question commonly addressed to the quantitative fidelity analysis (Behrensmeyer et al., 2000), it could allow answering “How much a taphocoenosis can resemble the “original” tanatocoenosis? The unit is Pleisto-Holocene in age and presents a shell-rich bed, containing a taxocoenosis equal or very similar to that registered in the dead assemblages of the Touro Passo River, at species level (Kotzian and Simões, 2006, Martello et al, 2006). The homonymous river also constitutes the ancient sedimentary environment, where the Touro Passo Formation was generated (Bombin, 1976), and the taphonomic signatures of its molluscan tanatocoenoses were previously studied, according to modern methodology and quantitative analysis, by Kotzian and Simões (2006).Thus, a quantitative comparison between the dead and fossil molluscan assemblages should be easily conducted.

TOURO PASSO FORMATION

The Touro Passo Formation is a Pleistocene-Holocene deposit, which crops out along the margins of the Touro Passo River, Southern Brazil. It was deposited in cold and dry climate, and correlates in age with the Sopas Formation (Uruguay) and Luján Formation (Argentina) (Bombin, 1976; Martinez and Rojas, 2004). The unit is composed by two members, which were described by Bombin (1976). The lower member is rudaceous, encloses reworked mammal fossils of Pleistocene age (13,000 to 12,000 yr BP), and lies in erosional unconformity over the basalts of the Serra Geral Formation (Jurassic-Cretaceous). The upper member is muddy, constituted by siltic clay and siltic sand, showing locally a level of volcanic ash. It presents the majority of the fossils and also archaeological material (12,000 to 3,500 yr BP). This member is overlain by recent sediments, where subfossil freshwater mollusk and younger archaeological material are also found (Bombin, 1976).

The molluscan fauna from the Touro Passo Formation is constituted by gastropods such as *Heleobia piscium*, *H. parchappei*, *H. australis*, *Potamolithus lapidum*, *P. petitianus* and *Gundlachia* sp., and bivalves such as *Anodontites trapesialis*, *Leila blainvilliana*, *Diplodon delodontus wymani*, *Diplodon* sp. (Bombin, 1976; Oliveira & Milder, 1990; E. Oliveira, personal communication, 2004). This taxocoenosis is equal at generic level, and equal or very similar at species level, to the present molluscan assemblage found in the Touro Passo Stream (Kotzian and Simões, 2006).

STUDIED AREA

The Touro Passo River is a tributary of the Uruguay River, located in western Rio Grande do Sul State, Southern Brazil (29°45'S; 57°05'W) (Fig. 1). The channel morphology is predominantly meandering to braided, with straight sectors (Bombin, 1976). According to the Instituto Nacional de Meteorologia (2007), the mean annual temperature varies between 18°C and 20°C and the mean annual precipitation is 1,250 mm, which allow classifying the climate as subtropical (Cfa2, Köppen classification). Particularly in the studied region, the climate determines the occurrence of torrential rains and dry periods. During the flooding, the base level of the river is controlled by the base level of the Uruguay River, which may dam the former up to 15 km from its mouth (Bombin, 1976).

The majority of the outcrops containing rich-mollusk beds are commonly covered by water, and their exposure occurs only in the rare episodes of extreme drought periods. The two outcrops selected for analysis are located in sites previously investigated in the study on the taphonomic signatures of the molluscan dead assemblages of the Touro Passo River (Kotzian and Simões, 2006). Both are localized in the "meandering sector" of the river (see Kotzian and Simões, 2006), in channels delimitating a vegetated alluvial island (=point bar) (Fig. 1A), and are commonly exposed (not covered by the water) all along the year.

The outcrop 1 is situated in the left margin of the main channel of the Touro Passo River. The fossiliferous bed is located right below a dark soil layer, commonly intersected by roots of the vegetation of the island (Fig. 1B, D). The rich-fossil bed has, approximately, 4-5 meters of extension and is about 20 cm thick (Fig. 1D). The outcrop 2 is situated in the left margin of the secondary channel (Fig. 1C), and is poorer in fossils than outcrop 1. Its fossiliferous “bed” is located far bellow the soil layer, near the riverbed, and the fossil content is scarce. It is approximately 20 cm thick, and the length is not traceable along the outcrop.

The massive nature of the sediments of the studied outcrops does not allow interpreting accurately its sedimentary depositional environment. However, some characteristics of the shell beds of both outcrops suggest that they were generated in settings similar to the present day environment of the Touro Passo River. The shell beds studied, as well as other fossiliferous levels of the Touro Passo Formation, exhibits small thickness and extension, a feature also observed in other coeval correlatives units (Sopas and Dolores Formations; Martinez and Rojas, 2004; Ubilla et al., 2004). The rich-shell bed of the outcrop 1 also shows loosely-packed bioclasts (according to Kidwell (1991) classification) and chaotic fabric, and is represented by high numbers of fragments and disarticulated shells, as will be discussed latter, including rare bivalves burrowed in life position (Fig. 2H) and/or with embryonic shells (Fig. 2C). Additionally, two *Diplodon delodontus wymani* shells dated with ^{14}C AMS yielded ages of cal. BP 19,570 to 18,570 and cal. BP 20,690 to 19,020 (Kotzian et al., 2005). Ongoing studies (Simões et al. 2007) using Electron Spin Ressonance (ESR) generate similar data, and the ages varies from 12,885 yr BP to 25,059 yr BP. In other words, the shell beds may represent episodes of rapid deposition, such as lateral accretion processes, which ultimately generated the point bar where the fossils were found, and their associated microhabitats. Nowadays, the vegetated alluvial island exhibits numerous small channels and swampy ponds, formed during the floods, which accumulate dead and live mollusks (Martello et al., 2006). These habitats could also have originated the chaotic biofabric and the lens-shape of the studied shell-bed.

MATERIALS AND METHODS

Whenever possible, the fossil mollusks samplings followed the “bed by bed” procedure suggested by Simões and Ghilardi (2000). In outcrop 1, richer in fossils, we selected four 3D blocks for analysis, in a vegetation–bare site. Three blocks with dimensions of 20 cm x 20 cm x 10 cm (length x width x height) and one exhibiting 80 cm x 60 cm x 20 cm (length x width x height) were selected. In a site covered by the vegetation, where the fossil bed is intersected by roots, we delimited four “3D blocks” for the study, three with 20 cm x 5 cm x 20 cm (length x width x height) and one with 160 cm x 20 cm (length x width x height). In outcrop 2, poorer in fossils, we selected three 20 cm x 10 cm x 20 cm (length x width x height) 3D blocks. In both outcrops, the “bed by bed” sampling was conducted using four 5 cm thick levels (1, 2, 3, 4, from the top to the base). All mollusks remain greater than 1 mm was removed by hand, enclosed in plastic bags and carried to the laboratory for investigation. The voucher specimens are deposited in the Fossil Mollusks Collection of the Department of Biology, Universidade Federal de Santa Maria.

The taphonomic profile (taphonomic signatures) was constructed in an analogous way utilized by Kotzian and Simões (2006), taking hand of several available studies on the nature and the classification of taphonomic signatures (Davies et al. 1989; Parsons and Brett, 1991; Kidwell et al. 2001**;** Henderson et al. 2002; Lazo, 2004; Parsons-Hubbard, 2005; Lockwood and Work, 2006). It is noteworthy that some features are exclusively found in the taphocoenosis, such as shell infilling and external/internal non-organic dark spots (Fig. 2B, Tables 3 and 4), as discussed bellow, while others previously registered in the molluscan dead assemblage (Kotzian and Simões, 2006) are missing in the fossil assemblage (e.g., “proteinaceous” parts and encrusting organisms) or rarely preserved (muscle scars).

The taphonomic signatures analyzed and their scores, characterization and possible origin are shown in Table 1 and Figure 2. Each shell and shell fragment received a unique identifying number, and was classified at species or genus level, whenever possible, based on extensive regional malacofauna descriptions (see references in Veitenheimer-Mendes et al., 1992; Martinez and Rojas, 2004; Mansur and Pereira, 2006; Martello et al., 2006). The specimens were examined under a stereomicroscope at 10x magnification (Kidwell et al., 2001), and the taphonomic variables were counted for presence/absence (1/0, Table 1), resembling the Parsons-Hubbard (2005) procedure, in order to obtain a semi quantitative database similar to that of Kotzian and Simões (2006).

It should be noted that some attributes are not useful for all the material examined. For example, the umbo and the muscle scars are lacking in many small fragments, avoiding the study of the taphonomic condition related to them. These attributes were further suppressed for the analysis in some specimens. On the other hand, some characteristics are not mutually exclusive, and can be found together in the same shell surface, such as the small and large pits, the organic sheets and the rhyzoconcretions (Fig. 2A, G; Tables 3 and 4). Thus the N value varies according the taphonomic signature and assemblage considered.

The analysis was conducted in an exhaustive approach (Kowalewski et al. 2003), i.e., including fragments, and the bivalves and gastropods were studied separately, in order to allow comparisons with the data obtained by Kotzian and Simões (2006).

Mann-Whitney U comparisons of taphonomic signatures between dead and fossil assemblages (Supplementary Data) showed no size class-related and fragmentation degree-related differences (but see Kidwell et al. 2001 and Kowalewski and Hoffmeister, 2003 for different results). Thus, all mollusk shell or fragment greater than 1 mm was included in the analysis. In addition, a 91% similarity in species abundance and taxonomic composition was observed between levels (1, 2, 3, 4) of each block, when utilizing Jaccard similarity index. In other words, there are no sensitive “bed by bed” differences. Thus, and also considering the scarcity of fossil mollusks of the outcrop 2, all levels and blocks collected are here treated as a single sampling unit.

The absence of statistical differences in the “bed by bed” analysis mentioned above and the chaotic biofabric of the shell beds suggest that the studied taphocoenosis was formed rapidly, possibly during the ancient lateral accretion process (see Material & Methods), which generated the two complementary point bars, which determine the “meandering to braided” morphology showed by some sector (Fig. 1A) of the present day channel. Henceforth, when comparing taphonomic signatures between the dead/fossil assemblages we used only the data concerning the tanatocoenosis of the “meandering sector” of the Touro Passo River, studied by Kotzian and Simões (2006). However, their original database was adapted to the sharing or equivalent characteristics of both assemblages, which were analyzed using scores adopted by Lockwood and Work (2006; see also Parsons-Hubbard, 2005).

We also utilized the Mann-Whitney U test for comparing the taphonomic profile of the taphocoenosis and tanatocoenosis. For demonstrating differences between both assemblages, we provide the Z values (with correspondent *p*-value) obtained by the test (Table 2), only for shared taphonomic characteristics of both dead and fossil assemblages. In order to avoid any spurious similarities between the assemblages analyzed, we adopted a *p*-value <0.001 to consider the comparisons significant. The mean proportions (and 95% confidence intervals) of each taphonomic feature (taphonomic profile) of the molluscan taphocoenosis from the Touro Passo Formation are presented in Table 3. All statistical treatment was performed utilizing SPSS package, version 11.01, and PAST software (Hammer et al. 2001).

RESULTS

The taphonocoenosis studied was constituted by the gastropods *Heleobia* aff. *piscium, H*. aff. *parchappei*, *H*. aff. *bertoniana* and *Potamolithus* aff. *orbignyi*, *P*. aff. *lapidum* and *P*. *callosus*? and by the bivalves *Cyanociclas limosa* [=*Neocorbicula limosa*], *Diplodon delodontus wymani*, *Diplodon rhuacoicus, Diplodon parallelopipedon*, *Diplodon* sp., *Anodontites* sp., and *Monocondylaea minuana*. The bivalves comprehend about 90.4% of the 2879 specimens collected, and were represented specially by fragments (n = 2558).

The taphonomic profile of the fossil bivalves is characterized by extremely high (> 90%) frequencies of fragmentation, disarticulation and loss of muscle scars, and also by high percentages (> 80%) of partial loss of sculpture, foliated fragmented edge, loss or erosion of the hinge, and loss of anterior adductor muscle scar (see Fig. 2, Tables 2 and 3). All the gastropods showed some degree of fragmentation, and high frequencies (> 80%) of foliated fragmented edge and partial loss of sculpture (Table 4). Shell infilling was more frequent in bivalves from the taphocoenosis than in bivalves from the tanatocoenosis (Table 2), but no differences were detected between gastropods and bivalves from the taphocoenosis ($p>0.05$).

The fossil and dead assemblages showed statistically significant differences for about nine taphonomic features (Table 2). The frequency of fragmentation was extremely high in the taphocoenosis, contrasting with the tanatocoenoses, which was dominated by large fragments and slightly fragmented shells (Tables 3 and 4; Kotzian and Simões, 2006). In the fossil assemblage, the percentage of the articulated valves was very low when comparing to the tanatocoenosis. The determination of right/left valves was hindered by the small size (mean size= 1,063 cm, median=0,9 cm) and high fragmentation degree presented by the fossils. Cracks were relatively rare in both assemblages, but gastropods were more frequently cracked in the tanatocoenosis than in the taphocoenosis (Table 2). In bivalves, small and very-chipped margins and sharp margin texture were more frequent in specimens from the tanatocoenosis than in those from the taphocoenosis, but foliated margin was more frequent in the latter (Fig. 6C). For the gastropods, foliated margin was absent in the dead assemblage and the polished condition was more frequent in the tanatocoenosis than in the taphocoenosis (Fig. 6D).

The fragmented shell edge texture (for bivalves and gastropods) consisted of high frequencies of foliated texture, followed, numerically, by decreasingly percentages of polished and sharp textures (Fig. 4). This profile was the opposite of that found in the tanatocoenosis, in which the foliated texture showed the lowest frequency, numerically followed by increasingly frequencies of polished and sharp textures. In bivalves, sharp fragmented margin texture was higher in the tanatocoenosis ($Z= 4.153$, $p<0.001$) than in the taphocoenosis. Foliated texture was higher in bivalves ($Z= 9.927$, $p<0.001$) and gastropods ($Z= 9.601$, $p<0.001$) of the taphocoenosis than in the mollusks of the tanatocoenosis (see also Fig. 4). The bivalves of the taphocoenosis showed higher hinge alteration than those of the tanatocoenosis (Table 2, see also Table 3), and although the proportion of natural/eroded hinges was similar in both assemblages, the frequencies of altered and natural hinges were respectively higher and lower in the taphocoenosis than in the tanatocoenosis (Table 2). The taphocoenosis also exhibited significantly higher percentages of loss of muscle scars than the tanatocoenosis (Table 2).

Differently from the dead assemblage, the majority of the fossil mollusks showed external sculpture total or partially lost, and high percentages of foliated texture (Fig. 5). But surprisingly, large pitting was more frequent in bivalves of the tanatocoenosis than in those of taphocoenosis (Table 2). Polished sculpture was more frequent in gastropods of the taphocoenosis than those of the tanatocoenosis (Fig. 5).

The taphocoenosis showed significantly more inorganic precipitations (Table 2). The non organic spots were significantly more frequent in fossil than in dead assemblage (Table 2). In fact, in the tanatocoenosis, the non organic spots were only observed in bivalves, at low frequency. Inorganic precipitations, in general, were more frequent in the taphocoenosis than in the tanatocoenosis (Table 2). In gastropods, organic sheets were more frequent in the taphocoenosis than in the tanatocoenosis, but oxide deposits were more frequent in latter (Table 2).

DISCUSSION

Our study provides the first quantitative description of differences in taphonomic signatures between dead and fossil mollusk assemblages. For the freshwater fossil mollusk, it also constitutes one of the few assessments to taphonomic signatures with a quantitative approach.

The absence of some taphonomic characteristics, or their condition/state, previously registered in the dead assemblage (Kotzian and Simões, 2006), such as “proteinaceous” parts (periostracum, gastropod operculum and bivalve ligament) and encrusting organisms, is not surprising. The preservation of organic parts is extremely rare in fossils (Kidwell and Flessa, 1996; Behrensmeyer et al., 2000), and previous studies on quantitative taphonomy of fossil marine mollusks did not assigned the occurrence of the attributes mentioned above (Brett and Baird, 1986; Zuschin and Stanton, 2002; Nielsen and Funder, 2003; Yesares-Garcia and Aguirre, 2004). Besides, the encrusting organisms frequently found in the dead assemblage studied are represented predominantly by egg capsules of *Potamolithus* (Kotzian and Simões, 2006), organic in constitution. Hence, the absence of encrustation probably represents the absence of well skeletonized encrusting taxa, if they ever existed in the ancient Touro Passo

River. However, altered organic remains were exclusively assigned in the taphocoenosis. The taphonomic signature “organic sheets” is brownish-to-darkish thin covering observed in wide areas of the shell surface (Table 1, Figure 2B). It is certainly organic in origin, given its immediate reaction with Coomassie Blue reagent (a widely used reagent for quantification of proteins in organic tissues and fluids; Bradford, 1976; Sapan et al., 1999).

The non-organic spots (Table 1; Fig. 2A) are by far the most interesting signature also found exclusively in the taphocoenosis. Apparently, they resemble periostracum remains due to their dark color. However, as they are also found in the internal surface of the shells, we suggest that the spots could be induced or generated by alterations of other types of tissues. Stressing the origin of this kind of taphonomic signature is beyond our scope in this study. However, we suggest that the spots may be composed of some kind of iron oxide. It was already investigated that some bacteria, under anoxic and/or anaerobic conditions, may use Fe^{3+} ion as the ultimate electron acceptor, and this can occur *in situ* with decomposing organic matter (Lovley and Phillips, 1986; Petrovich, 2001; Crowe et al., 2007). In this way, the reduced iron could have been adsorbed to the shell, if the decomposing organic matter were the periostracum and/or another mollusk organic tissue.

It is important to emphasize that the non-organic dark spots and the rhyzoconcretions assigned in the dead assemblage (the former was not formally registered as the latter by Kotzian and Simões, 2006, Fig. 2A) were rare and found in “chalky” specimens. Ongoing study on time-averaging, focusing the dead and fossil assemblages of Touro Passo River, using ESR (Simões et al., 2007), showed that the “chalky” bivalves of the former could be 287 to 57,530 years BP in age. In other words, they were clearly reworked from the outcrops, and eventually carried to the riverbed, i.e., non-organic dark spots and the rhyzoconcretions, are exclusive taphonomic characteristics of the taphocoenosis.

Shell infilling by sediments and shell deformation were also particular attributes of the fossil assemblage. Shell infilling was observed in gastropods and articulated bivalve shells, but was more common in the latter (Table, 2). This condition allows suggesting that the shells from the Touro Passo Formation could be prone to forming molds. In fact, one deformed internal mold of a mussel was assigned in the river margin (Fig. 2E). Shell deformation was rarely registered and determined by cracks in some gastropods. We also found few articulated shells of *Cyanocyclas limosa* containing embryonic shell (Fig. 2C).

Comparing the taphonomic signatures of the dead and fossil assemblages studied, the majority (21 out of 26, considering bivalves and gastropods separately) exhibited significantly differences. One clearly contrasting difference refers to the fragmentation. In the tanatocoenosis, the fragmentation was rare (Kotzian and Simões, 2006), suggesting that a similar profile will be found in the taphocoenosis. Surprisingly, the latter showed high percentage of fragmented specimens, and severe fragmentation degree (> 80%; Table 3, Fig. 2-3). Kotzian and Simões (2006) attributed the scarcity of fragments in the shells of the dead assemblages to the rapid dissolution of shells (due to the acidic condition of the water) in the Touro Passo River. In other words, they vindicated that the dissolution process initiates very early, soon after death, decomposing the shells after they could be either mechanically or chemically cracked (but see Newell et al., 2007 for chemically-induced mechanisms of breakage in Unionid shells). Considering that the original fossil assemblage was also probably submitted to such processes and conditions, the origin of the fragmentation of the mollusk shells of the Touro Passo Formation should be caused by different factors.

We suggest that the intense fragmentation assigned in the fossil assemblage was neither physical/biogenic, nor chemical, concerning pre-burial conditions. One of the most convincing evidence for a post burial origin is the presence of rhizoconcretions, a striking diagenetic feature, yielded by mineral (calcium carbonate) accumulation around living or dead plant roots (Klappa, 1980). This artifact is a strong indicator of pedogenesis (Retallack, 1997, 2004), generally occurring combined to carbonate concretions (Gibling et al., 2005; Sinha et al., 2006). Rhyzoconcretions and carbonate concretions are very common in Quaternary sediments, especially in floodplain and channel deposits (Retallack, 2004, Sinha et al., 2006). The primary source of the former has been attributed to mollusks shells, which usually occurs in these sediments (McBride and Milliken, 2006). Carbonate concretions occurs in many sites throughout the Touro Passo Formation (Bombin, 1976), including the studied outcrops. They origin are also associated with pedogenesis and, as emphasized by Rosa et al. (2004), by oscillations of the phreatic level near the soil surface. We suggest that the fossil shells could be dissolved, in order to form the carbonate concretions. The “carbonate concretion-like” internal mold found in the river margin (Fig. 2E) clearly shows the pervasiveness of this process. In other words, the fossil mollusks are undergoing post burial dissolution processes, which could weaken and/or destroy certain shell regions, yielding chemical (in origin) fragmentation.

Another important evidence for the diagenetic origin of the fragmentation can be found in the foliated texture of the edge of fragmented shells. In marine settings, the foliated texture is commonly related to biological (microbial) alteration of shells (Davies et al., 1989, Best and Kidwell, 2000a). However, we suggest another origin for this signature in the fossil shells studied. In the dead assemblages, the frequency of the foliated texture in fragmented edges is extremely low in bivalves (in gastropods this value is zero). As a matter of fact, the fragmented edges are predominantly sharp (fresh) in the tanatocoenosis (Kotzian and Simões, 2006). This indicates that in the dead assemblage, when fragmentation does occur, there is little alteration of edge surface. Thus, we must assume a post burial explanation, which could easily join the chemical (dissolution) origin proposed above for the shell fragmentation. However, it must be considered that some fragmentation can occur during the sampling, as previously mentioned by Kidwell et al. (2001). Many times, when trying to remove some bivalve shells or fragments from the sediment, the specimens broke. But in this case, the fragmented edge shows a clearly fresh aspect.

Other differences between the taphonomic signatures of the dead/fossil assemblages are probably pre burial in origin, although intensified by diagenetic processes, especially by post burial dissolution. The partial loss of the shell sculpture and the foliated nature of the reminiscent ornamentation are two predominant features in mollusks from the Touro Passo Formation (Tables 2-4, Fig. 5). In the tanatocoenosis, the majority of the specimens was totally or partially covered by the periostracum (Kotzian and Simões, 2006), which avoids the water-promoted dissolution of the shells. In other words, their sculpture is well preserved. However, after the incorporation in the sediment, the "new-taphocoenosis" lose the proteinaceous parts (e.g. periostracum), becoming prone to diagenetic process. Hence, dissolution-related signatures, such as the loss of the sculpture and foliated texture, are intensified. Experiments conducted by Neves et al. (2007) with bivalves of the Touro Passo River, clearly show that the dissolution are at least two times faster in specimens of *Anodontites* sp. and *Diplodon* sp. artificially destitute of periostracum than in intact shells.

Hinge erosion (Table 2) is another feature more frequent in the taphocoenosis than in the tanatocoenosis. As previously discussed by Kotzian and Simões (2006), in the latter, this signature could be generate by a combination of dissolution and abrasion (= corrasion, see Brett and Baird, 1986). We suggest that the high frequency of hinge erosion in the taphocoenosis was yielded by the porewater within the sedimentary column (Garrison et al., 1969; Cai et al., 2006, Newell et al., 2007; but see also Kidwell et al., 2005; Best et al., 2007 for substrate-related selectivity in shell dissolution). High frequencies of absence of muscle scars in fossil bivalves (Table 2, 3) are probably yielded by the same processes.

Although several taphonomic signatures of the tanatocoenosis could be intensified by diagenetic processes, some dissolution-related characteristics here analyzed did not show signals of being affected by them. Large pits, a feature clearly promoted by dissolution (Staff et al., 2002; Kotzian and Simões, 2006, Best et al., 2007), are much common in bivalves of the tanatocoenosis than in the specimens of the taphocoenosis (Table 2). This apparently unexpected result was determined by the usual presence of periostracum in mollusks of the dead assemblage, as mentioned above. Pitting and even the holes assigned in the tanatocoenosis were commonly originated under the periostracum covering (Kotzian and Simões, 2006). In fact, minor signs of dissolution may also occur *in vivo* and may not be taphonomic in origin (Best & Kidwell, 2000a; Lazo, 2004), and can be observed in live mussels of the Touro Passo River (personal observation). Additionally, as already discussed, some shells found in the Touro Passo River bed are certainly reworked fossil shells. Kotzian and Simões (2006) gave emphasis that the thick-shelled fossil bivalves (e.g. *Diplodon*) were more frequent in the river channel than other mollusks. In other words, they could have contributed to the higher frequencies of large pits in the tanatocoenosis (Table 3; Brown et al., 2005).

The higher disarticulation found in taphocoenosis (Table 2) could lead us to interpret this pattern as an artifact of the high levels of fragmentation and post burial dissolution (early diagenesis; Davies et al., 1989; Parsons and Brett, 1991), as previously mentioned by (Kowalewski and Hoffmeister, 2003).

CONCLUSIONS

In spite of its young geological age, the taphocoenosis from the Touro Passo Formation does not preserve satisfactorily the taphonomic signatures of its original molluscan tanatocoenosis. As expected, some attributes, especially the proteinaceous, are missing, while others, such as rhyzoconcretions, are exclusively assigned in the fossil assemblage. Additionally, the frequency of several dissolution-related signatures originally registered in the dead assemblages is increased, due to possible diagenetic processes. Porewater probably intensified the dissolution of shell attributes, such as sculpture, and also fostered the erosion of the bivalves hinge and muscle scars. Carbonate concretions and especially rhyzoconcretions found in the outcrops use the fossil shells as a main (carbonate) supply, intensifying their alteration and destruction. Dissolution-related processes also yielded the most strikingly differences between both assemblages. The noteworthy and unexpected high degree of fragmentation observed in the fossil mollusks could not be explained by physical and/or chemical pre burial processes, such pre burial transport. It was certainly originated by post burial dissolution, as confirmed by the foliated texture of the fragmented margins.

The results here obtained suggest that the preservation potential of the taphonomic signatures of the dead assemblages is not very good, and that the fossil assemblages contain some exclusive and/or altered characteristics, which could introduce biases concerning environmental factors or processes. For instance, the taphonomic signature of the shells from the Touro Passo Formation should easily take us to propose that the taphocoenosis lived in more energetic and acidic environment than that really occupied by their original dead assemblage. In other words, taphonomic signatures of fossil assemblages can be strongly biased, and needs the aid of other sources of information, in order to be useful for paleoecological reconstructions.

ACKNOWLEDGMENTS

Sergio Martinez (Universidad de La Republica, Montevideo, Uruguay) and Marcello G. Simões (UNESP, Botucatu, Brazil) made useful comments on the initial project. Átila da Rosa and Saul Milder (UFSM) helped, lending maps, photographs and literature. Édison V. de Oliveira (PUCRS, Uruguaiana, Brazil) gently accompanied us in the initial field trip and assigned unpublished data. Camila K. Fagundes (UFSM post-graduate student) and Ana Emília Siegloch (USP, Ribeirão Preto, Brazil) helped in field work. We are also very grateful to undergraduate students João H.N. Franco, Fernanda Stüker and Gabriela F. Soberón for laboratory assistance. This paper is part of Fernando Erthal M.Sc dissertation project.

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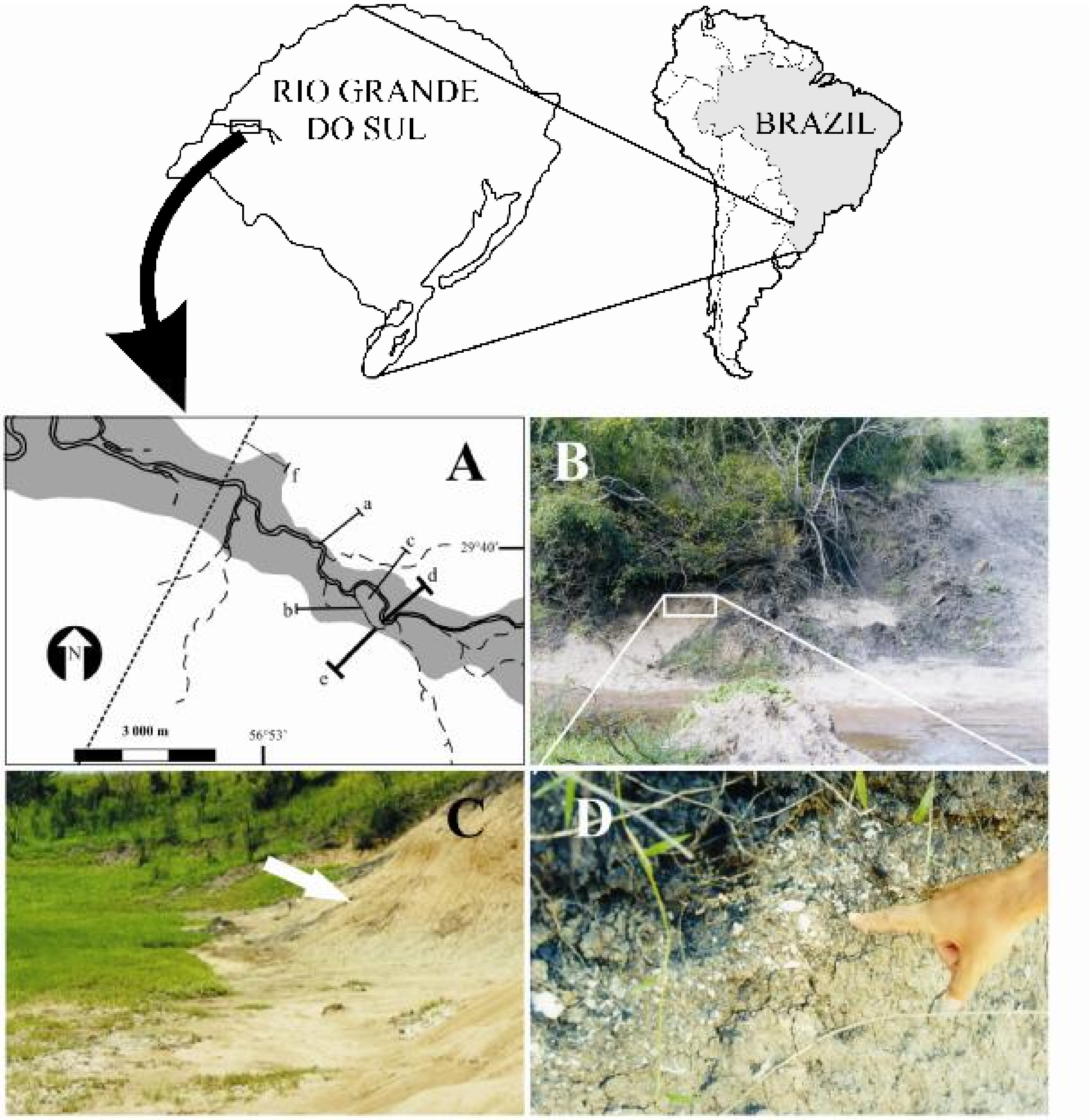

FIGURE 1— A) Location map of the studied area, showing the middle sector of the Touro Passo River, western Rio Grande do Sul State, southern Brazil. B) General view of the outcrop 1, showing the vegetation and the soil layer over the fossiliferous bed (white square). C) General view of outcrop 2. The arrow shows the position of the fossiliferous “bed”. D) Detailed view of outcrop 1, in the area delimited by the white square of figure 1-B, showing the fossil-rich bed. Explanation: a) Main channel of the Touro Passo River; b) Secondary channel; c) vegetated alluvial island (point bar); d) location of the outcrop 1; e) location of the outcrop 2; f) Road BR 472.

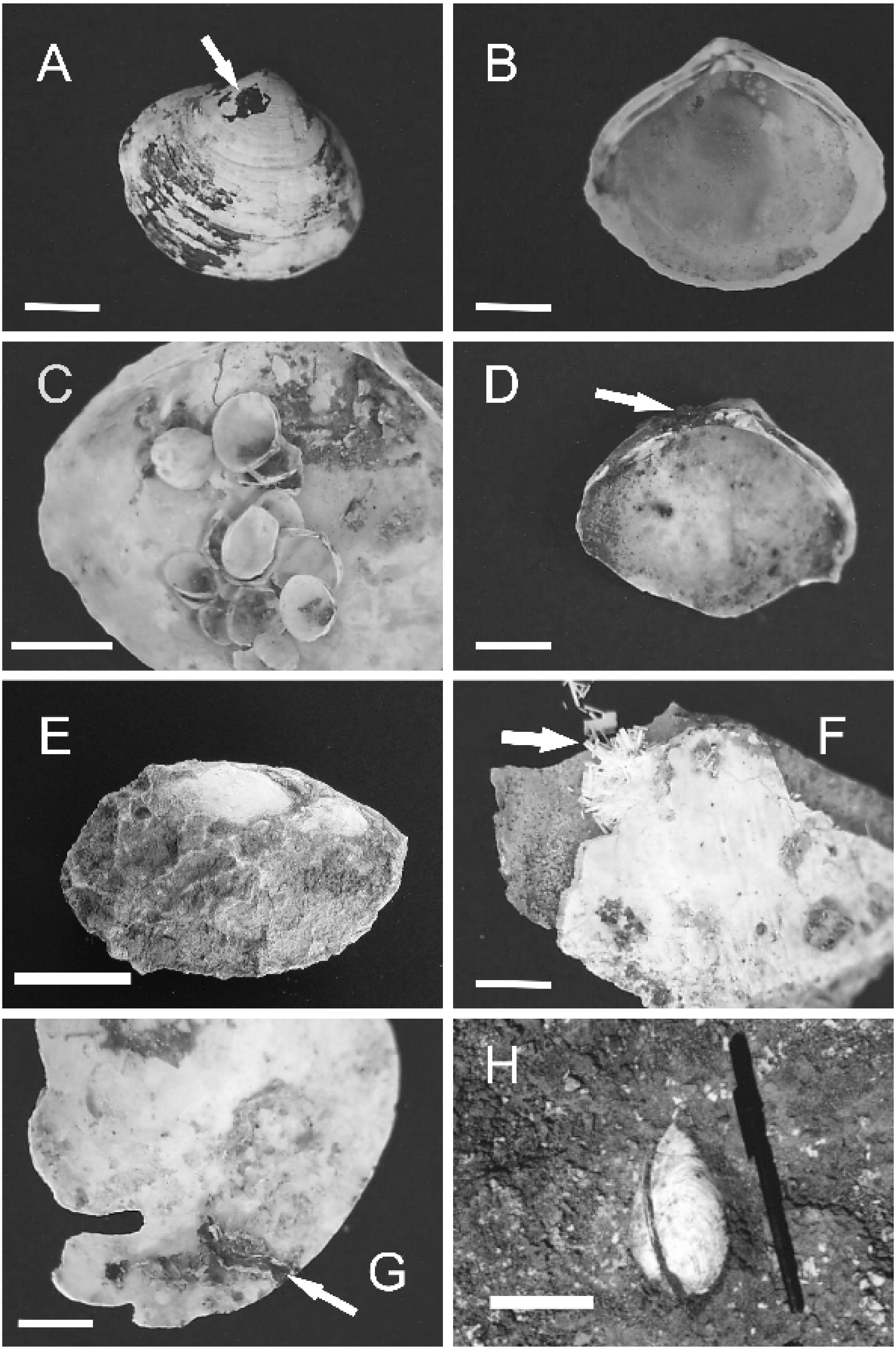
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FIGURE 2—Some taphonomic signatures of the fossil mollusks from the Touro Passo Formation. A) Non-organic spots (arrow) on the external surface of the shell of *Cyanocyclas limosa* (VsqD-4279, left valve). B) Organic sheet covering the internal surface of the shell of *C. limosa* (Ds3D-4080, right valve. C) Shell of *C. limosa* containing embryonic shells (Ds3D-4033, left valve). D) Shell of *C. limosa* (Ds3D-4039, left valve), showing oxide deposit (arrow) and marginal fragmentation. E) “Carbonate concretion-like” internal mold of an unidentified mussel (225). F) Foliated external surface of a fragment of a Unionoid shell (Gs3D-3593), showing the lose of crystallites from the outer, prismatic layer (arrow). G) Internal view of a rhyzoconcretion (arrow) on a shell fragment (Ds3D-3998). The dark filling of the lumen probably represents root remains. H) *Diplodon delodontus wymani* shell buried in life position (*in situ*) in the outcrop 1. Scale bar = 2 mm for A, B, D, F and G. Scale bar = 4 mm for C. Scale bar = 20 mm for E and H. (Fig. H was photographed by Átila da Rosa)

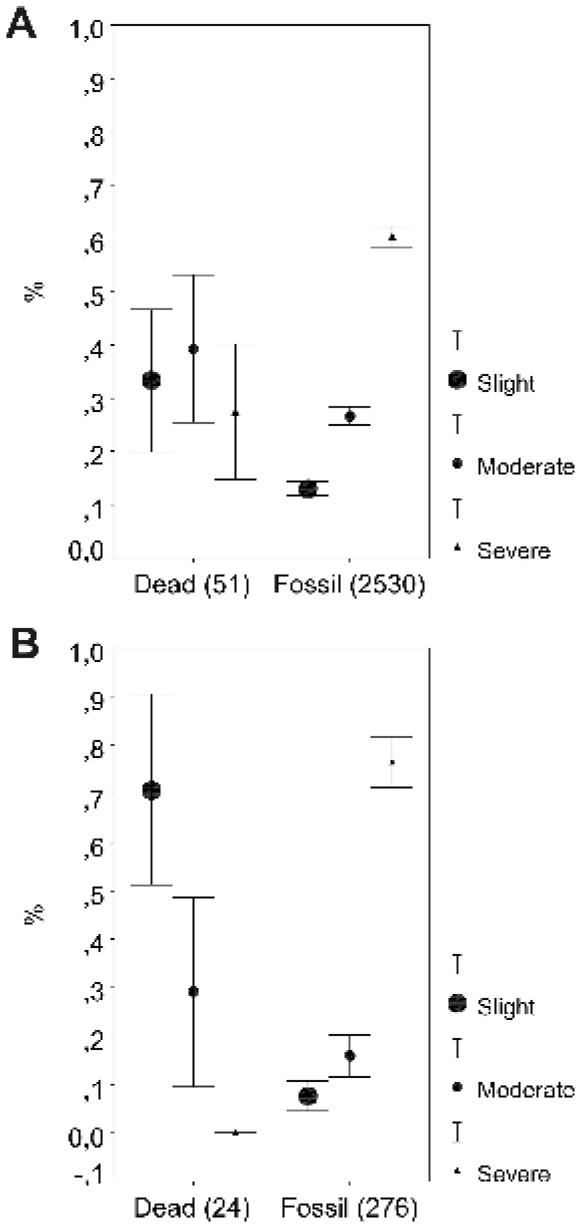

FIGURE 3—Frequency of different degrees (slight, moderate, severe) of fragmentation. Bars represent 95% confidence intervals. (N values for each assemblage are given within parenthesis in the x-axis category). A) Bivalves. B) Gastropods.

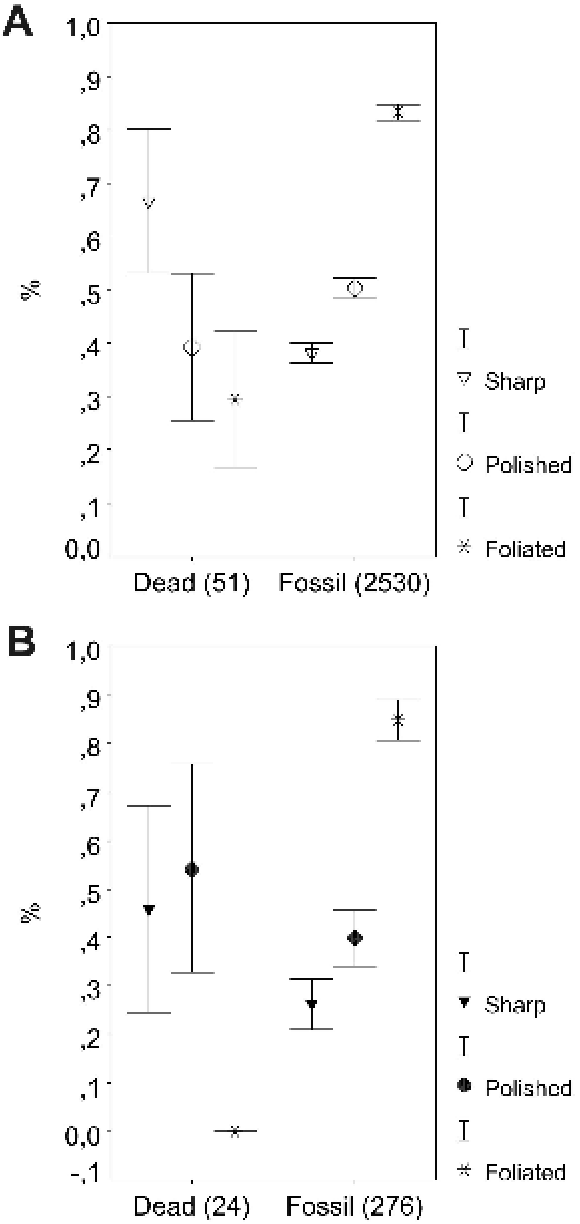

FIGURE 4—Frequency of different (sharp, polished, foliated) fragmented edge textures. Bars represent 95% confidence intervals (N values are provided within parenthesis in the category x-axis). A) Bivalves. B) Gastropods. See text for significant differences.

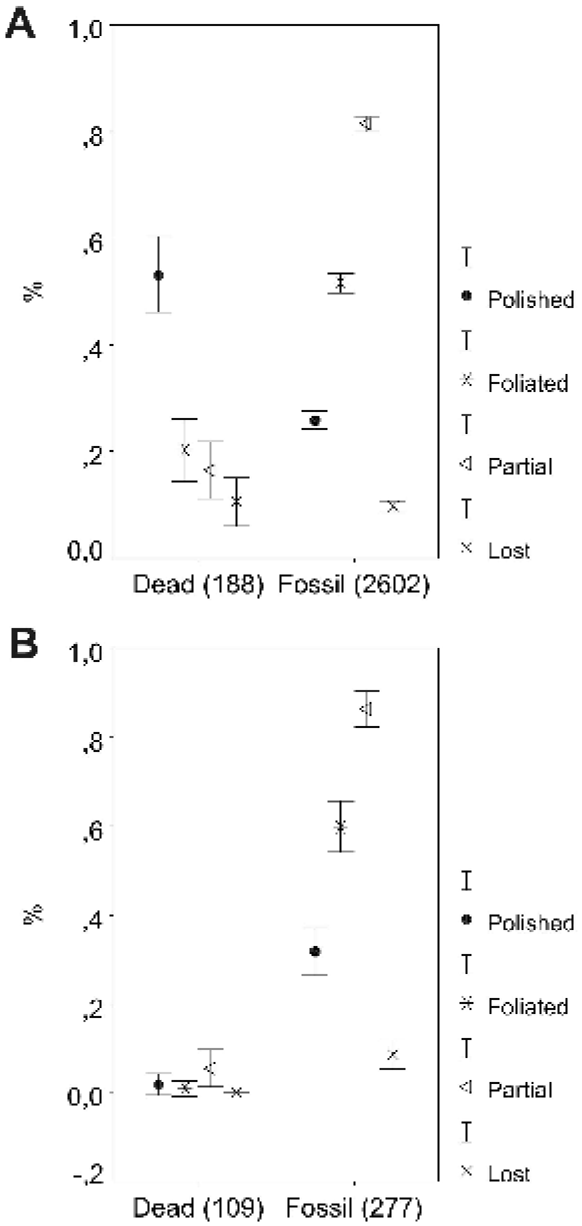

FIGURE 5—Frequency of sculpture condition (presence, texture). Bars represent 95% confidence intervals (N values for each assemblage are given within parenthesis in the category x-axis). A) Bivalves. B) Gastropods. See text for significant differences.

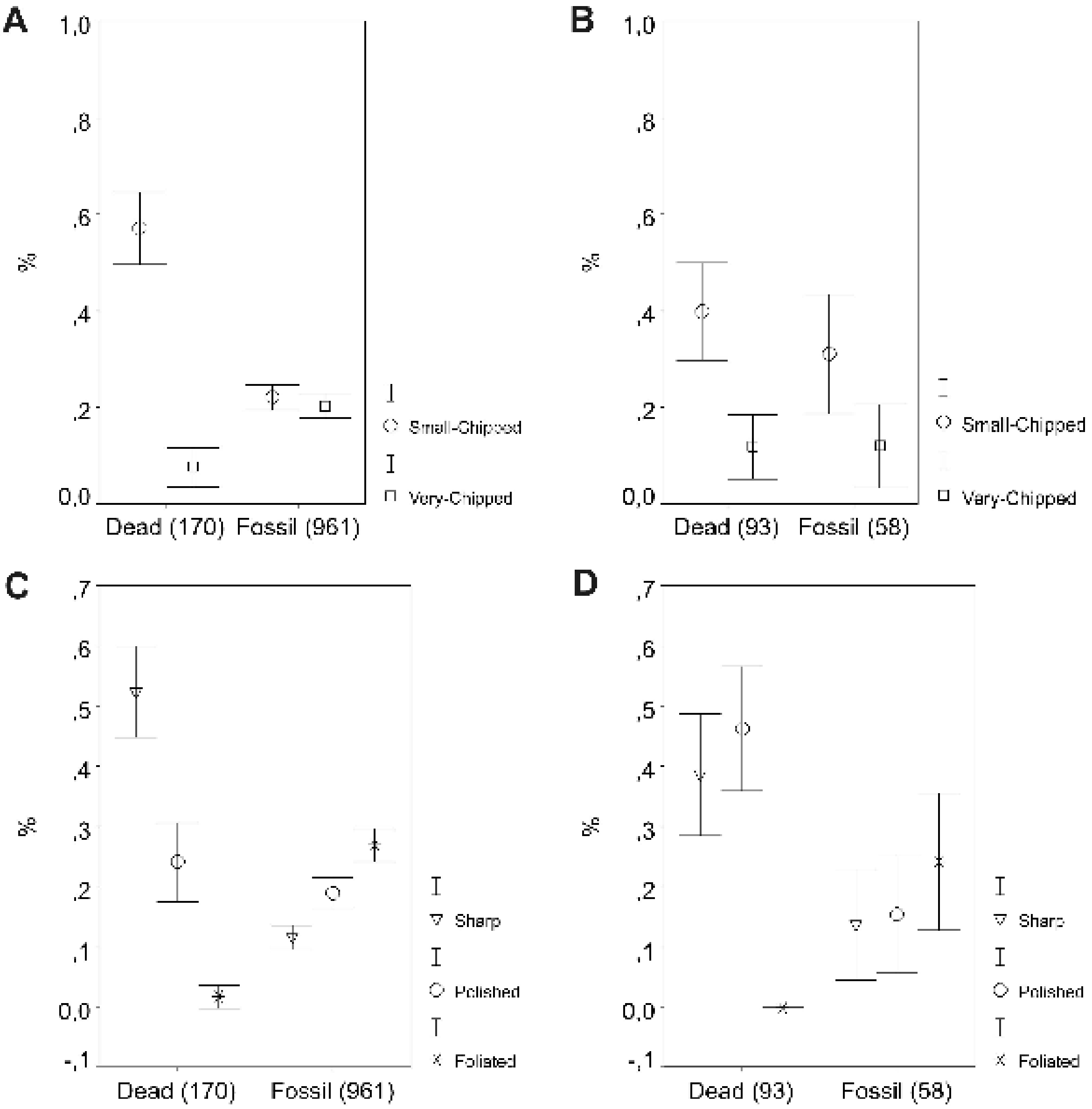

FIGURE 6—Frequency of edge rounding (A and B) and texture (C and D). Bars represent 95% confidence intervals (N values for each assemblage are given within parenthesis in the category x-axis). A) and C) Bivalves. B) and D) Gastropods.

TABLE 1—Taphonomic signatures analyzed in mollusks from the Touro Passo Formation, and their rank and semi-quantitative scales, with some observations. Asterisk denotes non-mutually exclusive attributes.

Taphonomic Signature	Score	Observation
1. Disarticulation	1/0 (present/absent)	
Right Valve		
Left Valve		
2. Fragmentation	1/0 (present/absent)	
Slight	1	< 50% of the surface lost
Moderate	2	50% - 80% of the surface lost
Severe	3	> 80% of the surface lost
3. Cracks	1/0 (present/absent)	
4. Edge rounding*		
Small-chipped	1/0 (yes/no)	
Very-chipped	1/0 (yes/no)	
5. Edge texture*		
Sharp	1/0 (yes/no)	fresh aspect
Polished	1/0 (yes/no)	smooth aspect
Foliated	1/0 (yes/no)	laminated rough aspect
6. Fragmented edge texture*		
Sharp	1/0 (yes/no)	fresh aspect, recently broken
Polished	1/0 (yes/no)	smooth aspect
Foliated	1/0 (yes/no)	laminated rough aspect (Fig. 2F)
7. Umbo/Apex alteration	1/0 (yes/no)	eroded but not broken
8. Surface pitting*		
Small pitting	1/0 (present/absent)	superficial punctuations
Large pitting	1/0 (present/absent)	(Fig. 2A, F)
9. Sculpture presence		
Present	1/0 (present/absent)	
Partially present	1/0 (present/absent)	
Lost	1/0 (present/absent)	
10. Sculpture texture*		
Natural	1/0 (present/absent)	present
Polished	1/0 (present/absent)	smooth aspect
Foliated	1/0 (present/absent)	laminated aspect; Fig 2F.
11. Hinge		
Natural	1/0 (present/absent)	
Eroded	1/0 (present/absent)	

12. Muscle Scars		
Palial line	1/0 (present/absent)	
Anterior aductor	1/0 (present/absent)	
Posteiror aductor	1/0 (present/absent)	
13. Precipitations	1/0 (present/absent)	
14. Rhyzoconcretions*		calcareous tubes (Fig. 2G)
Internal	1/0 (present/absent)	
External	1/0 (present/absent)	
15. Organic sheets	1/0 (present/absent)	brown plates organic in origin (Fig 2B)
16. Oxide deposits	1/0 (present/absent)	iron oxide-like deposits (Fig. 2D)
17. Non-organic spots*		non-organic dark thin sheets, possibly same origin as 15 (Fig. 2A)
Internal	1/0 (present/absent)	
External	1/0 (present/absent)	
18. Shell infilling	1/0 (present/absent)	filled with sediment

TABLE 2—Z and P-values of Mann-Whitney U test, for comparisons of shared taphonomic signatures between dead and fossil assemblages. Positive Z values represent higher damage frequency in the taphocoenosis. Negative Z values represent higher damage in the tanatocoenosis. Significant values ($p<0.001$, see Material and Methods) are in bold. Asterisk denotes missing observations in gastropods.

Variable	Bivalves	p-value	Gastropods	p-value
Disarticulation	$Z_{188,445} = 9.961$	**0.000**	*	*
Right valve	$Z_{111,410} = 3.168$	0.002	*	*
Fragmentation	$Z_{188,2602} = 35.257$	**0.000**	$Z_{109,277} = 16.476$	**0.000**
Cracks	$Z_{188,2602} = -0.368$	0.713	$Z_{109,277} = -3.523$	**0.000**
Umbo/Apex condition	$Z_{188,314} = -0.468$	0.640	$Z_{108,277} = 2.022$	0.043
Surface pitting				
Small pitting	$Z_{188,2602} = -0.561$	0.575	$Z_{109,277} = -2.111$	0.035
Large pitting	$Z_{188,2606} = -5.907$	**0.000**	$Z_{109,277} = -2.787$	0.005
Hinge erosion presence	$Z_{173,476} = 9.619$	**0.000**	*	*
Muscle scars absence	$Z_{172,2292} = 37.876$	**0.000**	*	*
Palial line	$Z_{152,68} = 7.531$	**0.000**	*	*
Anterior adductor	$Z_{152,68} = 2.750$	0.006	*	*
Posterior adductor	$Z_{152,68} = 5.869$	**0.000**	*	*
Precipitations	$Z_{188,2602} = 7.704$	**0.000**	$Z_{109,277} = 6.764$	**0.000**
Rhyzoconcretions				
Internal	$Z_{44,1366} = 2.464$	0.014	$Z_{34,191} = 2.801$	0.005
External	$Z_{44,1366} = 1.187$	0.235	$Z_{34,191} = 2.026$	0.043
Organic sheets	$Z_{44,1366} = 0.486$	0.627	$Z_{34,191} = 6.631$	**0.000**
Oxide deposits	$Z_{44,1366} = 2.736$	0.006	$Z_{34,191} = -6.997$	**0.000**
Non-organic spots	$Z_{188,2602} = 14.891$	**0.000**	$Z_{109,24} = 11.506$	**0.000**
External	$Z_{188,1678} = 19.547$	**0.000**	$Z_{109,180} = 11.529$	**0.000**
Internal	$Z_{188,1678} = 16.577$	**0.000**	$Z_{109,180} = 11.448$	**0.000**
Shell infilling	$Z_{188,266} = 15.637$	**0.000**	$Z_{109,24} = 2.402$	0.016

TABLE 3—Taphonomic profile of the bivalve assemblage from the Touro Passo Formation. Data are presented as frequency (mean percentage) with 95% Confidence Interval, and the respective N value of each attribute.

Attribute	N	95% C. I.
Disarticulation	445	92 ± 2.5
Right Valve	410	54 ± 4.8
Left Valve	410	46 ± 4.8
Fragmentation	2602	97 ± 0.6
Slight	2530	13 ± 1.3
Moderate	2530	27 ± 1.7
Severe	2530	60 ± 1.9
Cracks	2602	5 ± 0.8
Small-Chipped Margin	961	22 ± 2.6
Very-Chipped Margin	961	20 ± 2.5
Sharp Margin	961	12 ± 2.0
Polished Margin	961	19 ± 2.5
Foliated Margin	961	27 ± 2.8
Sharp Fragmented Edge	2530	38 ± 1.9
Polished Fragmented Edge	2530	50 ± 1.9
Foliated Fragmented Edge	2530	83 ± 1.4
Umbo alteration	314	70 ± 5.1
Small pitting	2602	55 ± 1.9
Large pitting	2602	34 ± 1.8
Polished sculpture	2602	26 ± 1.7
Foliated sculpture	2602	52 ± 1.9
Partial sculpture	2602	81 ± 1.5
Lost sculpture	2602	10 ± 1.1
Eroded hinge	476	88 ± 2.9
Hinge absent	2602	82 ± 1.5
Scars absent	2292	97 ± 0.7
Palial line	68	84 ± 8.7
Anterior aductor	68	12 ± 7.7
Posterior aductor	68	74 ± 10.4
Precipitations	2602	52 ± 1.9
Rhyzoconcretions		
Internal	1366	34 ± 2.5
External	1366	18 ± 2.0
Organic sheets	1366	42 ± 2.6
Oxide deposits	1366	36 ± 2.5
Non-organic spots	2602	64 ± 1.8
External	1678	76 ± 2.0
Internal	1678	70 ± 2.2
Shell infilling	266	75 ± 5.2

TABLE 4—Taphonomic profile of the gastropods assemblage from the Touro Passo Formation. Data are presented as frequency (mean percentage) with 95% Confidence Interval, and the respective N value of each attribute.

Attribute	N	95% C. I.
Fragmentation	277	100
Slight	276	8 ± 3.2
Moderate	276	16 ± 4.3
Severe	276	76 ± 5.0
Cracks	277	4 ± 2.3
Small-Chipped Margin	58	31 ± 11.9
Very-Chipped Margin	58	12 ± 8.3
Sharp Margin	58	14 ± 8.9
Polished Margin	58	16 ± 9.4
Foliated Margin	58	24 ± 10.9
Sharp Fragmented Edge	276	26 ± 5.2
Polished Fragmented Edge	276	40 ± 5.8
Foliated Fragmented Edge	276	85 ± 4.2
Apex alteration	277	47 ± 5.8
Small pitting	277	52 ± 5.9
Large pitting	277	32 ± 5.5
Polished sculpture	277	32 ± 5.5
Foliated sculpture	277	60 ± 5.8
Partial sculpture	277	86 ± 4.1
Lost sculpture	277	9 ± 3.4
Precipitations	277	69 ± 5.4
Rhyzoconcretions		
Internal	191	19 ± 5.5
External	191	11 ± 4.4
Organic deposition	191	62 ± 6.9
Oxide deposition	191	35 ± 6.7
Non-organic spots	277	65 ± 5.6
External	180	69 ± 6.7
Internal	180	69 ± 6.7
Shell infilling	24	58 ± 19.7

SUPPLEMENTARY DATA

SUPPLEMENTARY TABLE 1—Results for Mann-Whitney U test (Z values) for comparisons between taphonomic signatures, according size-class, of dead assemblages of the Touro Passo River (Kotzian and Simões, 2006) and fossil assemblages from the Touro Passo Formation. Three databases are compared: Complete = with all size-classes; Restrictive 1 (R1) = fragment size <0.5 cm and fragmentation degree >80% unconsidered, and; Restrictive 2 (R2) = fragment size <1.0 cm and fragmentation degree >80% unconsidered.

	Complete	p-value	R1	p-value	R2	p-value
Disarticulation	-9.961	0.000	-9.598	0.000	-9.316	0.000
Right Valve	-3.168	0.002	-3.289	0.001	-3.112	0.002
Fragmentation	-40.813	0.000	-37.167	0.000	-32.421	0.000
Edge rounding						
Small-chipped	-9.096	0.000	-9.151	0.000	-9.275	0.000
Very-chipped	-4.057	0.000	-4.089	0.000	-4.022	0.000
Edge texture						
Sharp	-13.142	0.000	-13.130	0.000	-13.119	0.000
Polished	-4.646	0.000	-4.541	0.000	-4.526	0.000
Foliated	-9.019	0.000	-9.030	0.000	-8.956	0.000
Fragmented edge texture						
Sharp	-4.080	0.000	-3.654	0.000	-3.059	0.002
Polished	-0.910	0.363	-1.082	.279	-1.258	0.208
Foliated	-14.004	0.000	-13.577	0.000	-12.281	0.000
Umbo condition	-0.468	0.640	-0.440	0.660	-0.498	0.618
Apex condition	-2.022	0.043	-2.108	0.035	-2.309	0.021
Surface pitting						
Small pitting	-1.611	0.107	-0.962	0.336	-0.548	0.584
Large pitting	-6.450	0.000	-5.847	0.000	-5.131	0.000
Sculpture presence						
Partial	-26.432	0.000	-24.712	0.000	-22.279	0.000
Absent	-1.644	0.100	-1.884	0.060	-2.266	0.023
Sculpture condition						
Polished sculpture	-2.917	0.004	-2.906	0.004	-2.949	0.003

Foliated sculpture	-12.916	0.000	-12.234	0.000	-11.074	0.000
Hinge erosion	-24.271	0.000	-21.910	0.000	-18.522	0.000
Muscle scars presence	-40.304	0.000	-36.504	0.000	-31.801	0.000
Palial line	-7.531	0.000	-7.393	0.000	-7.163	0.000
Anterior aductor	-2.750	0.006	-2.816	0.005	-2.665	0.008
Posterior aductor	-5.869	0.000	-5.706	0.000	-5.181	0.000
Precipitations	-9.132	0.000	-8.703	0.000	-8.538	0.000
Rhyzoconcretions						
Internal	-4.281	0.000	-4.579	0.000	-5.282	0.000
External	-2.540	0.011	-2.797	0.005	-2.969	0.003
Organic sheets	-3.980	0.000	-3.707	0.000	-3.008	0.003
Oxide deposits	-2.991	0.003	-3.187	0.001	-3.226	0.001
Non organic spots	-19.510	0.000	-19.793	0.000	-20.241	0.000

4. CONCLUSÕES E PERSPECTIVAS

As assembléias de moluscos do Rio Touro Passo não estão bem preservadas na Formação Touro Passo, tanto em termos de fidelidade quantitativa (e.g., riqueza, abundância e ordem de dominância de espécies), quanto no que se refere à assinaturas tafonômicas. A riqueza de espécies de moluscos da Formação Touro Passo é pouco parecida com a das assembléias vivas (45% de espécies vivas também encontradas fósseis) e mortas (58% de espécies mortas também encontradas fósseis) do Rio Touro Passo. A pequena similaridade entre a tafocenose e as associações atuais é creditada à tendenciamentos não-tafonômicos, como o empobrecimento da malacofauna atual e a introdução de espécies alienígenas. Desse modo, a fidelidade quantitativa pode ser uma importante ferramenta para estudos de Biologia da Conservação, uma vez que permite o acesso a informações hoje perdidas, mas armazenadas no registro sedimentar, como a informação sobre a biodiversidade original.

As assinaturas tafonômicas de moluscos fósseis revelam tendenciamentos estritamente relacionados a processos diagenéticos ou paleoambientais, que atuaram na tafocenose estudada. O perfil tafonômico geral da tafocenose mostra que a dissolução química das conchas é muito intensa após o soterramento, tal como demonstrado pela freqüência de rizoconcreções, o que pode ter resultado na alta freqüência de fragmentação de suas conchas e o estado geral de grande degradação apresentado pelas mesmas. Ou seja, os danos observados em conchas fósseis não podem ser usados para interpretações de fatores ambientais, com base nos resultados obtidos em tanatocenoses. Se assim fosse, poderia ser inferido que os moluscos da Formação Touro Passo, habitaram um antigo Rio Touro Passo com condições de águas mais ácidas e mais energéticas, já que a taxocenose encontrada não é representativa desse tipo de ambiente.

Os resultados obtidos também mostram que mais estudos sobre a origem das assinaturas em meio fluvial são necessários, pois os dados aqui apresentados são pontuais e pioneiros, já que se trata do primeiro registro de assinaturas tafonômicas em moluscos de água doce. Quanto à fidelidade quantitativa, devem ser investigadas áreas não impactadas, embora atualmente seja difícil encontrar ambientes de águas continentais não alterados.

Este trabalho pode servir como base de comparação para estudos regionais mais amplos, como a investigação de padrões de conservação da fidelidade quantitativa no registro sedimentar pleistocênico, e assim verificar possíveis tendências gerais de perda de espécies atuais. Também pode ser utilizado para determinar padrões regionais (i.e., escala de bacia) de possível seletividade na preservação de espécies no registro sedimentar.

Também é necessário testar a origem das assinaturas tafonômicas em moluscos de habitats semelhantes, preferencialmente em rios de morfologia meandrante e determinar padrões mais amplos de dano tafonômicos em moluscos de água doce, atuais e fósseis, de modo que interpretações paleoecológicas e paleoambientais se tornem mais confiáveis.

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6. ANEXO: PALAIOS AUTHOR’S GUIDELINES