UNIVERSIDADE ESTADUAL PAULISTA

Instituto de Geociências e Ciências Exatas

Campus de Rio Claro

BIVALVES PERMIANOS DA FASE DE CONTINENTALIZAÇÃO DAS BACIAS DO GONDWANA OCIDENTAL: SISTEMÁTICA, PALEOGEOGRAFIA E BIOESTRATIGRAFIA

Juliana Machado David

Orientador: Prof. Dr. Marcello Guimarães Simões

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Dissertação de Mestrado elaborada junto ao Curso de Pós-Graduação em Geologia Regional - Área de Concentração em Bacias Sedimentares, para obtenção do Título de Mestre em Geologia Regional.

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- Juliana Machado David -

Rio Claro, 19 de novembro de 2010

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Para os meus pais. Sempre.

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“Um homem deveria examinar por si mesmo a grande pilha de estratos superpostos e ver os riachos carregando argila e as ondas desgastando as falésias marinhas para poder compreender algo sobre a duração do tempo passado, cujos monumentos vemos em todo o nosso redor.”

Charles Darwin

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LISTA DE SIGLAS

IBB/UNESP - Instituto de Biociências, Universidade Estadual Paulista, Campus de Botucatu;

IG/SMA – Instituto Geológico, Secretaria do Meio Ambiente;

IGCE/UNESP – Instituto de Geociências e Ciências Exatas, Universidade Estadual Paulista, Campus de Rio Claro.

IGc/USP – Instituto de Geociências, Universidade de São Paulo, Campus São Paulo.

DGP – Sigla da Coleção Científica do Departamento de Paleontologia e Estratigrafia, Universidade de São Paulo, Campus São Paulo.

DZP – Departamento de Zoologia, Paleontologia. Sigla da Coleção Científica de Paleontologia do Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista, Campus de Botucatu.

URC MB – Sigla da Coleção Científica do Departamento de Geologia Aplicada, Instituto de Geociências e Ciências Exatas, Universidade Estadual Paulista, Campus Rio Claro.

RESUMO

O estudo de bivalves da Formação Gai-As, Permiano, área de Huab, NW da Namíbia, indicou a presença de espécies anteriormente conhecidas apenas no Grupo Passa Dois, Permiano, Bacia do Paraná, Brasil, possibilitando o aprimoramento das correlações estratigráficas entre as duas bacias. A fauna da Formação Gai-As ocorre em intervalos estratigráficos bem definidos, um na porção basal e outro na porção superior. Em ambos, a deposição final das conchas ocorreu sob a influência de eventos episódicos de alta energia. As espécies encontradas no intervalo basal compreendem *Cowperesia emerita*, *Terraia* cf. *altissima* e *Terraia* cf. *curvata*, enquanto no intervalo superior apenas *Huabiella compressa* gênero e espécie novos, e *Terraia* cf. *curvata* estão presentes Os táxons sugerem correlação entre a Formação Gai-As e a porção basal do Membro Serrinha, Formação Rio do Rasto. Adicionalmente, conforme dados prévios de literatura, na Formação Gai-As, logo acima das últimas ocorrências de bivalves do intervalo superior, existem tufos vulcânicos, cuja datação radiométrica de minerais de zircão indica idades em torno de 265+2.5 Ma., aproximadamente no limite Wordiano-Capitaniano. Essas idades são muito próximas das recentemente obtidas para minerais de zircão de cinzas vulcânicas na Formação Teresina (267±17 Ma.) e no Membro Serrinha 266.3±4.6 Ma. da Bacia do Paraná.

Palavras-chaves: Bivalves, área de Huab, Formação Gai-As, Biocorrelação, Formação Rio do Rasto.

ABSTRACT

The taxonomic study of bivalve mollusks of the Gai-As Formation, Permian, Huab area, Namibia, allowed the identification of species previously recorded only in the Permian Passa Dois Group, Paraná Basin, Brazil, improving the stratigraphical correlations between both basins. In the Gai-As Formation, bivalve shells are recorded in two well defined stratigraphical intervals, in the lower and upper portions. In both cases, the final deposition of the bivalve shells was a result of high energy episodic events. The species recorded in the lower portion are *Cowperesia emerita*, *Terraia* cf. *altissima* and *Terraia* cf. *curvata*. In the upper portion there are *Huabiella compressa* new gen. and sp., and *Terraia* cf. *curvata*. These bivalve species corroborate the correlation of Gai-As Formation to the lower portion of the Serrinha Member, Rio do Rasto Formation. Additionally, according to literature, in Gai-As Formation, fallout tuffs deposited immediately above the last occurrences of bivalves of the upper portion, bear zircon grains, whose radiometric shrimp U/Pb dating provided ages of 265±2.5 Ma., equivalent to the Wordian-Capitanian boundary. This age is very close to that recently recorded from zircon grains found in ash-beds of the Teresina Formation (267±17 Ma.) and the Serrinha Member (266.3±4.6 Ma.) of the Paraná Basin.

Key words: Bivalvia, Huab area, Gai-As Formation, Biocorrelation, Rio do Rasto Formation.

APRESENTAÇÃO

O presente documento procura sintetizar os dados e resultados obtidos nos 24 meses de realização da Dissertação de Mestrado, junto ao Programa de Geologia Regional (Análise de Bacias Sedimentares) do IGCE/UNESP, campus de Rio Claro, SP. O tema central da dissertação diz respeito ao estudo paleontológico dos moluscos bivalves, permianos, da Formação Gai-As, área de Huab, NW da Namíbia e suas implicações paleoecológicas e bioestratigráficas. O estudo, conforme será visto mais adiante, está fundamentado em uma coleção de fósseis obtidos pelo Dr. Frank Holzfoerster do Instituto de Geologia, da Universidade de Wuerzburg, Alemanha, a qual foi trazida ao Brasil, em 1998, pelo orientador da presente dissertação. Desde então, a despeito de sua importância taxonômica e bioestratigráfica, essa coleção permaneceu não estudada.

A estrutura do documento segue as normas do Programa de Pós-graduação do IGCE/UNESP e divide-se em três capítulos e demais anexos. O primeiro capítulo refere-se à Introdução, na qual é explorado o contexto em que a presente dissertação insere-se, bem como a motivação de sua realização e os objetivos da pesquisa desenvolvida. O segundo capítulo, que constitui o corpo principal da Dissertação, diz respeito ao estudo taxonômico, tafonômico e paleoecológico realizado sobre os bivalves permianos da Formação Gai-As, área de Huab, NW da Namíbia, contendo o artigo submetido à revista de paleontologia australiana Alcheringa, intitulado: “Permian bivalve mollusks from the Gai-As Formation, Northern Namibia: Systematics, Taphonomy and Biostratigraphy”. O terceiro capítulo trata das Considerações Finais, o qual engloba as conclusões, apresentando um texto integrador, expondo os principais resultados obtidos na dissertação, além das perspectivas de estudos futuros. Neste subitem do último capítulo são apresentados alguns resultados obtidos na revisão sistemática preliminar dos gêneros *Anhembia* e *Leinzia*, motivada pelo relato prévio na literatura de formas semelhantes à *Leinzia similis* na Formação Gai-As, área de Huab, NW da Namíbia.

Por fim, seguem-se aos elementos textuais desta dissertação, quais sejam os Anexos, que contêm duas figuras referentes aos gêneros *Anhembia* e *Leinzia*, além de um artigo no qual a aluna é co-autora, também sobre tema correlato à dissertação. De fato, durante o desenvolvimento do projeto de mestrado tornou-se inevitável à aluna travar contato mais estreito com os bivalves permianos da Bacia do Paraná, em especial, aos do Grupo Passa Dois. Nesse sentido, foram conduzidas, paralelamente, pesquisas

enfocando problemas ainda pendentes relativos a estes fósseis, maiormente, relacionados à taxonomia da fauna de bivalves do Grupo Passa Dois. Com isso, foi possível iniciar a revisão de alguns gêneros importantes para compreensão da sistemática e evolução da fauna da Formação Gai-As, bem como descrever outros relacionados à fase de continentalização da Bacia do Paraná (*e.g.*, Formação Rio do Rasto). De imediato, esses estudos produziram o artigo que se encontra presente nos anexos desta dissertação, intitulado "A new Permian bivalve (Megadesmidae, Plesiocyprinellinae) from the Serrinha Member, Rio Do Rasto Formation, Paraná Basin, Brazil". Cumpre lembrar que este artigo já foi publicado em julho de 2010, na Revista GEOLOGIA USP - SÉRIE CIENTÍFICA - Vol. 10 - Núm. 2 – pg. 13-21, publicada pelo Instituto de Geociências da Universidade de São Paulo (IGc/USP) .

1. INTRODUÇÃO

Moluscos bivalves estão entre os elementos mais comuns e conspícuos do registro fóssil do Grupo Passa Dois (Permiano), da Bacia do Paraná (MENDES, 1952; BEURLEN, 1957; RUNNEGAR; NEWELL, 1971; SIMÕES; ROCHA-CAMPOS; ANELLI, 1998), Brasil. As principais ocorrências provêm, principalmente, das biozonas de *Anhembia froesi* Mendes, 1949, *Pinzonella illusa* Reed, 1932, *Pinzonella neotropica* (Reed), 1932, e *Leinzia similis* Mendes, 1949, que ocorrem em sucessão estratigráfica nas formações Serra Alta, Teresina/Corumbataí e Rio do Rasto (vide ROHN, 1994). Existem menções também à presença de bivalves em rochas atribuíveis à Formação Irati, do Estado do Paraná, mas essas permanecem ainda não descritas (KAZUBEK; SIMÕES, 2003; LAGES, 2004).

A ocorrência de bivalves no Grupo Passa Dois, Bacia do Paraná é internacionalmente conhecida (vide WESSELINGH, 2007) por três motivos principais: a - o excelente estado de preservação dos fósseis, b - sua história evolutiva complexa e c - o alto grau de endemismo e disparidade morfológica dos gêneros e espécies presentes. As conchas fósseis ocorrem muitas vezes silicificadas, em coquinas ou arenitos bioclásticos, interpretados como tempestitos proximais (*e.g.*, SIMÕES; TORELLO; ROCHA-CAMPOS, 1996), e são dominadas por bivalves megadesmídeos, que claramente evoluíram de ancestrais marinhos presentes no Grupo Tubarão e em outras seqüências marinhas do Paleozóico da América do Sul (RUNNEGAR; NEWELL, 1971; SIMÕES; MARQUES; MELLO; ANELLI, 1997; SIMÕES; ROCHA-CAMPOS; ANELLI, 1998).

O alto grau de endemismo desta fauna é destacado desde Mendes (1952) e Beurlen (1957) e de fato, até 1984, não existiam ocorrências de bivalves do Grupo Passa Dois fora da Bacia do Paraná. No entanto, Cooper e Kensley (1984) registraram e ilustraram bivalves semelhantes, morfologicamente, aos das formações Serra Alta e Teresina/Corumbataí, na Formação Waterford (Permiano), Grupo Ecca, Bacia do Karroo, África do Sul. Consequentemente, os bivalves do Grupo Passa Dois não poderiam mais ser considerados restritos à Bacia do Paraná. Entretanto, Dickins (1992, p. 989) não aceitou completamente as identificações destes bivalves africanos. Dessa maneira, a ocorrência de bivalves permianos da Bacia do Paraná em depósitos da Bacia do Karoo é ainda questionável.

Alguns anos mais tarde, Horsthemke (1992) e Ledendecker (1992), baseados na presença de bivalves endêmicos, correlacionaram a Formação Gai-As, área de Huab,

NW Namíbia às formações Serra Alta e Teresina e à porção inferior da Formação Rio do Rasto, Bacia do Paraná. Por sua vez, Stollhofen, Stanistreet, Rohn, Holzfoerster e Wanke, (2000) e Wanke (2000) mencionaram a presença de bivalves permianos da Bacia do Paraná, assembléia de *Terraia altissima*, Formação Rio do Rasto (Membro Serrinha), na Formação Gai-As, NW Namíbia. Segundo Wanke (2000), a principal forma presente é *Leinzia similis*, um dos gêneros mais interessantes (morfologicamente) da fauna do Grupo Passa Dois, em razão da presença de uma expansão na porção anterior de suas conchas, denominada *rostrum* (vide discussões em RUNNEGAR; NEWELL, 1971; SIMÕES; ROCHA-CAMPOS; ANELLI, 1998; GHILARDI, 1999; MELLO; SIMÕES; MARQUES; GHILARDI, 1999). Entretanto, a despeito das implicações evolutivas, paleoambientais e bioestratigráfica destas ocorrências africanas, estes bivalves nunca foram ilustrados, nem formalmente descritos.

1.1. DELIMITANDO O PROBLEMA

Os bivalves do Grupo Passa Dois evoluíram em ambiente do tipo lago/mar (vide ROHN, 1994), sob condições de extremo isolamento geográfico e salinidade variável (RUNNEGAR; NEWELL, 1971; SIMÕES; ROCHA-CAMPOS; ANELLI, 1998). Trata-se do mais antigo exemplo conhecido de evolução *in situ* na história evolutiva dos moluscos bivalves (WESSELINGH, 2007). Porém, a despeito dos enormes avanços ocorridos na compreensão da evolução (SIMÕES; MARQUES; MELLO; ANELLI, 1997; SIMÕES; ROCHA-CAMPOS; ANELLI, 1998), da gênese das concentrações fossilíferas (SIMÕES; TORELLO; ROCHA-CAMPOS, 1996; SIMÕES; KOWALEWSKI, 1998; SIMÕES; TORELLO; MELLO; GHILARDI, 2000; SIMÕES; TORELLO, 2003; ROHN; MEGLHIORATTI; CORDEIRO-SILVA, 2007; NEVES, 2009), paleoecologia (GHILARDI, 1999) e distribuição bioestratigráfica da fauna (ROHN, 1994), vários problemas ainda persistem referentes à sistemática, história evolutiva e morfologia funcional daqueles bivalves. Paralelamente, novas ocorrências foram descobertas em rochas permianas da Namíbia, demonstrando que a distribuição paleobiogeográfica de alguns gêneros era, possivelmente, mais ampla do que o suposto anteriormente.

A ocorrência de *Leinzia similis* na Formação Gai-As, Namíbia, sugerida por vários autores (STOLLHOFEN; STANISTREET; ROHN; HOLZFOERSTER; WANKE, 2000; WANKE, 2000; ROHN, 2007) reveste-se de grande importância do ponto de vista bioestratigráfico. No Grupo Passa Dois, essa espécie está confinada aos

níveis estratigráficos referentes ao Membro Serrinha, na parte inferior da Formação Rio do Rasto (ROHN, 1994, 2007). Há mais de um século a questão da idade do Grupo Passa Dois vem sendo debatida na literatura, com autores argumentando a favor de uma idade permiana ou triássica, ao menos para parte do topo do Grupo Passa Dois. Na borda leste da Bacia do Paraná, o topo do Grupo Passa Dois é representado pela Formação Rio do Rasto (veja síntese em ROHN, 1994, 2007), cujos fósseis de conchostráceos, plantas vasculares e anfíbios são indicativos de idade pré-Triássica, recentemente confirmada pelos dados geocronológicos de Rocha-Campos, Basei e Dos Santos, (2009). Nesse sentido, a suposta presença de *L. similis* nos depósitos da Formação Gai-As, área de Huab, NW Namíbia, reveste-se de grande importância, pois nesta Formação africana esses fósseis são encontrados em horizonte fossilífero, pouco abaixo de tufos vulcânicos, cuja datação radiométrica de minerais de zircão indicam idades de aproximadamente 265+2.5 Ma (limite Wordiano-Capitaniano) (STOLLHOFEN; STANISTREET; ROHN; HOLZFOERSTER; WANKE, 2000; WANKE, 2000; ROHN, 2007). Porém, conforme acima referido, esses fósseis nunca foram ilustrados ou formalmente descritos e poderiam constituir informação adicional e independente a favor de uma idade pré-Triássica para os depósitos coevos do Grupo Passa Dois, da Bacia do Paraná.

Em decorrência dos comentários expostos acima, a pesquisa desenvolvida têm como tema central o estudo taxonômico e tafonômico das ocorrências de moluscos bivalves de idade permiana da Formação Gai-As, área de Huab, NW Namíbia, incluindo interpretações paleobiológicas, paleoecológicas e bioestratigráficas. Ele insere-se na linha de pesquisa desenvolvida pela Dra. Rosemarie Rohn Davies e pelo Dr. Marcello G. Simões que, há mais de duas décadas, têm envidado esforços no sentido de compreender a evolução da fauna de moluscos do Grupo Passa Dois, bem como das condições ambientais reinantes durante o intervalo de tempo referente ao Grupo Passa Dois, com especial atenção à borda leste da Bacia do Paraná. Por fim, o estudo aqui proposto, envolvendo as ocorrências do continente africano, poderá fornecer novos dados para o entendimento da evolução, distribuição geográfica e significado bioestratigráfico desses bivalves.

1.2. OBJETIVOS

Em razão do acima exposto, a presente dissertação de Mestrado tem como objetivos principais:

1- a descrição e identificação taxonômica dos bivalves fósseis da Formação Gai-As, da Namíbia;

2- o estudo tafonômico dos bivalves da Formação Gai-As, Namíbia, com a finalidade de entender os processos e ambientes de fossilização dessas conchas, no contexto paleoambiental de seu intervalo de ocorrência;

3- a análise do significado bioestratigráfico dos bivalves da Formação Gai-As, Namíbia;

4- revisão sistemática preliminar do gênero *Anhembia* e *Leinzia*, das formações Serra Alta, Corumbataí e Rio do Rasto.

Conforme já comentado na apresentação desse documento, além dos objetivos acima, durante o desenvolvimento do mestrado foi possível travar contato com outros bivalves fósseis do Grupo Passa Dois, Bacia do Paraná, em especial do Membro Serrinha, Formação Rio do Rasto, resultando na descrição de um novo gênero de bivalve para este intervalo estratigráfico (vide anexo).

1.3. MATERIAIS E MÉTODOS

O presente projeto de mestrado se valeu de três conjuntos de dados, sendo o primeiro a pequena coleção de bivalves fósseis provenientes da Formação Gai-As, NW da Namíbia, os quais se encontram no Laboratório de Paleozoologia Evolutiva do IBB/UNESP. O segundo compreendeu os espécimes de *Anhembia* e *Leinzia* provenientes das formações Serra Alta, Corumbataí e Rio do Rasto, pertencentes a quatro coleções científicas, ou seja, IBB/UNESP, IG/SMA, IGCE/UNESP e IGc/USP. O terceiro conjunto de dados englobou materiais da Formação Rio do Rasto, já preparados e parcialmente estudados, os quais estavam depositados no IGc/USP.

Os materiais estudados e os métodos de análises empregados no estudo em desenvolvimento aparecem detalhadamente descritos em cada um dos artigos que compõem esse documento de dissertação. Em linhas gerais, do ponto de vista taxonômico, os procedimentos metodológicos a serem seguidos são os mesmos descritos em Simões *et al.* (1997), sendo que a classificação está fundamentada em Runnegar e Newell (1971) e Runnegar (1974). A preparação física, moldagem e fotografia dos exemplares seguiram Mello (1999) e Anelli (1999). Já a descrição tafonômica, especialmente das ocorrências da Namíbia, seguiram Kidwell *et al.* (1986), Brett e Baird (1986) e Fürsich e Oschmann (1986, 1993).

2. BIVALVES PERMIANOS DA FORMAÇÃO GAI-AS, ÁREA DE HUAB, NW NAMÍBIA

2.1. COMPROVANTE DE SUBMISSÃO DO ARTIGO

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2.2. PERMIAN BIVALVE MOLLUSKS FROM THE GAI-AS FORMATION, NORTHERN NAMIBIA: SYSTEMATICS, TAPHONOMY, AND BIOSTRATIGRAPHY

JULIANA M. DAVID, MARCELLO G. SIMÕES, LUIZ E. ANELLI, ROSEMARIE ROHN AND FRANK HOLZFOERSTER

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Fossil bivalves from two horizons in the Gai-As Formation of NW Namibia are tentatively correlated with mid-Permian taxa of the Passa Dois Group of Brazil, supporting the concept that the Paraná Basin extended into Africa. The Namibian fauna includes a new genus and species, *Huabiella compressa*, which was previously confused with Brazilian taxa. The taphonomy of the bivalve-rich strata indicates deposition under the influence of episodic events, such as storms. The Gai-As Formation directly overlies the mesosaurid-bearing deposits of the Huab Formation, indicating a significant unconformity when compared to the more complete succession of the Passa Dois Group, Paraná Basin, Brazil. The studied bivalve assemblages are no younger than 265±2.5 Ma (mid-Permian), based on U/Pb radiometric dating of zircons from tuffs.

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Key words: Bivalvia, Megadesmidae, Permian, Huab area, Gai-As Formation, biostratigraphy, Rio do Rasto Formation.

DURING the late Palaeozoic, large areas of western Gondwana (South America and Africa) were covered by an extensive inland sea in which part of the Permian successions of the Paraná (Brazil, Argentina, Paraguay and Uruguay), Karoo (South Africa) and Huab (NW Namibia) basins were deposited. In the late Early Permian, this large inland sea was either isolated or had a restricted connection to the Permian oceans. As demonstrated by the Permian succession of the Paraná Basin (*ca* 281–265 Ma, Holz *et al.* 2010), this inland sea was very shallow, with variable salinity regimes (hypersaline, brackish, and freshwater) due to climatic changes (humid to arid: Rohn 1994, Holz *et al.* 2010). Benthic faunas within this inland sea were dominated by bivalve molluscs that flourished despite the conditions of high environmental stress and extreme geographic isolation (Mendes 1952, Runnegar & Newell 1971, Simões *et al.* 1998, 2000). This is one of the oldest known examples of a molluscan long-lived fauna that evolved within an epeiric sea (Wesselingh 2007). The fauna was endemic, with high morphological disparity and was dominated by megadesmid bivalves, which had clearly evolved from marine ancestors (Runnegar & Newell 1971, Simões *et al.* 1997, 1998).

At least 24 generic names had been applied to bivalves from the Paraná Basin prior to the publication of the benchmark monograph on Permian Passa Dois Group molluscs

by Runnegar & Newell (1971). None of these names has been applied to species or genera found outside the Paraná Basin (Runnegar & Newell 1971). Cooper & Kensley (1984) were the first authors to record bivalves in the Permian deposits of the South African Waterford Formation, Ecca Group (Karoo Basin), ascribing them to typical Permian genera of the Paraná Basin. Consequently, the bivalves could no longer be considered endemic to the Paraná Basin, although Dickins (1992, p. 989) did not fully accept the identifications of the African forms by Cooper & Kensley (1984). As a result, this particular Karoo Basin fauna needs to be fully revised and re-described. Therefore, the occurrence of Permian bivalves in common with the Paraná Basin (Brazil, Uruguay and Paraguay) in deposits of the Karoo Basin has remained questionable.

A new Permian bivalve occurrence was recorded in lacustrine deposits of the Gai-As Formation (Huab Basin, NW Namibia) by Ledendecker (1991, 1992), who identified *Terraia altissima* (Holdhaus, 1919), a taxon known from the upper portion of the Passa Dois Group (Rio do Rasto Formation) of the Paraná Basin in Brazil and Uruguay. This information was confirmed by Holzfoerster (2000, 2002), Stollhofen *et al*. (2000) and Wanke (2000), and further occurrences were recorded, together with the discovery of bivalves tentatively assigned to *Leinzia similis* (Holdhaus, 1918). Unfortunately, these bivalve molluscs were not properly figured or described. Given the importance of bivalves for biocorrelation and the need for detailed descriptions of the fossil assemblage, the German sedimentologists contacted Brazilian palaeontologists and sent the fossils for further study. This paper aims to: (1) identify and describe the Permian bivalves of the Gai-As Formation, Namibia; (2) compare the fauna with coeval assemblages of the Paraná Basin, Brazil, and (3) describe the taphonomic features of the bivalve assemblages.

Geological setting

The Permian succession of the Huab area in northern Namibia (Fig. 1), comprises two sedimentary successions that include fluvio-marine deposits (Verbrandeberg, Tsarabis and Huab formations) and lacustrine deposits (Gai-As and Doros formations; Figs 2, 3). These deposits were described by Stranistreet & Stollhofen (1999), Holzfoerster (2000, 2002), Stollhofen *et al.* (2000) and Wanke (2000), and their relevant results are summarized below.

Insert Figures 1, 2, 3

The lacustrine sequence, yielding unique bivalve shells, reaches 170 m thick and initiates with the Gai-As Formation, which is divided into lower and upper subunits (Holzfoerster 2000, 2002, Stollhofen *et al.* 2000, Wanke 2000; Fig. 3). The Gai-As Formation is separated from the underlying marine, mesosaurid-bearing deposits of the Huab Formation by a significant hiatus (Wanke 2000), and is succeeded unconformably by the sandy deposits of the Doros Formation. The Gai-As and Doros formations represent an overall shallowing and coarsening-upward interval (Holzfoerster 2000, 2002, Stollhofen *et al.* 2000, Wanke 2000). The lower Gai-As deposits comprise 65 m of laminated claystones and mudstones representing a hemi-pelagic facies association, whereas the upper Gai-As deposits comprise mainly mudstones with interbedded limestones, sandstones and fallout tuffs resembling a shallowing-upward lacustrine association. The overlying Doros Formation is characterized by sandstones and conglomerates with subordinate interbeds of mudstones and limestones representing a lake-margin facies association.

Within the lacustrine sequence, bivalves occur in both the lower and upper Gai-As deposits (Fig. 3). The lower unit of the Gai-As Formation, from which part of our samples were derived, is widespread in the central Huab region. According to

Holzfoerster (2000, 2002), Stollhofen *et al.* (2000) and Wanke (2000), the basal strata of the Gai-As Formation comprise reddish to violet, mostly laminated argillaceous to silty shales, containing 1–3 cm thick tabular interbeds of normally graded, medium-grained sandstones and a few 10–50 cm thick, laminated limestone beds (Fig. 3). This informally named lower Gai-As Formation (Stollhofen *et al.* 2000) contains at least two widespread beds with conspicuous concentrations of bivalve shells (Wanke 2000).

The informally named upper Gai-As Formation (Stollhofen *et al.* 2000), thins from 80 m at the Namibian coast to 10–20 m thickness inland and comprises red–violet mudstones containing minor tabular sandstone interbeds, laminated or small-scale cross-bedded limestone, and fallout tuff deposits. Eastwards, intense pedogenic modification is apparent. The fine- to medium-grained sandstones, 1–10 cm thick, are normally graded and show rare hummocky cross-bedding, basal load casts, wave-rippled tops and *Monocraterion*-like escape structures (Holzfoerster 2000, 2002, Wanke 2000). They are interpreted as tempestite or turbidite beds arranged in a thickening- and coarsening-upward architecture. At least four horizons of interlaminated limestone/sandstone beds (single layers 2–5 cm thick) contain conspicuous concentrations of articulated and disarticulated bivalve shells.

Systematic palaeontology

Nearly 20 small (15 cm long) slabs of fossiliferous sediment from the Gai-As Formation were available for study, originally collected in Namibia by one of us (Frank Holzfoerster). The bivalves occur in mudstone and very fine sandstone. The samples are housed in the scientific collection of the Zoology Department of the São Paulo State University, Botucatu campus, under the code DZP. The material comprises 28 shells, some of which were mechanically extracted, following standard palaeontological

techniques described by Feldmann *et al*. (1989). However, many shells were kept in the original matrix for taphonomic studies.

The suprageneric systematics for the anomalodesmatans and crassatellaceans follows Morris *et al*. (1991). The morphological terminology and systematic classification of megadesmids is based on Mendes (1952), Runnegar & Newell (1971), Runnegar (1974) and Simões *et al*. (1997). The mode of life of Gai-As bivalves has been interpreted from shell morphology, dimensions and muscle scars (where preserved) following Stanley (1970).

Subclass HETEROCONCHIA Hertwig, 1895

Superorder HETERODONTA Neumayr, 1883

Order VENEROIDA Adams & Adams, 1856

Superfamily CRASSATELLOIDEA Férussac, 1822

Family Uncertain

Terraia Cox, 1934

Type species. *Terraia altissima* (Holdhaus, 1918); Late Permian, Brazil.

Terraia sp. cf. **T**. **altissima** (Holdhaus, 1918) **(**Fig. 4A–E)

Material examined. Four single silicified shells (DZP-18706, 18707, 18708, 18711) and one internal mould (DZP-18710).

Locality and unit. Huab region, Namibia, lower Gai-As Formation, Huab Sedimentary Basin.

Age. Permian, Wordian.

Description. Shell small, equivalved, inequilateral, elongate. Two well-defined posterior umbonal carinae extending from umbonal region to the postero-dorsal and postero-ventral angles, each ridge bearing 6–7 visible protuberances (knobs; Fig. 4A–D), which are visible in the internal moulds (Fig. 4B, E). The ventral carina is always stronger; the dorsal carina borders the escutcheon. Umbones low, extending beyond the dorsal margin, with slightly prosogyrous beaks. Anterior margin strongly rounded (Fig. 4B); ventral margin broadly arcuate (Fig. 4D); posterior margin angular where intercepted by the two posterior carinae, and straight between (Fig. 4B). External ornament of co-marginal spaced growth lines. Ligament, muscle scars and hinge features unknown.

*Remarks***.** The shell shape and external ornament of the Gai-As specimens are very similar to *Terraia altissima* (Fig. 4F), which is common in bivalve assemblages from the basal part of Rio do Rasto Formation, Paraná Basin, Brazil. The six to seven protuberances (knobs) on the posterior-umbonal carinae are similar to those found in specimens of *T. altissima* from the Paraná Basin (Runnegar & Newell 1971, p. 49, fig. 21, Rohn 1994, p. 361, fig. 169-1), but the Namibian specimens lack the slight flexure of the ventral margin anterior to the posterior-umbonal carina (see Fig. 4F). The hinge is not visible in the Huab material, making a more accurate comparison with specimens figured by Runnegar & Newell (1971) difficult. Consequently, the Namibian specimens are identified as *Terraia* sp. cf. *T. altissima* (Holdhaus 1918).

Insert table I

Terraia sp. cf. **T**. **curvata** (Reed, 1929) (Fig. 4G–H)

Material examined. One silicified shell (DZP-18712) and one external mould (DZP-18709).

Locality and unit. Huab region, Namibia, lower and upper Gai-As Formation, Huab Basin.

Age. Permian, Wordian.

Description. Shell small, subtriangular, anterior margin broadly rounded and slightly angular where it intercepts dorsal margin; dorsal margin posterior to umbo, slightly arched, descending steeply to small obliquely truncated respiratory margin. External surface of shell with two arched, posterior umbonal carinae; the second carina being close to dorsal margin. Posterior margin appears truncated between the carinae. Umbones low, subcentral, with slightly prosogyrous beaks. External ornament of co-marginal spaced growth lines. Hinge and muscle scars not preserved.

Remarks. The Gai-As Formation specimens are very similar to *Terraia curvata* described from Brazil by Reed (1929, pl. I, figs 6, 7). The muscle scars and hinge are not preserved in the Namibian specimens, making a more accurate comparison difficult. *Terraia curvata* occurs with *Terraia altissima* in the Serrinha beds of the Rio do Rasto Formation, Paraná Basin. These forms are morphologically similar, and Mendes (1952) tentatively suggested that *Terraia curvata* might be a junior synonym of *T. altissima* (for discussion, see Beurlen 1953, 1954). Beurlen (1954, 1957), however, regarded the general shell profile and hinge structure of both species as distinct. The Namibian

specimens of *Terraia* sp. cf. *T. curvata* have a more equilateral shell that bears two well-defined arched carinae. The shell of *Terraia altissima* on the other hand, is more posteriorly elongated and has straighter posterior carinae, which bear well-defined projections. As specimens of *Terraia curvata* from the Paraná Basin (Serrinha Member), show well-preserved anterior muscle scars and hinge features (see Reed 1929), which are unknown in the Gai-As bivalves, we have identified the Namibian specimens as *Terraia* sp. cf. *T. curvata*.

Insert table II

Insert Figure 4

Superorder ANOMALODESMATA Dall, 1899

Order PHOLADOMYOIDA Newell, 1965

Superfamily PHOLADOMYOIDEA (King) Gray, 1847

Family MEGADESMIDAE Vokes, 1967

Huabiella gen. nov.

Type-species. *Huabiella compressa* gen. et sp. nov.

Diagnosis. Shell small, compressed, very elongate and posteriorly expanded. Anterior margin of shell with poorly defined expansion; umbonal carina well marked, extending diagonally from beak to posterior-ventral margin.

Etymology. After the Huab area in northern Namibia.

Remarks. Huabiella can be distinguished from other Permian bivalves by a combination of external and internal characters. A well-defined rostrum is present in *Leinzia* Mendes, but absent in *Huabiella*. We do not consider the similar pattern of ornamentation of *Huabiella* (from Namibia) and *Leinzia* (from the Paraná Basin) to be a strong argument for con-specificity. Hammer (2000) has shown that the growth processes responsible for the concentric co-marginal ribs in bivalves, result from an oscillation in the regulatory system involving purely mechanical factors. This evaluation seems valid since among Permian megadesmids of the Paraná Basin, co-marginal ribs are found in genera as distinct as *Cowperesia* Mendes, 1952 and *Leinzia*. The main difference between *Huabiella* and *Leinzia*, besides the shell shape, is the absence of a well-defined rostrum in the anterior margin of the Namibian genus. The anterior margin of *Huabiella* shells has a small projection, very similar to that found in *Holdhausiella* Mendes, 1952 and *Favalia* Mendes, 1962 from the Corumbataí and Teresina formations (see Runnegar & Newell 1971, p. 41, fig. 16 and p. 43, fig. 17, respectively). However, in *Holdhausiella* and *Favalia* the hinge is edentulous and the posterior margin of the shell is straight.

Huabiella compressa sp. nov. (Fig. 5A–K)

Type Material. Six internal moulds (DZP-18687, 18690, 18691, 18692, 18693) and two external moulds (DZP-18688, 18689). Holotype, DZP-18686. Paratypes, DZP-18687, 18688, 18689, 18690, 18691, 18692, 18693.

Diagnosis. Huabiella shell ornamented by regularly spaced angular commarginal rugae.

Locality and unit. Huab region, Namibia, upper Gai-As Formation, Huab Basin.

Age. Permian, Wordian.

Description. Shell small, very elongate, posteriorly expanded, equivalved, inequilateral, compressed to very compressed. Dorsal and ventral margins subparallel; umbones low, beaks slightly prosogyrous. Anterior dorsal margin only slightly pronounced anteriorly; posterior margin straight or nearly so. Umbonal carina well marked, narrow and sharply rounded, extending diagonally from beak to posterior-ventral angle; delimiting a smooth, concave, elongate, triangular area below posterior dorsal margin. External ornamentation of regularly spaced rounded co-marginal rugae, separated by angular grooves. Rugae terminate abruptly against the posterior-umbonal carina without any projections. Ligament external, parivincular. Hinge and muscle scars unknown.

Discussion. *Huabiella compressa* superficially resembles *Leinzia similis* (Fig. 5L) from the middle to upper part of the Serrinha Member (Rio do Rasto Formation), and understandably, some authors (Stollhofen *et al.* 2000, Wanke 2000) have preliminarily assigned the Gai-As shells to this species. However, despite the relatively poor preservation of the examined specimens, the small anterior expansion in *H. compressa* is in no way comparable to the anterior rostrum of *Anhembia froesi* Mendes, and *L. similis*. The anterior expansion observed in *Huabiella compressa* is more similar to that recorded in other Permian megadesmids, such as *Holdhausiella elongata* (Holdhaus, 1918) and *Favalia arcuata* Mendes, 1962. In addition, *Huabiella compressa* shells lack protuberances at the intersection of the umbonal carina with the co-marginal rugae, or spinose projections along the posterior dorsal margin as in *L. similis* (see Runnegar & Newell 1971, p. 53). It should be noted that *Huabiella compressa* is very similar to specimens figured by Beurlen (1957, pl. 4, figs 23, 34–36) from the Serrinha Member of the Rio do Rasto Formation. These specimens were designated *Leinzia curta*

Beurlen, 1957, but were never formally described and no type material was selected. The illustrations are hand drawings and not photos. *Leinzia curta* should, therefore, be regarded as a *nomen nudem*. Rohn (1994, fig. 167-6) also recorded bivalves from the Serrinha Member that were similar to Beurlen's drawings, but these were never fully described.

Insert table III

Insert Figure 5

Cowperesia Mendes, 1952

Discussion. Runnegar & Newell (1971) suggested that *Cowperesia* Mendes, 1952 is a junior subjective synonym of *Pyramus* Dana, 1847. The following generic characters are listed for *Pyramus* by Runnegar & Newell (1971, p. 35): "shell oval, equivalved, with low umbones, inwardly directed beaks, and rounded to angular posterior umbonal slopes; lunule and escutcheon narrow, often poorly defined; valve margins closed anteriorly and ventrally, but usually with small siphonal gape; shell smooth or with ornament of coarse concentric ribs; ligament opisthodetic, parivincular, external, attached to short dorsally reflected nymphs; hinge virtually edentulous or with variably developed tooth beneath beak of right valve and socket in left; valve margin in front of socket may be thickened to fit beneath corresponding edge of right valve; true lateral teeth absent; adductor muscle scars subequal; pallial line relatively wide, continuous, not extended above adductor scars; pallial sinus small or absent; pedal protractor and anterior and posterior retractor scars present in all species; elevator muscle scar present in most species at apex of umbonal cavity."

Based on these characters, we had difficulty accepting the suggested synonymy of *Cowperesia* and *Pyramus* for the following reasons: 1**,** adult shells of *Cowperesia* are

very small, compressed to very compressed, whereas shells of *Pyramus* are normally large and inflated; 2**,** the elevator scar is absent in all specimens of *Cowperesia*, as are the adductor accessory muscle scars “a”, “b”, and “ava” figured for *Pyramus* (see Runnegar 1966, 1967); 3**,** the lunule and escutcheon are absent in *Cowperesia*, but are usually present in *Pyramus*; 4**,** the ornamentation of *Cowperesia* shells is typically of fine co-marginal rugae, which differs from the coarser concentric ribs of *Pyramus*; 5**,** the pallial sinus of *Cowperesia* is deeper than that present in most species of *Pyramus*; 6**,** the hinge of *Cowperesia* always bears a blunt tooth in the right valve, whereas *Pyramus* is normally edentulous.

Cowperesia emerita (Reed 1929) (Fig. 6A–H, J–K)

Material. Six specimens with silicified shell remains (DZP-18696, 18697, 18699, 18700, 18701, 18702) and six internal moulds (DZP-18694, 18695, 18698, 18703, 18704, 18705).

Locality and unit. Huab region, Namibia, lower Gai-As Formation, Huab Basin.

Age. Permian, Wordian.

Description. Shell small, subtriangular, equivalved, equilateral, equant to moderately elongate (elongation index: 1.17–1.24), very compressed (inflation = obesity index of 2.26). Two well-defined, slightly curved posterior umbonal carinae present, one extending from the umbonal region to the posterio-ventral angle and the other close to the posterior dorsal margin (Fig. 6A, C). Very weak projections evident where co-marginal growth lines cross the umbonal carina. Projections not visible on internal moulds (Fig. 6D). External ornament of fine, co-marginal growth lines, superimposed

by widely spaced, broad co-marginal rugae that are apparent on internal moulds (Fig. 6B, D). Umbones low with pointed prosogyrous beaks. Well-marked muscle insertion scars visible on the umbonal region of internal moulds (Fig. 6J, K), with radiating striated muscle tracks below (Fig. 6D, E). Right valve with well-developed triangular tooth below beak (Fig. 6G, L). Left valve has large triangular socket below beak, and a well-defined tooth to anterior (Fig. 6 H, I). Lateral teeth absent.

Remarks. *Cowperesia anceps* (Reed, 1935), *C. emerita* (Reed, 1935), and *C. camposi* Mendes, 1952 are the only known species of *Cowperesia*. However, *C. camposi* may be conspecific with *C. anceps*, as the type specimens are similar to Reed's original illustrations and only small differences in ornamentation separate the two species (Runnegar & Newell 1971). As far as we know, *C. anceps* and *C. emerita* do not occur together at the same stratigraphic level in the Permian of the Paraná Basin. The Namibian material closely resembles *C. emerita* in shell shape, ornamentation and hinge features (see Fig. 6J, L for comparison). This is further supported by specimens from the upper part of the Teresina Formation in the Tiaraju region (Klein 1997), Rio Grande do Sul State, and from the Serrinha Member of the Rio do Rasto Formation, illustrated by Rohn (1994, p. 358, fig. 166-1a, b; p. 360, fig. 168-7-9).

Insert table IV

Insert Figure 6

Palaeoautoecology

The bivalve fauna of the Gai-As Formation is of low diversity, particularly when compared with coeval faunas of the mid-Permian deposits of the Paraná Basin (see

Runnegar & Newell 1971, Simões *et al*. 1998). However, the Huab fauna is dominated by the same bivalve groups that are found in the Passa Dois Group of the Paraná Basin, namely megadesmids and veneroids. In this context, the abundance of megadesmid genera is of particular interest because they are also common in Permian marine faunas of Australia and New Zealand (see Runnegar 1967, Runnegar & Newell 1971, Simões *et al*. 1997). Megadesmids were infaunal, suspension-feeding bivalves that appear to have had robust shells with a stout opisthodetic ligament, edentulous hinge or have a blunt tooth in the right or both valves (Runnegar 1967, Runnegar & Newell 1971, Simões *et al*. 1997). They were active infaunal bivalves (shallow, intermediate and deep burrowers) that flourished in shallow waters with soft substrates (Runnegar 1974, Runnegar & Newell 1971, Simões *et al*. 1997).

Cowperesia emerita and *Huabiella compressa* are the typical megadesmids of the lower and upper Gai-As Formation, respectively. *Cowperesia emerita* has thin, very compressed and non-elongated shells (elongation index 1.04-1.17, see Stanley 1970). The occurrence of closed-articulated shells of *C. emerita* in very fine sediments of the lower Gai-As Formation (Fig. 7G) indicates that this species may have lived in a soupy, fine-grained substrate. As commented by Stanley (1970), due to the maintenance of negative buoyancy, a good strategy in such conditions of soft, muddy bottoms is to keep the shell thin and compressed. Species of *Cowperesia* from the Paraná Basin bear deeply impressed anterior, protractor muscle scars in addition to a small, but very well defined pallial sinus. These features may indicate an active, intermediate, burrowing lifestyle (see Runnegar 1974). Similar conclusions may be applicable to *Huabiella compressa* shells, of which the splayed valves are also found in fine-grained sediments. As the species name indicates, their shells are compressed, thin, non-gaped, and very elongate (elongation index 2.32-3.05, see Stanley 1970). Again this may be a strategy

for bouyancy in a fine-grained substrate of low density and viscosity (Stanley 1970), with a shallow to intermediate burrowing strategy.

Terraia sp. cf. *T. altissima* is elongate to very elongate (elongation index 1.50–1.63, see Stanley 1970). Both species (*Terraia* sp. cf. *T. altissima* and *Terraia* sp. cf. *T. curvata*) have relatively robust shells. Similar to other thick-shelled Veneroida, these may have been active burrowers in shallow water substrates (Stanley 1970, p. 68, Runnegar & Newell 1971). The shells of *Terraia* sp. cf. *T. altissima* and *Terraia* sp. cf. *T. curvata* are always disarticulated and, owing to their different lifestyle, they may not have lived in direct association with the other forms (*C. emerita* and *H. compressa*) during life.

Taphonomy

The taphonomic analysis presented herein is probably biased, as the samples were primarily collected for taxonomic purposes and not according to standard taphonomic procedures (e.g. Kidwell *et al.* 1986, Kidwell 1991, Kidwell & Holland 1991, Fürsich & Oschmann 1993, Simões & Kowalewski 1998). Fortunately, some slabs were large enough to be vertically sectioned for descriptions and allowed observation of some taphonomic characters (e.g. degree of packing and shell orientation). Since few samples were available, our analysis is only qualitative. The description follows the terminology suggested by Kidwell (1991) and Kidwell & Holland (1991).

The lower Gai-As Formation comprises a 35 m thick sequence of reddish to violet, mostly laminated mudrocks containing thin (1–3 cm) tabular interbeds of normally graded, fine- to medium-grained sandstones and a few laminated limestones, 10–50 cm thick (Fig. 3; Holzfoerster 2000, 2002, Wanke, 2000). In this succession, at least two extensive shale horizons incorporate layers, up to 4 cm thick, of accumulated bivalve

shells (Wanke 2000). The bivalves are both articulated and disarticulated and are chaotically distributed within the matrix (Fig. 7G). Closed articulated shells of *Cowperesia emerita* are common, and are associated with disarticulated valves of *Terraia* sp. cf. *T. altissima* and *Terraia* sp. cf. *T. curvata*. Some closed articulated shells have fragile structures preserved, such as the ligament (Fig. 7E). The shells are silicified without signs of abrasion, encrustation or bioerosion. Some closed articulated specimens bear geopetal infillings of sediment (matrix) and calcite (Figs 7C, D). In some cases, disarticulated shells, including *Cowperesia emerita* and *Terraia* sp. cf. *T. altissima*, are nested (Figs 6G, 7F).

Insert figure 7

The Upper Gai-As Formation comprises a 10–80 m thick sequence of red violet mudstones with minor tabular sandstone interbeds, laminated or small-scale cross-bedded limestone, and laminated rhyolitic to dacitic fallout tuff (Holzfoerster 2000, 2002, Stollhofen *et al*. 2000). Some interlaminated limestone/sandstone beds are characterized by conspicuous concentrations of *Huabiella compressa* shells in a single, 2–5 cm thick layer with sparse specimens of *Terraia* sp. cf. *T. curvata*. *Cowperesia emerita* and *Terraia* sp. cf. *T. altissima* appear to be absent. All shells are represented by moulds (see also Stollhofen *et al.* 2000). The shells are commonly disarticulated and in a concave-down orientation. Rare splayed shells were also found (Holzfoerster 2000, 2002).

In summary, the bivalve assemblages of the lower and upper Gai-As Formation are formed by a mixture of autochthonous to parautochthonous species (*C. emerita* and *H. compressa*, respectively) and allochthonous (transported) shells (*Terraia* sp. cf. *T. altissima* and *Terraia* sp. cf. *T. curvata*) when present. However, these observations must be viewed with caution owing to the small size of the examined collection.

Palaeoenvironment

Despite the qualifications outlined above, the bivalve shell concentrations of the Gai-As Formation exhibit a range of taphonomic signatures that are useful for palaeoenvironmental interpretations. At least two associations are present, characterized by particular preservational styles and taphonomic histories.

As indicated by Holzfoerster (2000, 2002), Stollhofen *et al*. (2000) and Wanke (2000), the thick succession of mudstones of the basal portion of the Gai-As Formation was deposited predominantly from suspension fallout in a hemi-pelagic setting within a large body of water. However, the calm background conditions that prevailed in this lacustrine environment were frequently disrupted by episodic high-energy events. For example, within the lower Gai-As section the sandstone beds were interpreted as event beds, such as tempestites and turbidites (Holzfoerster 2000, 2002, Stollhofen *et al*., 2000, Wanke, 2000). Indeed, the presence of chaotically disposed, stacked and nested bivalve shells in the matrix would supplement this, and the occurrence of specimens with closed articulated valves (*Cowperesia emerita*), some with preserved ligament (Fig. 7E), are good indicators of abrupt burial associated with high-energy events (see Aigner 1985, Fürsich & Oschmann 1986, 1993, Kidwell *et al.* 1986, Simões *et al.* 1996, Simões & Kowalewski 1998). Both *Cowperesia emerita* and *Terraia* sp. cf. *T. altissima* were shallow burrowers, and the closed articulated shells that are chaotically arranged in the matrix are good indicators of disruption of bivalves that were alive prior to final burial. This disruption may have been caused by turbulent flows in offshore bottoms, as indicated by the presence of nested shells (Figs 6G, 7F) that were subsequently buried by very fine grained sediments from suspended mud. Although closed-articulated, some shells may represent winnowed and reworked re-fossilized material. For example, many articulated shells of *Cowperesia emerita* have geopetal structures (Figs 7C, D), i.e.

infillings clearly divided into sediments and calcite crystals – the calcite precipitated in the hollow upper space of the valves. According to the inclined position of the geopetal structures within the bed, it is easy to conclude that the shells were reworked. The infilling of some closed shells corroborates this interpretation because it is composed of sediment that is different from that of the muddy matrix that encloses the shells (Fig. 7B). Other specimens are completely filled with muddy sediment equivalent to the surrounding matrix (Fig. 7A). According to various authors (Seilacher 1973, Fürsich 1978, Brett & Allison 1998, Klein & Simões 1998, Simões & Torello 2003), these features suggest reworking and repeated burial of shells over long time periods on bottoms that were continuously being affected by storms or turbidites (see also Wani 2001, p. 622).

Additional evidence for deposition under high-energy conditions with exhumed and disarticulated shells settling from suspension is manifest by the presence of concave-up, nested and disarticulated shells (Kidwell *et al.* 1986, Fürsich & Oschmann 1993, Simões *et al.* 1996, Simões & Kowalewski 1998). Hence, these taphonomic observations corroborate previous interpretations by Holzfoerster (2000, 2002), Stollhofen *et al.* (2000) and Wanke (2000) based on sedimentological evidence alone.

The shell beds of the lower part of the Gai-As Formation are composite concentrations (*sensu* Kidwell 1991), deposited during high-energy events (storms or turbitidy flows) that show disharmonic time-averaging (see Kowalewski, 1996; Simões & Kowalewski 1998). This taphonomic context is equivalent to many Permian shell beds of the Passa Dois Group of the Paraná Basin (see Klein & Simões 1998, Simões *et al.* 1996, Simões & Kowalewski 1998, Simões & Torello 2003, Neves 2009, Neves *et al.* 2010).

One of the main taphonomic features of the shell-rich layers in the upper part of the Gai-As Formation is the presence of articulated and disarticulated valves of *Huabiella*

compressa in concave-down attitude to bedding (see also Holzfoerster 2000, 2002, Stollhofen *et al*. 2000, Wanke 2000). *Huabiella compressa* was a shallow burrower that may have lived in a soupy, fine-grained bottom, as suggested by their thin, compressed shells with commarginal rugae (see also Ghilardi 1999). The articulated specimens of *Huabiella compressa* are those with the two valves splayed open on the bedding plane. Because bivalve molluscs shells are known to dry out and splay, it is highly unlikely that open shells of *Huabiella compressa* lying at the sediment/water interface could have been transported intact and articulated (see also Allmon 1985, Selover *et al*. 2005). The splayed shells of *Huabiella* may represent dead molluscs dislodged during high-energy events that became mixed with previously dead molluscs lying on the bottom. *Huabiella compressa* shells were elongate, nearly flat, with a small, opisthodetic, parivincular ligament and no hinge teeth (edentulous). It is arguable that the lack of teeth and the fragile ligament favours disarticulation if the shells are submitted to prolonged exposure on the sea floor. This suggests that, these splayed shells of *Huabiella* are good indicators of rapid (but not abrupt) burial. However, because splayed shells were preferentially preserved in a concave-down position, this may indicate that after settling, these shells experienced brief exposure to bottom currents that overturned both splayed and disarticulated shells into a more hydrodynamically stable positions. The preservation of splayed shells in a concave-down position suggests low-energy conditions following the exhumation event but relatively rapid subsequent burial, preventing the complete disarticulation of valves (Cantalamessaa *et al*. 2005).

Biostratigraphy and correlation

The age and vertical and lateral extent of the Namibian Gai-As sediments are well resolved following the studies of Horsthemke (1992), Ledendecker (1992), Holzfoerster

(2000, 2002), Stollhofen *et al.* (2000) and Wanke (2000). Based on the occurrence of the bivalves, Horsthemke (1992) and Ledendecker (1992) correlated the Gai-As Formation with the Serra Alta, Teresina, and lower Rio do Rasto formations of Brazil, and with the Collingham to Waterford Formations of South Africa. However, studies by Holzfoerster (2000, 2002), Stollhofen *et al*. (2000) and Wanke (2000) have demonstrated that in northern Namibia, coeval Permian beds to the entire post-Whitehill Formation (Ecca Group), Collingham to Waterford formations, in the Main Karoo Basins, of South Africa and the greater part of the Passa Dois Group (Serra Alta and Teresina formations) of Brazil, are poorly preserved or missing (Stollhofen *et al*. 2000). Based on the probable presence of *Leinzia similis*, Stollhofen *et al*. (2000) suggested correlation of the Gai-As Formation with the informal *Terraia altissima* Biozone (Rohn 1994) of the Rio do Rasto Formation, Paraná Basin, Brazil. However, as revealed here *Leinzia similis* is not recognized in Namibia, and the presence of *Cowperesia emerita*, indicates possible correlation with intervals of the lower portion (Serrinha Member) of the Rio do Rasto Formation. The occurrence of *Terraia* sp. cf. *T. altissima* and *Terraia* sp. cf. *T. curvata* in the Namibian fauna may constitute additional evidence for the biocorrelation above (but see comments in the section below). In addition, it is pertinent to note that *Huabiella compressa* is very similar to *Leinzia curta* (*nomen nudum*) recorded by Beurlen (1957), and to some non-described specimens illustrated by Rohn (1994, Fig. 167-6), from the basal part of the Rio do Rasto Formation (Serrinha Member).

Radiometric dating of zircon grains from tuff beds within the top part of the Gai-As succession provide U/Pb ages of 265±2.5 Ma (Holzfoerster 2000, 2002, Wanke 2000). This age, according to the International Stratigraphic Chart of 2009 (Walker & Geissman 2009), corresponds to the Wordian/Capitanian boundary in the Guadalupian (Middle Permian). More significantly, recent U/Pb ages obtained from zircon grains

from ash-fall beds in coeval Permian rocks of the Paraná Basin indicate ages of 267±17 Ma for the Teresina Formation, and 266.3±4.6 Ma for the Serrinha Member of the Rio do Rasto Formation (Rocha-Campos *et al.* 2009). Consequently, the tuff layers are of probable equivalent age (Wordian) in both countries, reinforcing correlations made by previous authors (Holzfoerster 2000, 2002, Stollhofen *et al.* 2000, Wanke 2000).

Summary

The discovery of typical South America Permian "endemic" bivalves in Namibia reinforces the idea that the fauna of the Passa Dois Group (Mendes 1952, Runnegar & Newell 1971, Simões *et al.* 1998) was not confined to the South American portion of the Permian sea that covered the southern region of Gondwana during Wordian times. The lacustrine environment represented by the Namibian deposits was probably an extension of the huge epicontinental sea of the Paraná Basin. The best record of this fauna in terms of preservation, abundance and stratigraphic completeness is found in Brazil.

The Gai-As bivalve occurrences are potentially significant for stratigraphic correlation and age determination. The species identified as *Terraia* sp. cf. *T. altissima*, and *Terraia* sp. cf. *T. curvata* are not necessarily different to *T. altissima* and *T. curvata* in South America, but the Namibian forms lack the preservational details for definitive attribution to the Brazilian taxa. Therefore, future research in Namibia must focus on the search for better preserved specimens that may clarify the specific relationships between these species of *Terraia*.

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References

ADAMS, H. & ADAMS, A., 1856. *The genera of Recent Mollusca*, Volume 3. John von Voorst, Paternaster Row, London, liv + 661 pp.

AIGNER, T., 1985. Storm depositional systems: Dynamic stratigraphy in modern and ancient shallow marine sequences. *Lecture Notes in Earth Sciences 3*, i-x + 174 pp.

ALLMON, R.A., 1985. “Butterflied” bivalves as paleoenvironmental indicators. *Geological Society of America Abstracts Programs 17*, 512–512.

BEURLEN, K., 1953. Considerações sobre alguns lamilibranquios das Camadas Terezina, no Paraná. *Divisão Geológica e Mineralógica do Brasil 142*, 1–41.

BEURLEN, K., 1954. As faunas de lamelibranquios do sistema Gonduwânico no Paraná. In *Paleontologia do Paraná Volume Comemorativo do 10˚ Centenário do Estado do Paraná*, F.W. LANGE, ed., Curitiba, Brasil, 107–136.

BEURLEN, K., 1957. Faunas salobras fósseis e o tipo ecológico-paleogeográfico das faunas Gondwânicas no Brasil. *Anais da Academia Brasileira de Ciências 29*, 229–241.

BRETT, C. & ALLISON, P.A., 1998. Paleontological approaches to the environmental interpretation of marine mudrocks, In *Shales and Mudstones*, J. SCHIEBER, W. ZIMMERLE & P. SETHI, eds, Schweizerbartsche Verlagsbuchandlung (Nagel u. Obermiller), Stuttgart, 301–349.

CANTALAMESSAA, G., CELMAA, C.D. & RAGAINIB, L., 2005. Sequence stratigraphy of the Punta Ballena Member of the Jama Formation (Early Pleistocene, Ecuador): insights from integrated sedimentologic, taphonomic and paleoecologic analysis of molluscan shell concentrations. *Palaeogeography, Palaeoclimatology, Palaeoecology 216*, 1–25.

CATUNEANU, O., WOPFNER, H., ERIKSSON, P.G., CAIRNCROSS, B., RUBDGE, B.S., SMITH, R.M.H. & HANCOX, P.J., 2005. The Karoo Basins of south-central Africa. *Journal of African Earth Sciences 43*, 211–253.

COOPER, M.R. & KENSLEY, B., 1984. Endemic South America Permian bivalve mollusks from the Ecca of South Africa. *Journal of Paleontology 58*, 1360–1363.

COX, L.R., 1934. Triassic Lamellibranchia from Uruguay. *Annals and Magazine of Natural History 13*, 264–273.

DALL, W.H., 1889. On the hinge of pelecypods and its development, with an attempt toward a better subdivision of the group. *American Journal of Science 38*, 445–462.

DANA, J.D., 1847. Descriptions of fossil shells of the collections of the exploring expedition under the command of Charles Wilkes, U.S.N., obtained in Australia, from the lower layers of the coal formation in Illawarra, and from a deposit probably of nearly the same age at Harper's Hill, Valley of the Hunter. *American Journal of Science and Arts 4*, 1151–1160.

DICKINS, J.M., 1992. Permian geology of Gondwana countries: An overview. *International Geology Review 34*, 986–1000.

FELDMANN, R.M., CHAPMAN, R.E. & HANNIBAL, J.T., 1989. *Paleotechniques*. The Paleontological Society Special Publication, New York, liv + 358 pp.

FÉRUSSAC, A.E., 1822. *Tableaux systématiques des animaux mollusques*. A. Bertrand, Paris and London, liv + 111 pp.

FÜRSICH, F.T., 1978. The influence of faunal condensation and mixing on the preservation of fossil benthic communities. *Lethaia 11*, 243–250.

FÜRSICH, F.T. & OSCHMANN, W., 1986. Storm shell beds of *Nanogyra virgule* in the Upper Jurassic of France. *Neues Jahrhuch für Geologie und Paläontologie Abhandlungen 172*, 141–161.

FÜRSICH, F.T. & OSCHMANN, W., 1993. Shell beds as tools in basin analysis: the Jurassic of Kachchh, western India. *Journal of Geological Society of London 150*, 169–185.

GHILARDI, R.P., 1999. *Paleoautoecologia dos bivalves do Grupo Passa Dois (Neopermiano), no Estado de São Paulo: bivalves fósseis como indicadores da dinâmica sedimentar*. MSc dissertation, University of São Paulo. 160 pp. (unpublished)

GRAY, J.E., 1847. A list of the genera of recent Mollusca, their synonyms and Types. *Proceedings of the Zoological Society of London 15*, 129–219.

HAMMER, O., 2000. A theory for the formation of commarginal ribs in mollusc shells by regulative oscillation. *Journal of Molluscan Studies 66*, 383–392.

HERTWIG, C.W.T.R., 1895. *Lehrbuch der Zoologie*. Gustav Fischer, Boulder, liv + 599 pp.

HOLDHAUS, K., 1918. Sobre alguns lamelibrânquios fósseis do sul do Brasil. *Serviço Geológico e Mineralógico 2*, 1–24, 2 pls.

HOLZ, M., FRANÇA, A.B., SOUZA, P.A., IANNUZZI, R. & ROHN, R., 2010. A stratigraphic chart of the Late Carboniferous/Permian succession of the eastern border of the

Paraná Basin, Brazil, South America. *Journal of South American Earth Sciences 29*, 381–399.

HOLZFOERSTER, F., 2000. *Sedimentology, stratigraphy and synsedimentary tectonics of the Karoo Supergroup in the Huab and Waterberg-Erongo areas, N-Namibia*. PhD thesis, University of Würzburg, 298 pp. (unpublished)

HOLZFOERSTER, F., 2002. Sedimentology, stratigraphy and synsedimentary tectonics of the Karoo Supergroup in the Huab and Waterberg-Erongo areas, N-Namibia. *Beringeria 30*, 1–144.

HORSTHEMKE, E., 1992. Fazies der Karoosediment in der Huab-Region, Damaraland, NW-Namibia. *Göttinger Arbeiten zur Geologie und Paläontologie 55*, 1–102.

KIDWELL, S.M., 1991. The stratigraphy of shell concentrations. In *Taphonomy: releasing the data locked in the fossil record*, P.A. ALLISON & D.E.G.BRIGGS, eds, Plenum Press, New York, 211–290.

KIDWELL, S.M. & HOLLAND, S.M., 1991. Field description of coarse bioclastic fabrics. *Palaios 6*, 426–434.

KIDWELL, S.M., FÜRSICH, F.T. & AIGNER, T., 1986. Conceptual framework for the analysis and classification of shell concentrations. *Palaios 1*, 228–238.

KING, W., 1844. On a new genus of paleozoic shells. *Annals and Magazine of Natural History 1*, 313-317.

KLEIN, C., 1997. *Contribuição ao estudo das concentrações fossilíferas do Grupo Passa Dois na região de Tiarajú, RS e suas implicações paleoambientais.* MSc dissertation, University of the Rio do Sinos Valley, 132 pp. (unpublished)

KLEIN, C. & SIMÕES, M.G., 1998. Tafonomia de pelecípodes da Formação Teresina (Permiano), Tiaraju, RS, Brasil. *Anais da Academia Brasileira de Ciências 70*, 617–625.

KOWALEWSKI, M., 1996. Time-averaging, overcompleteness and the geological record. *Journal of Geology 104*, 317–326.

LEDENDECKER, S., 1991. *Stratigraphie der Karoosedimente der Huabregion (NW-Namibia) und deren Koorrelalion mit zeitäquivalenten Sedimenten des Paranàbeckens (Südamerika) un des Groben Karrobeckens (Südafrika) unter besonderer Berücksichtigung der ü berrequonalen geodynamischen und klimatishen Entwicklung Westgondwanas.* PhD Thesis, Georg-August-University, 87 pp. (unpublished)

LEDENDECKER, S., 1992. Stratigraphie der Karoosedimente der Huabregion (NW-Namibia) und deren Koorrelalion mit zeitäquivalenten Sedimenten des Paranàbeckens (Südamerika) un des Groben Karrobeckens (Südafrika) unter besonderer Berücksichtigung der ü berrequonalen geodynamischen und klimatishen Entwicklung Westgondwanas. *Göttinger Arbeiten zur Geologie und Paläontologie 54*, 1–87.

MENDES, J.C., 1952. Formação Corumbataí na região do Rio Corumbataí (estratigrafia e descrição dos lamelibrânquios). *Boletim da Faculdade de Filosofia Ciências e Letras 145*, Série Geologia *8*, 1–119.

MENDES, J.C., 1962. Lamelibrânquios permianos do oólito de Angatuba, Estado de São Paulo. *Boletim da Sociedade Brasileira de Geologia 11*, 37–56.

MORRIS N.J., DICKINS, J.M. & ASTAFIEVA-URBAITIS, K., 1991. Upper Paleozoic anomalodesmatan Bivalvia. *Bulletin of the British Museum of Natural History, (Geology) 47*, 51–100.

NEUMAYR, M., 1883. Zur Morphologie des Bivalvenschlosses. *Kaiserlich Königlice Akademie der Wissenschaften zui Wien. Naturwissenschaftlich-Mathematische Classe Sitzungsberichte, Abtheilung 1, 88*, 385–418.

NEWELL, N.D., 1965. Classification of the Bivalvia. *American Museum Novitates 2206*, 1–25.

NEVES, J.P., 2009. *Tafonomia das rochas carbonáticas conchíferas das formações Teresina e Rio do Rasto (Permiano, Bacia do Paraná)*. MSc dissertation, University of the State of São Paulo, 90 pp. (unpublished)

NEVES, J.P., ROHN, R. & SIMÕES, M.G., 2010. Tafonomia de biválvios em calcários oolíticos da Formação Teresina (Bacia do Paraná, Permiano médio, Prudentópolis, PR). *Geologia USP, Série Científica*, *10*, 19–36.

REED, F.R.C., 1929. Faunas Triassicas do Brasil. *Serviço Geológico e Mineralógico do Brasil 9*, 1–83.

REED, F.R.C., 1935. Some Triassic lamellibranchs from Brazil and Paraguay. *Geological Magazine 847*, 33–42.

ROCHA-CAMPOS, A.C., BASEI, M.A. & SANTOS, P.R., 2009. Depósitos de cinza vulcânica no Neopaleozóico da Bacia do Paraná: datação radiométrica (SHRIMP) e possíveis implicações cronoestratigráficas e paleoambientais. *Boletim de Resumos da Reunião Anual da Sociedade Brasileira de Paleontologia - Núcleo SP*, 8.

ROHN, R., 1994. *Evolução ambiental da Bacia do Paraná durante o Neopermiano no leste de Santa Catarina e do Paraná*. PhD thesis, University of São Paulo, 250 pp. (unpublished)

RUNNEGAR, B., 1966. Systematics and biology of some desmodont bivalves from the Australian Permian. *Journal of Geological Society of Australia 13*, 373–386.

RUNNEGAR, B., 1967. Desmodont bivalves from the Permian of eastern Australia. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, Australia 96*, 1–108.

RUNNEGAR, B., 1974. Evolutionary history of the bivalve Subclass Anomalodesmata. *Journal of Paleontology 48*, 904–939.

RUNNEGAR, B. & NEWELL, N.D., 1971. Caspian-like relict molluscan fauna in the South American Permian. *Bulletin of the American Museum of Natural History 146*, 1–66.

SCHÄFER, W., 1972. *Ecology and Paleoecology of Marine Environments*. Chicago Press, Chicago, liv + 568 pp.

SEILACHER, A., 1973. Biostratinomy: the sedimentology of biologically standardized particles. In *Evolving concepts in sedimentology*, R.N. GINSBURG, ed., John Hopkins University Press, Baltimore 159–177.

SELOVER, R.W., GASTALDO, R.A. & NELSON, R.E., 2005. An estuarine assemblage from the Middle Devonian Trout Valley Formation of Northern Maine. *Palaios 20*, 192–197.

SIMÕES, M.G. & KOWALEWSKI, M., 1998. Shell beds as paleoecological puzzles: a case study from the Upper Permian of the Paraná Basin, Brazil. *Facies 38*, 175–196.

SIMÕES, M.G. & TORELLO, F.F., 2003. Modelo de tafofácies para os moluscos bivalves do Grupo Passa Dois (Formações Serra Alta, Teresina e Corumbataí), Permiano Superior, Bacia do Paraná, Brasil. *Revista Brasileira de Geociências 33*, 1–10.

SIMÕES, M.G., TORELLO, F.F. & ROCHA-CAMPOS, A.C., 1996. Gênese e classificação da Coquina de Camaquã, Formação Corumbataí (Neopermiano), na Região de Rio Claro, SP. *Anais da Academia Brasileira de Ciências 68*, 545–557.

SIMÕES, M.G., ROCHA-CAMPOS, A.C. & ANELLI, L.E., 1998. Paleoecology and Evolution of Permian pelecypod assemblages (Paraná Basin) from Brazil. In *Bivalves- An Eon of evolution: paleobiological studies honoring Norman D. Newell*, P.A. JOHNSTON & J.W. HAGGART, eds, University of Calgary Press, Calgary, 443–452.

SIMÕES, M.G., MARQUES, A.C., MELLO, L.H.C. & ANELLI, L.E., 1997. Phylogenetic analysis of the genera of the extinct Family Megadesmidae (Pelecypoda,

Anomalodesmata), with remarks on its paleoecology and taxonomy. *Journal of Comparative Biology 2*, 75–90.

SIMÕES, M.G., KOWALEWSKI, M., TORELLO, F.F., GHILARDI, R.P. & MELLO, L.H.C., 2000. Early onset of modern-style shell beds in the Permian sequences of the Parana Basin: implications for the Phanerozoic trend in bioclastic accumulations. *Revista Brasileira de Geociências 30*, 499–503.

STANLEY, S.M., 1970. Relation of shell form to life habitats of the Bivalvia (Mollusca). *Memoir of the Geological Society of America 125*, 1–296.

STOLLHOFEN, H., STRANISTREET, I.G., ROHN, R., HOLZFOERSTER, F. & WANKE, A., 2000. The Gai-As lake system, northern Namibia and Brazil. In *Lake Basins Through Space and Time*, E.H. GLERLOWSKI-KORDESCH & K.R. KELTS, eds, AAPG Studies in Geology Volume 46, AAPG, Tulsa, 87–108.

STRANISTREET, I.G. & STOLLHOFEN, H., 1999. Onshore equivalents of the main Kudu gas reservoir in Namibia. In *Oil and Gas Habitats of the South Atlantic*, N. CAMERON, R. BATE & V. CLURE, eds, Geological Society Special Publication 153, Geological Society, London, 345–365.

VOKES, H.E., 1967. Genera of the Bivalvia: a systematic and bibliographic catalogue. *Bulletins of American Paleontology 51*, 111–393.

WALKER, J.D. & GEISSMAN, J.W., 2009. *Geologic Time Scale*. Geological Society of America, doi: 10.1130/2009.

WANKE, A., 2000. *Karoo-Etendeka Unconformites in NW Namibia and their Tectonic Implications*. Ph.D. thesis, Würzburg University, 116 pp. (unpublished)

WANI, R., 2001. Reworked ammonoids and their taphonomic implications in the Upper Cretaceous of northwestern Hokkaido, Japan. *Cretaceous Research 22*, 615–625.

WESSELINGH, F.P., 2007. Long-lived lake molluscs as island faunas: a bivalve perspective. In *Biogeography, Time and Place: distributions, barriers and islands*, W. RENEMA, ed., Springer, Dordrecht, 275–314.

FIGURE CAPTIONS

Fig. 1. Schematic map of the Huab area, northwest Namibia (modified from Catuneanu *et al.* 2005). Inset: map of the outcrop belts of Gai-As Formation, and the type localities of the sections measured at the Klien Gai-As and north of Doros (see also Fig. 3, modified from Stollhofen *et al.* 2000).

Fig. 2. Sedimentary succession of the Huab area, northwest Namibia (modified from Stollhofen *et al.* 2000).

Fig. 3. Composite stratigraphic section of the Gai-As and Doros formations, measured at the Klien Gai-As and north of Doros type localities (see Fig. 1), showing the stratigraphic position of the bivalve shell beds studied (modified from Stollhofen *et al.* 2000).

Fig. 4. **A–E**, *Terraia* sp. cf. *T. altissima* (Holdhaus, 1918), Gai-As Formation, Huab area, Permian. **A**, External view of silicified left valve, DZP-18706, x 5.1; **B**, External view of silicified left valve, DZP-18707, x 7.9; **C**, External view of silicified left valve, DZP-18700, x 7.0; **D**, External view of silicified left valve, DZP-18711, x 3.8; **E**, Internal mould with silicified shell remains, right valve view, DZP-18710, x 3.2; **F**, *Terraia altissima*, Passa Dois Group, Paraná Basin, external view of a silicified left valve, FAC Pal.1868 (figure from Runnegar & Newell 1971), x 2.8; **G–H**, *Terraia* sp. cf. *T. curvata* (Reed, 1929), Gai-As Formation, Huab area, Permian. **G**, External view of incomplete silicified right valve, DZP-18712, x 9.3; **H**, Plasticine cast of external mould of right valve, DZP-18709, x 3.2.

Fig. 5. **A–H**, **J**, *Huabiella compressa* gen. et sp. nov., Gai-As Formation, Huab area, Permian. **A**, Plasticine cast of internal mould of left valve, holotype DZP-18686, x 1.8; **B**, Left valve view of internal mould, paratype DZP-18687, x 4.3; **C**, Detail of anterior region, paratype DZP-18686, x 2.7; **D**, Detail of anterior region, paratype DZP-18687, x 6.9; **E**, Plasticine cast of external mould of left valve, paratype DZP-18688, x 2.3; **F**, Latex cast of external mould of splayed valves, paratype DZP-18689, x 3.7; **G**, Internal mould of left valve, paratype DZP-18691, x 3.2; **H**, Latex cast of internal mould of left valve, paratype, DZP-18692, x 3.2; **I**, Plasticine cast of internal mould of left valve, paratype DZP-18690, x 2.3; **J**, Drawing representation based in the same specimen, x 2.3; **K**, Latex cast of internal mould of left valve, paratype DZP-18693, x 2.4; **L**, *Leinzia similis*, Serrinha Member, Rio do Rasto Formation, Paraná Basin, external mould of left valve, arrow indicates the characteristic anterior expansion of this species, DGP 7-85, x 2.7.

Fig. 6. **A–H**, **J–K**, *Cowperesia emerita* (Reed, 1929), Gai-As Formation, Huab area, Permian. **I**, **L**, *Cowperesia emerita* (Reed, 1929), Rio do Rasto Formation, Paraná Basin, Permian, specimens illustrated by Rohn (1994). **A**, External view of silicified left valve, DZP-18697, x 5.0; **B**, Incomplete internal mould with silicified shell remains, left valve, DZP-18699, x 5.4; **C**, External view of silicified left valve, DZP-18696, x 6.0; **D**, Internal mould of right valve, DZP-18703, x 5.6; **E**, Drawing representation of muscular pits, based in the same specimen, x 5.6; **F**, Incomplete internal mould with silicified shell remains, left valve, DZP-18702, x 4.3; **G**, Internal view of silicified right valve showing hinge features, DZP-18700, x 4.3; **H**, Internal view of silicified left valve showing hinge features, DZP-18701, x 6.5; **I**, Internal view of silicified left valve, showing the hinge features, x 3.2; **J**, Internal mould of right valve, DZP-18698, x 10.0;

K, Drawing representation of muscular pits, based on the same specimen, x 10.0; **L**, Internal mould of a right valve, x 3.3.

Fig. 7. Taphonomic features of bivalve shells of the Lower Gai-As Formation. **A**, Shell filled by muddy sediments (matrix), x 6,0; **B**, Articulated shells showing infillings that do not match with the surrounding matrix, x 6.0; **C–D**, Bivalve shells with distinct geopetal infills, x 7.0; **E**, Closed articulated valve with the external ligament preserved, x 20.0; **F**, Nested concave-up shells, x 12.0; **G**, Section showing articulated and disarticulated valves, chaotically oriented in the matrix, x 1.05. Note the predominance of closed articulated bivalve shells in lower portion of the sample.

TABLE CAPTIONS

Table I- Dimensions of specimens of *Terraia* sp. cf. *T. altissima*

Table II- Dimensions of specimens of *Terraia* sp. cf. *T. curvata*.

Table III- Dimensions of specimens of *Huabiella compressa* gen. et sp. nov.

Table IV- Dimensions of specimens of *Cowperesia emerita*.

Table I

Specimen	Valve	Length (mm)	Height (mm)	Elongation Index
DZP-18700	Left	---	4.23	---
DZP-18706	Left	11.07	6.79	1.63
DZP-18707	Left	7.86	4.48	1.75
DZP-18710	Right	---	13.04	---
DZP-18711	Left	14.63	9.69	1.50

Table II

Specimen	Valve	Length (mm)	Height (mm)	Elongation Index
DZP-18709	Right	19.43	---	---
DZP-18712	Right	---	4.13	---

Table III

Specimen	Valve	Length (mm)	Height (mm)	Elongation Index
DZP-18686	Left	31.28	12.10	2.58
DZP-18687	Left	13.58	4.44	3.05
DZP-18688	Left	---	14.42	---
DZP-18689	---	---	---	---
DZP-18690	Left	---	14.67	---
DZP-18691	Left	16.27	---	---
DZP-18692	Left	15.71	6.78	2.32
DZP-18693	Left	---	10.23	---

Table IV

Specimen	Valve	Length (mm)	Height (mm)	Elongation Index
DZP-18696	Left	---	7.55	---
DZP-18697	Left	7.89	7.56	1.04
DZP-18698	Right	4.09	3.52	1.16
DZP-18699	Left	6.86	5.92	1.15
DZP-18700	Right	9.22	8.03	1.14
DZP-18701	Left	---	---	---
DZP-18702	Left	9.36	7.95	1.17
DZP-18703	Right	---	6.83	---

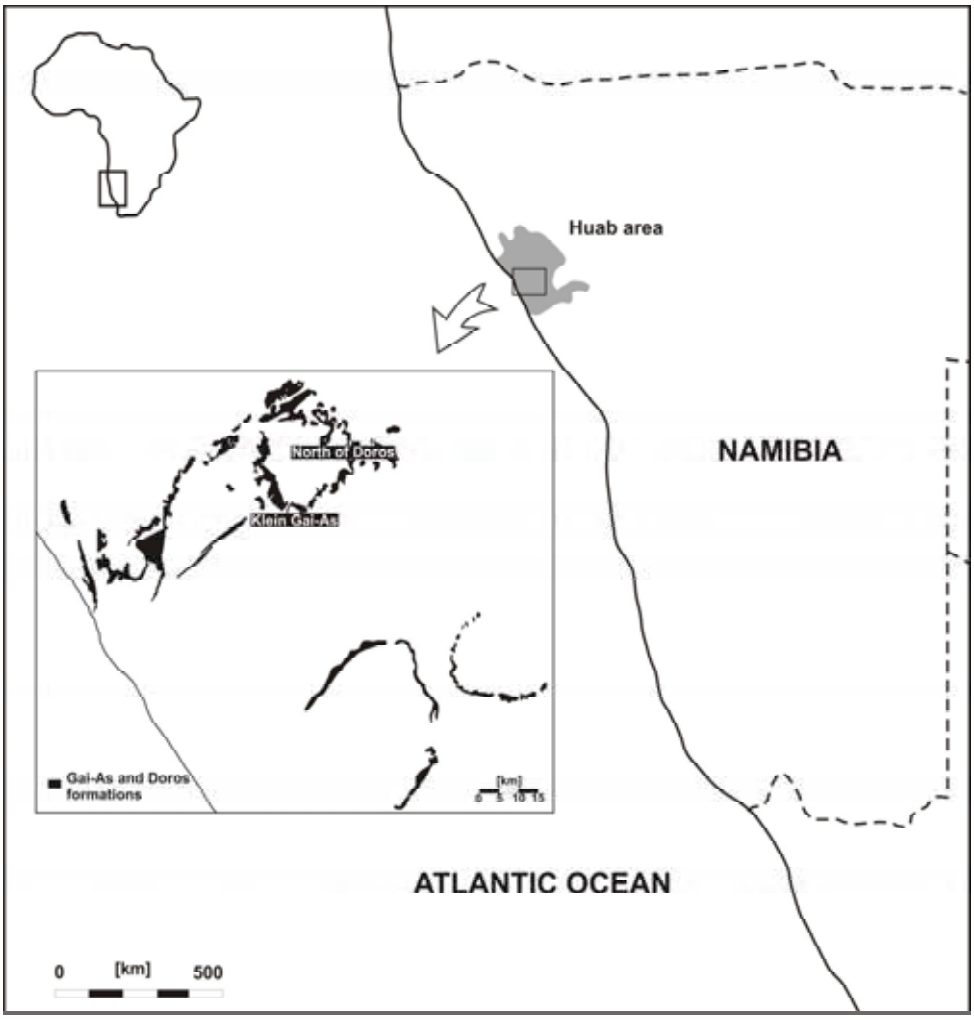
Huab area
NAMIBIA
North of Doros
Klein Gai-As
Gai-As and Doros formations
[km]
ATLANTIC OCEAN
0
[km]
500

Figure 1

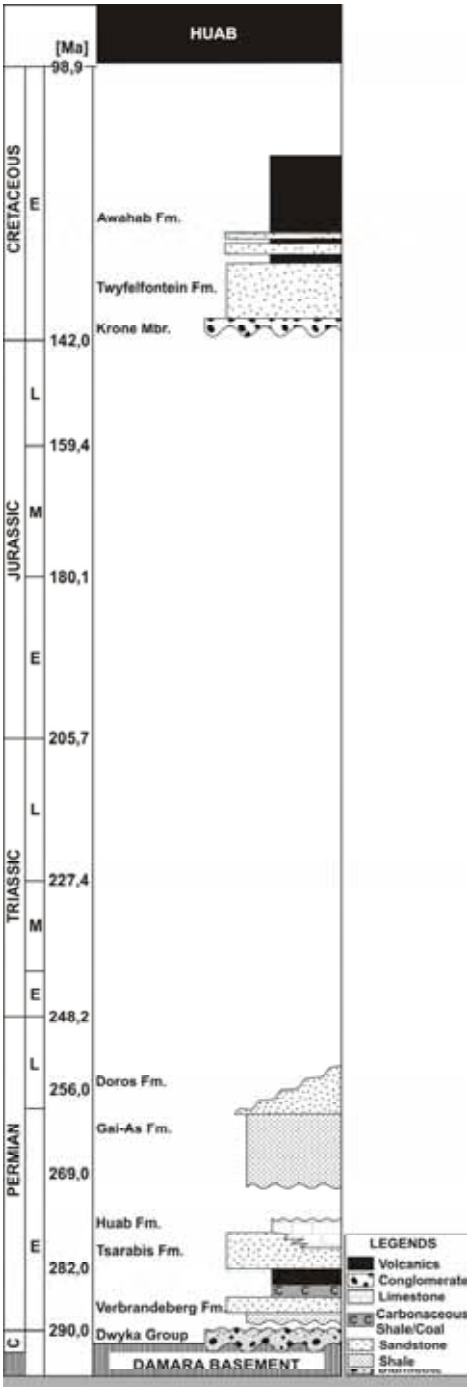
[Ma]
HUAB
98,9
CRETACEOUS
L
Awahab Fm.
Twyfelfontein Fm.
Krone Mbr.
142,0
L
159,4
JURASSIC
M
180,1
E
205,7
L
227,4
TRIASSIC
M
E
248,2
L
Doros Fm.
256,0
Gai-As Fm.
PERMIAN
269,0
Huab Fm.
E
Tsarabis Fm.
282,0
Verbrandeberg Fm.
290,0
C
Dwyka Group
DAMARA BASEMENT
LEGENDS
Volcanics
Conglomerate
Limestone
Carbonaceous Shale/Coal
Sandstone
Shale

Figure 2

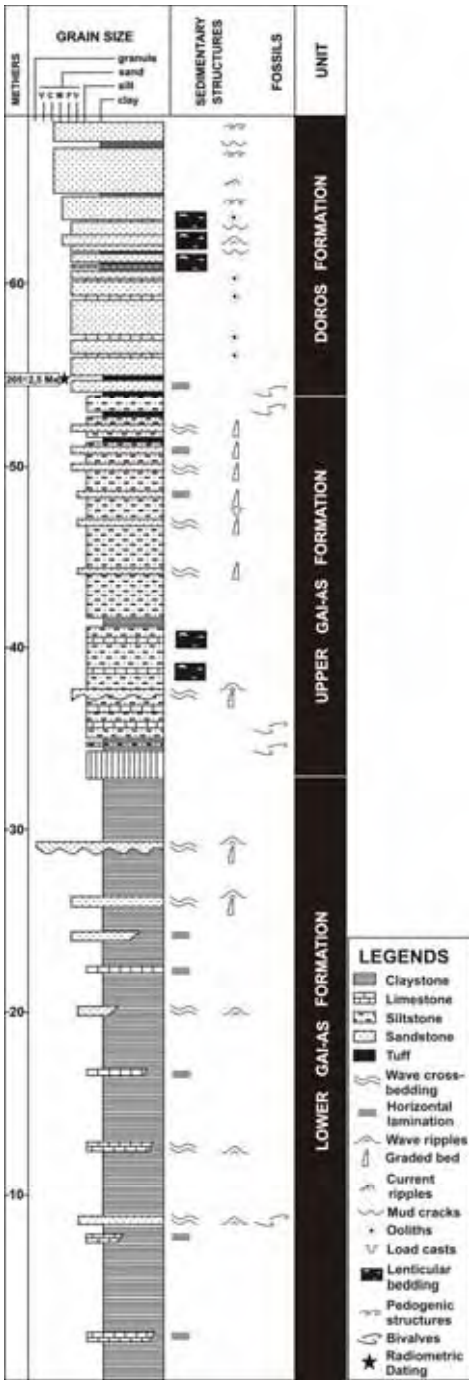
METHERS
GRAIN SIZE
granule
sand
silt
clay
V C M F V
SEDIMENTARY STRUCTURES
FOSSILS
UNIT
DOROS FORMATION
UPPER GAI-AS FORMATION
LOWER GAI-AS FORMATION
60
50
40
30
20
10
LEGENDS
Claystone
Limestone
Siltstone
Sandstone
Tuff
Wave cross-bedding
Horizontal lamination
Wave ripples
Graded bed
Current ripples
Mud cracks
Ooliths
Load casts
Lenticular bedding
Pedogenic structures
Bivalves
Radiometric Dating

Figure 3

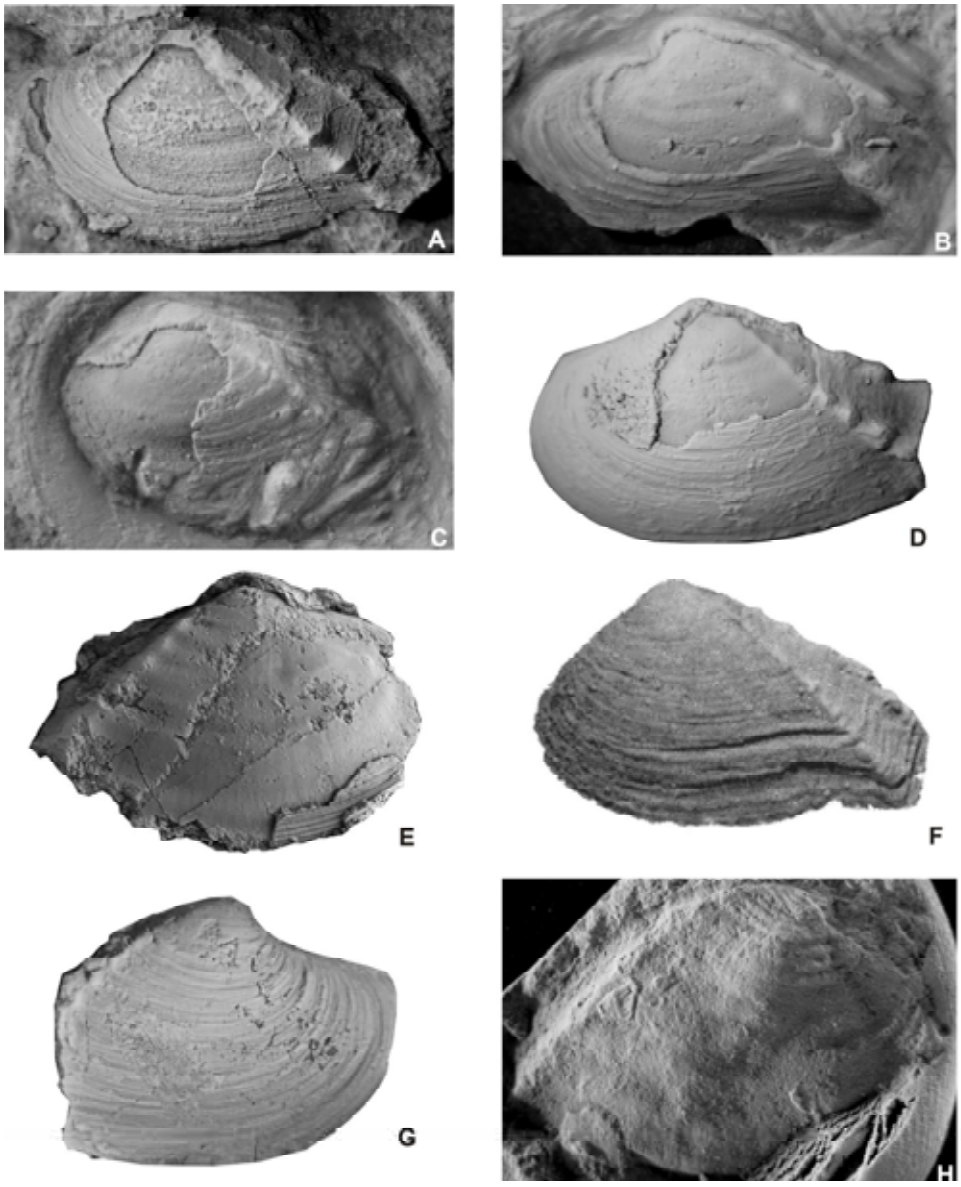

Figure 4

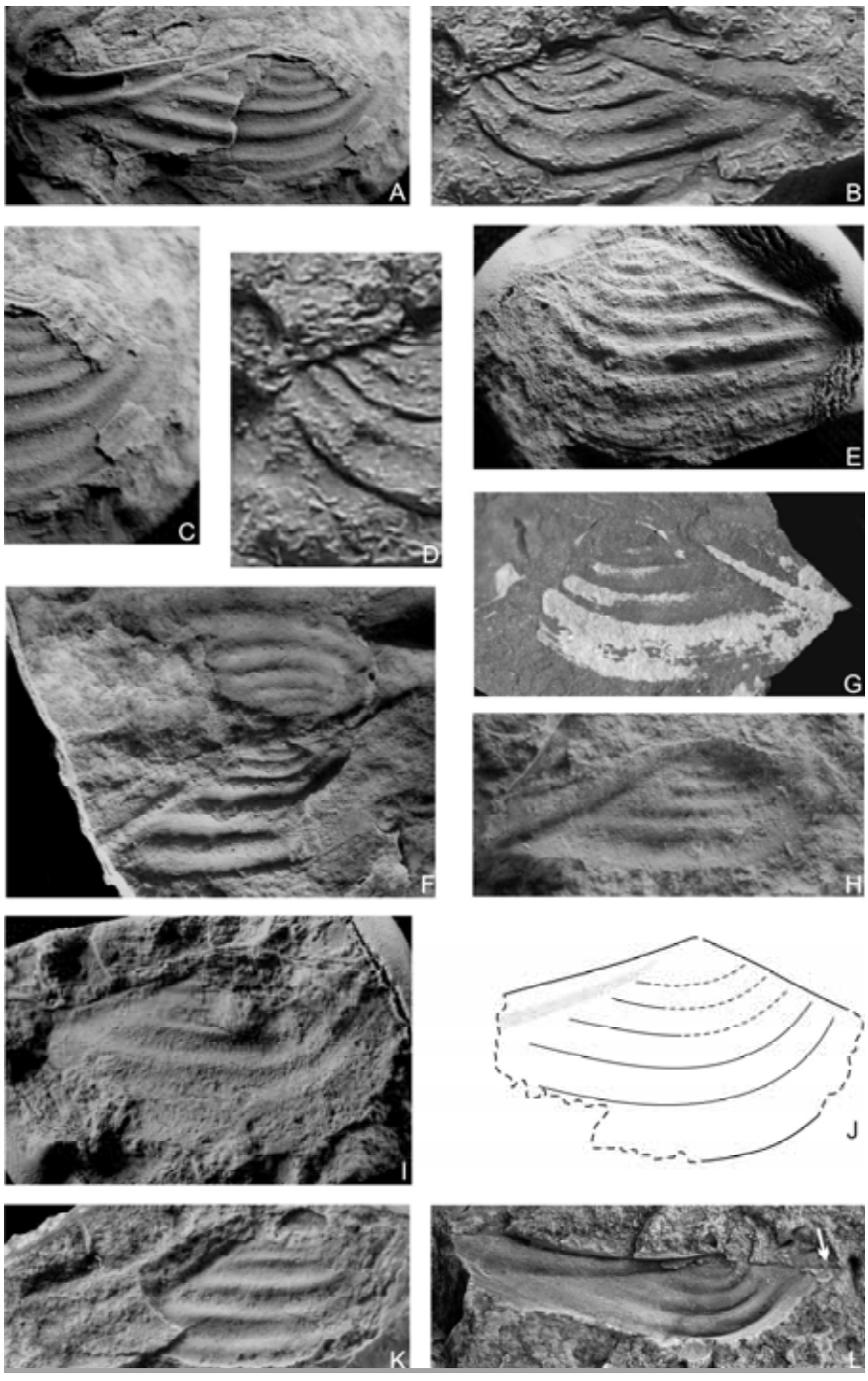

Figure 5

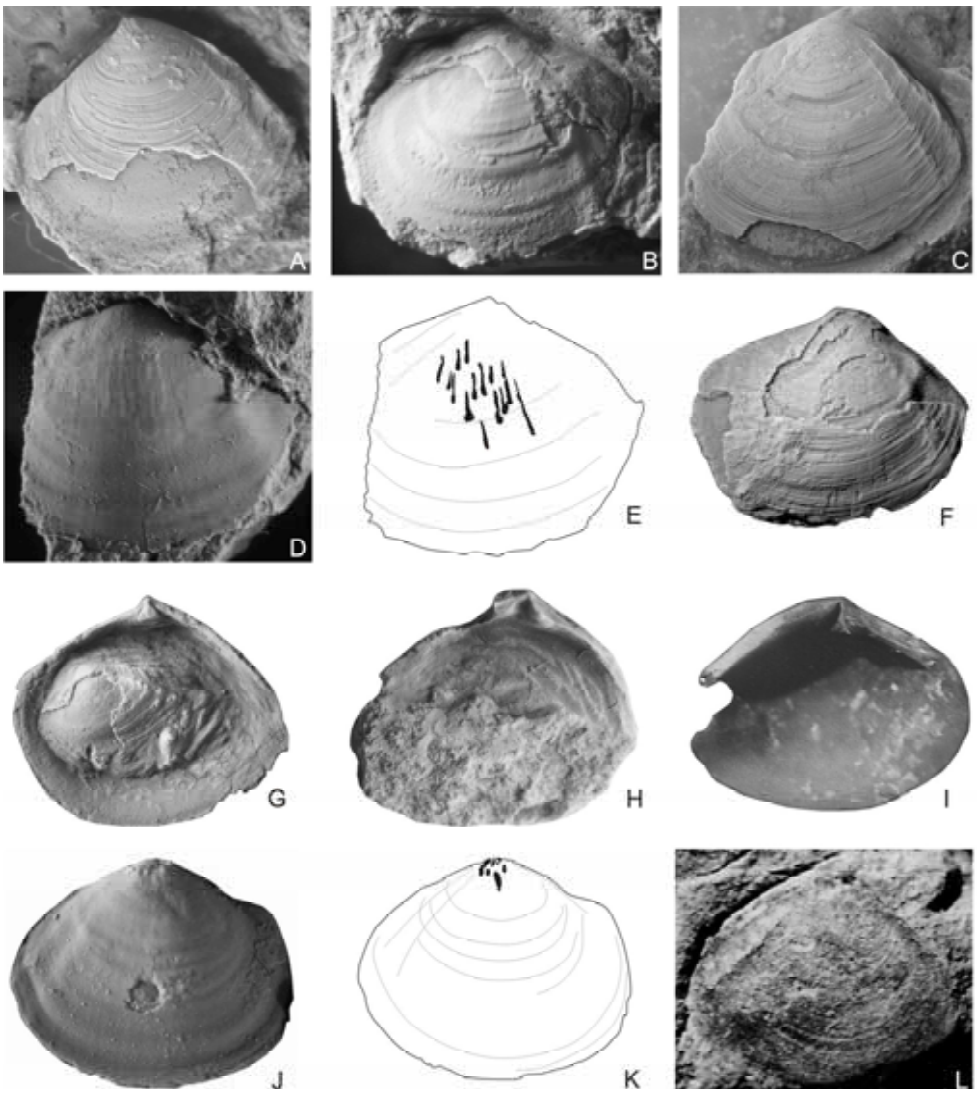

Figure 6

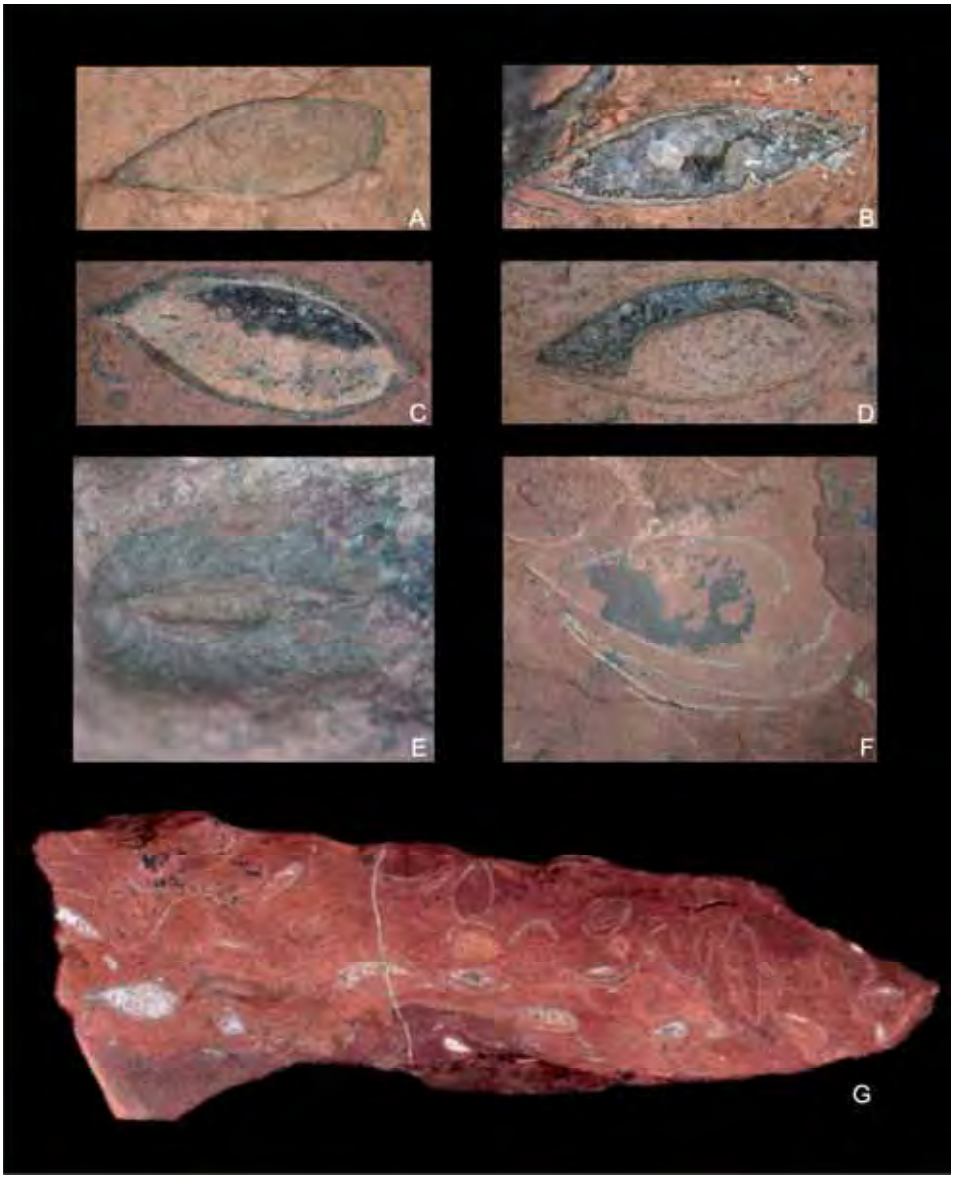

Figure 7

3. CONSIDERAÇÕES FINAIS

3.1. CONCLUSÕES

Os resultados dos dados disponíveis para o estudo dos bivalves da Formação Gai-As, área de Huab, NW da Namíbia, permitem sugerir que:

(a) Os atributos tafonômicos apresentados pelos bivalves das rochas da porção inferior da Formação Gai-As, área de Huab, NW da Namíbia, tais como a mistura de valvas articuladas e desarticuladas, a preservação de frágeis estruturas como o ligamento externo, a falta de sinais de abrasão, erosão ou incrustação, a presença de aninhamento e empilhamento de conchas, além do preenchimento de valvas articuladas pelo crescimento de cristais de calcita formando, em algumas situações, estruturas geoptais, indicam que os mesmos foram depositados por eventos de alta energia, exibindo alto grau de mistura temporal;

(b) Os atributos tafonômicos apresentados pelos bivalves das rochas da porção superior da Formação Gai-As, área de Huab, NW Namíbia, compreendem a presença de conchas em postura côncava para baixo, comumente desarticuladas, porém com raras conchas articuladas (*butterflied*). Este último atributo pode representar conchas mortas desalojadas durante eventos de alta energia, que foram misturadas junto às conchas previamente mortas que se encontravam no substrato, além de representar um ótimo indicador de um soterramento rápido, porém não abrupto. Entretanto, pelo fato das conchas estarem preferencialmente preservada em atitudes com a concavidade para baixo, elas podem indicar que, após acomodarem-se junto ao fundo, experimentaram um pequeno período de exposição, no qual correntes de fundo viraram as mesmas para uma posição hidrodinâmica mais estável;

(c) A diversidade de espécies de bivalves da Formação Gai-As, área de Huab, NW Namíbia é maior do que anteriormente conhecida, em conseqüência da identificação das espécies de *Terraia* cf. *altissima, Terraia* cf. *curvata* e *Cowperesia emerita*, além da descrição do novo gênero e espécie *Huabiella compressa*;

(c) Os dados bioestratigráficos provenientes da identificação das espécies de *Terraia* cf. *altissima, Terraia* cf. *curvata* e *Cowperesia emerita* na Formação Gai-As,

área de Huab, NW Namíbia, sugerem uma possível correlação com intervalos da porção basal (Membro Serrinha) da Formação Rio do Rasto, Bacia do Paraná, Brasil;

3.2. PERSPECTIVAS PARA ESTUDOS FUTUROS

Apesar da fauna de moluscos bivalves do Grupo Passa Dois, Bacia do Paraná, ser conhecida internacionalmente e representar o mais antigo exemplo conhecido de evolução *in situ*, na história evolutiva dos moluscos bivalves (WESSELINGH, 2007), muitos problemas ainda persistem quanto à história evolutiva e à sistemática desta fauna. De fato, a diversidade taxonômica dos bivalves do Grupo Passa Dois, Bacia do Paraná, permanece ainda obscura, devido ao parco e enviesado conhecimento desta fauna (SIMÕES; ANELLI; DAVID, 2010).

Os principais estudos relativos a esse assunto concentram-se nos bivalves referentes ao intervalo das biozonas de *Pinzonella illusa* e *Pinzonella neotropica*, nas porções médias e superiores das formações Teresina e Corumbataí (ROHN, 1994). Conforme destacado por Simões, Anelli e David (2010), diversas razões contribuem para este viés, entre elas, o fato dos bivalves destas biozonas serem encontrados em coquinas e arenitos bioclásticos, onde as conchas apresentam-se silicificadas e, frequentemente, bem preservadas. Por sua vez, os bivalves encontrados na Formação Irati (KAZUBEK; SIMÕES, 2003), na Formação Serra Alta (MARANHÃO, 1986) e nos Membros Serrinha e Morro Pelado, Formação Rio do Rasto (ROHN, 1994; ROHN; SIMÕES, 1997) continuam pouco e inadequadamente estudados. Por exemplo, os gêneros *Anhembia* (Mendes), 1949 e *Leinzia* Mendes, 1949 sempre se destacaram como uma das formas mais espetaculares da fauna de bivalves do Grupo Passa Dois, Bacia do Paraná, devido à sua morfologia incomum, marcada pela presença de *rostrum*. O primeiro ocorre em camadas da porção basal das formações Serra Alta e Corumbataí, enquanto o segundo encontra-se preservado em níveis estratigráficos referentes ao Membro Serrinha, na parte inferior da Formação Rio do Rasto. Desde quando foram propostos, a posição sistemática destes gêneros foi problemática, devido principalmente, ao precário conhecimento de sua anatomia interna.

Tanto Holdhaus (1918), quanto Reed (1929), ao examinarem espécimes atualmente atribuídos à *Leinzia similis*, que não apresentavam a expansão anterior característica desses gêneros, compararam respectivamente estes espécimes com os gêneros *Solenomorpha* e *Cuspidaria*. Mendes (1949), ciente desta expansão anterior, propôs o gênero *Leinzia*, contendo as espécies *Leinzia froesi*, *Leinzia gigantea* e *Leinzia*

similis. Em 1990, Mezzalira, Mendes e Maranhão sugeriram o gênero *Anhembia*, para diferenciar as formas presentes na base das formações Serra Alta e Corumbataí, *Leinzia froesi* e *Leinzia gigantea*, das ocorrentes (*Leinzia similis*) no Membro Serrinha da Formação Rio do Rasto. Os autores, entretanto, fundamentaram suas interpretações em caracteres biométricos, extraídos de um número reduzidos de exemplares, mostrando graus variados de distorção morfológica geral das conchas, devido à compactação, sendo que nenhuma sinapomorfia foi reconhecida pelos autores para diagnosticar o gênero *Anhembia*.

As afinidades sistemáticas dos gêneros *Leinzia* e *Anhembia* sempre foram de difícil reconhecimento, bem exemplificado pelas diferentes atribuições a famílias marinhas ou de afinidades incertas. Newell (1969), por exemplo, os atribuiu à Família Solenomorphidae, baseado na forma alongada da concha. Posteriormente, Runnegar e Newell (1971) mantiveram o gênero em família incerta, dentro dos crassateláceos, devido a uma interpretação equivocada dos caracteres das charneiras (vide abaixo). Mais recentemente, Mello, Simões, Marques e Ghilardi (1999) atribuíram as formas referentes a estes gêneros à Família Megadesmidae.

A análise tanto dos holótipos, quanto de material adicional destes dois gêneros, na tentativa de recuperar informações sobre a musculatura e charneira destes bivalves, reveste-se de grande importância para o entendimento do posicionamento taxonômico dos mesmos. Um re-exame de fósseis de *Leinzia* e *Anhembia* (Anexos, Figuras 1, 2), realizado durante o desenvolvimento deste mestrado, e motivado pelo reconhecimento anterior de formas semelhantes à *Leinzia similis* na Formação Gai-As, Bacia de Huab, NW Namíbia, possibilitou o resgate de detalhes preservados da musculatura e da charneira destes gêneros. Estes compreendem elementos importantes para a classificação (RUNNEGAR; NEWELL, 1971; SIMÕES; MARQUES; MELLO; ANELLI, 1997) e determinação do modo de vida (vide síntese em GHILARDI, 1999) desses bivalves.

O estudo de dois espécimes do gênero *Anhembia* (DGP 7-91, IG/SMA-774-I), permitiu o resgate das características do músculo anterior e da linha palial (Anexos, Figura 1b, f). Estas são morfologicamente semelhantes àquelas apresentadas pelos bivalves da Família Megadesmidae, que representa a família predominante entre os táxons do Grupo Passa Dois. A musculatura anterior dos táxons desta família é notavelmente recortada e irregular, assim como a apresentada pelos espécimes de *Anhembia*. Além disso, em alguns megadesmideos, como em *Astartila* e *Casterella*, a

linha palial apresenta um espessamento em sua porção anterior, exatamente como aquele observado no exemplar IG/SMA-774-I de *Anhembia* (vide também WASS, 1972).

Tais evidências sugerem uma possível relação de parentesco entre os táxons da Família Megadesmidae e o gênero *Anhembia*, a qual já havia sido destacada por Mello (1999). Segundo Simões, Marques, Mello e Anelli (1997), o monofiletismo desta família é suportado por um dente abrupto na valva direita. O fato do re-exame dos espécimes de *Anhembia* sugerir que este gênero possui uma charneira edentelosa, não invalida sua inclusão nesta família, já que outros megadesmideos, como *Roxoa*, *Holdhausiella* e *Casterella* também apresentam este tipo de charneira. Tal característica foi interpretada por Simões, Marques, Mello e Anelli (1997) como uma reversão de caráter, dentro da história filogenética do grupo.

Por sua vez, a análise de exemplares de *Leinzia similis* revelou que esta espécie apresenta uma fosseta triangular na valva esquerda (Anexos, Figura 2h) e, consequentemente, um dente triangular abrupto na valva direita, ou seja, uma charneira típica dos megadesmideos. Tanto o dente, quanto a ornamentação concêntrica, de *Leinzia similis* se assemelham à *Cowperesia* (MELLO, 1999). Tais evidências, assim como proposto por Mello (1999), também sugerem uma possível atribuição do gênero *Leinzia* à Família Megadesmidae.

Ambos os gêneros colonizaram fundos lamosos e a função da característica mais marcante dos mesmos, o rostrum, sempre permaneceu incerta na literatura. Savazzi e Peiye (1992) reconheceram esta mesma estrutura em um unioídeo vivente, *Arconaia lanceolata*, que sobrevive em substratos anóxicos e lamosos, ricos em metano. Alguns autores, tais como Simões; Rocha-Campos e Anelli, (1998, p. 447), Ghilardi (1999) e Mello (1999), levantaram a possibilidade desta estrutura morfológica estar relacionada com o desenvolvimento de processos simbióticos entre o bivalve e bactérias oxidantes, à moda do que ocorre com *Arconaia lanceolata* (vide SAVAZZI; PEIYE, 1992).

Conforme apresentado, existem evidências morfológicas que sugerem a atribuição dos gêneros *Anhembia* e *Leinzia* à Família Megadesmidae. Entretanto, somente um estudo mais detalhado dos espécimes existente, bem como a tentativa de aquisição de novos exemplares através da realização de novos trabalhos de campo e coleta, é imprescindível para viabilizar o entendimento das afinidades sistemáticas destes dois gêneros, contribuindo para o conhecimento da evolução e sistemática da fauna de moluscos bivalves do Grupo Passa Dois, Bacia do Paraná.

4. REFERÊNCIAS BIBLIOGRÁFICAS

ANELLI, L.E. *Invertebrados neocarboníferos das formações Piauí (Bacia do Parnaíba) e Itaituba (Bacia do Amazonas): taxonomia; análise cladística das subfamílias Oriocrassatellinae (Crassatellacea, Bivalvia) e Neospiriferinae (Spiriferoidea, Brachiopoda).* 1999. 184f. Tese (Doutorado em Geologia Sedimentar) - Instituto de Geociências, Universidade de São Paulo, São Paulo, 1999.

BERURLEN, K. Faunas salobras fósseis e o tipo ecológico-paleogeográfico das faunas Gondwânicas no Brasil. *Anais da Academia Brasileira de Ciências*, Rio de Janeiro, v.29, n.2, p. 229-241. 1957.

BRETT, C.; BAIRD, G.C. Comparative taphonomy: a key to paleoevironmental interpretation based on fossil preservation. *Palaios*, Tulsa, v.1, p. 207-227. 1986.

COOPER, M.R.; KENSLEY, B. Endemic South America Permian bivalve mollusks from the Ecca of South Africa. *Journal of Paleontology*, Tulsa, v.58, p. 1360-1363. 1984.

DICKINS, J.M. Permian geology of Gondwana countries: An overview. *International Geology Review*, Columbia, v.34, n.10, p. 986-1000. 1992.

FÜRSICH, F.T & OSCHMANN, W. Storm shell beds of *Nanogyra virgule* in the Upper Jurassic of France. *Neues Jahrhuch für Geologie und Paläontologie Abhandlungen*, Stuttgart, v.172, p. 141–161. 1986.

FÜRSICH, F.T.; OSCHMANN, W. Shell beds as tools in basin analysis: the Jurassic of Kachchh, western India. *Journal of Geological Society of London*, Londres, v.150, p. 169-185. 1993.

GHILARDI, R.P. *Paleoautoecologia dos bivalves do Grupo Passa Dois (Neopermiano), no estado de São Paulo: bivalves fósseis como indicadores da dinâmica sedimentar*. 1999. 162f. Dissertação (Mestrado em Geologia Sedimentar) - Instituto de Geociências, Universidade de São Paulo, São Paulo, 1999.

HOLDHAUS, K. Sobre alguns lamellibranchios fosseis do sul do Brasil. *Serviço Geológico e Mineralógico do Brasil*, Rio de Janeiro, Monografia 2, p. 1-24. 1918.

HORSTHEMKE, E., Fazies der Karoosediment in der Huab-Region, Damaraland, NW-Namibia. *Göttinger Arbeiten zur Geologie und Paläontologie*, Göttingen, v. 55, p.1-102. 1992.

KAZUBEK, M.F.; SIMÕES, M.G. Permian bivalves of the Irati Formation (Passa Dois Group, Paraná Basin) and their paleoecological significance. In: XVIII Congresso

Brasileiro de Paleontologia, 2003, Brasília. *Boletim de Resumos...*, Brasília: Sociedade Brasileira de Paleontologia, 2003. p. 161-161.

LAGES, L.C. *A Formação Irati (Grupo Passa Dois, Permiano, Bacia do Paraná) no furo de sondagem FP-01-PR (Sapopema, PR)*. 2004. 117f. Dissertação (Mestrado em Geologia Regional) - Instituto de Geociências e Ciências Exatas, Universidade Estadual Paulista, Rio Claro, 2004.

LEDENDECKER, S. Stratigraphie der Karoosedimente der Huabregion (NW-Namibia) und deren Koorrelalion mit zeitäquivalenten Sedimenten des Paranàbeckens (Südamerika) un des Groben Karrobeckens (Südafrika) unter besonderer Berücksichtigung der ü berrequonalen geodynamischen und klimatishen Entwicklung Westgondwanas. *Göttinger Arbeiten zur Geologie und Paläontologie*, Göttingen, v.54, p. 1-87. 1992.

KIDWELL, S.M.; FÜRSICH, F.T.; AIGNER, T. Conceptual framework for the analysis and classification of shell concentration. *Palaios*, Tulsa, v.1, p. 228-238. 1986.

MARANHÃO, M. S. A. S. *Contribuição ao conhecimento da malacofauna das camadas basais da Formação Corumbataí (Permiano) Estado de São Paulo*. 1986. 89f. Dissertação (Mestrado em Geologia Sedimentar) - Instituto de Geociências, Universidade de São Paulo, São Paulo, 1986.

MELLO, L.H.C. *Análise cladística dos bivalves do Grupo Passa Dois (Neopermiano), Bacia do Paraná, Brasil: implicações taxonômicas, evolutivas e paleobiogeográficas*. 1999. 160f. Dissertação (Mestrado em Geologia Sedimentar) - Instituto de Geociências, Universidade de São Paulo, São Paulo, 1999.

MELLO, L.H.C.; SIMOES, M.G.; MARQUES, A.C.; GHILARDI, R.P. Taphonomy, paleoecology and cladistics: a case study in Permian bivalves. In: The Geologycal Society of America Annual Meeting, 1999, Denver. *Geological Society of America Annual Meeting Program and Abstracts.*..Denver: Geological Society of America, 1999. p. 468-468.

MENDES, J.C. Novos lamelibrânquios fósseis da Série Passa Dois (Sul do Brasil). *Boletim do Departamento Nacional de Produção Mineral*, Rio de Janeiro, n.133, p. 1-40. 1949.

MENDES, J. C. A Formação Corumbataí na região do Rio Corumbataí (estratigrafia e descrição dos lamelibrânquios). *Boletim da Faculdade de Filosofia Ciências e Letras, Série Geologia*, São Paulo, v.8, n.145, p. 1-119. 1952.

MEZZALIRA, S.; MENDES, J.C.; MARANHÃO, M.S.A.S. *Anhembia*: novo gênero de bivalves do Grupo Passa Dois- Permiano. *Revista do Instituto Geológico*, São Paulo, v.11, n.1, p. 51-54. 1990.

NEVES, J.P. Tafonomia das rochas carbonáticas conchíferas das formações Teresina e Rio do Rasto (Permiano, Bacia do Paraná). 2009. 72f. Dissertação (Mestrado em Geologia Regional) - Instituto de Geociências e Ciências Exatas, Universidade Estadual Paulista, Rio Claro, 2009.

NEWELL, N.D. Classification of Bivalvia. In: MOORE, R.C. (Ed.). *Treatise on Invertebrate Paleontology, Pt. N, Mollusca 6, Bivalvia*. Lawrence: Geological Society of America and University of Kansas Press, 1969. p. N205-N218.

REED, F.R.C. Faunas Triassicas do Brasil. *Serviço Geológico e Mineralógico do Brasil*, Rio de Janeiro, Monografia 9, p.1-83. 1929.

ROCHA-CAMPOS, A.C.; BASEI, M.A.; DOS SANTOS, P.R. Depósitos de cinza vulcânica no Neopaleozóico da Bacia do Paraná: datação radiométrica (shrimp) e possíveis implicações cronoestratigráficas e paleoambientais. In: Reunião Anual da Sociedade Brasileira de Paleontologia - Núcleo SP, 2009, Guarulhos. *Boletim de Resumos*...São Paulo: Sociedade Brasileira de Paleontologia – São Paulo, 2009. p. 8.

ROHN, R. *Evolução ambiental da Bacia do Paraná durante o Neopermiano no leste de Santa Catarina e do Paraná.* 1994. 2v. Tese (Doutorado em Geologia Sedimentar) - Instituto de Geociências, Universidade de São Paulo, São Paulo, 1994.

ROHN, R. The Passa Dois Group (Paraná Basin, Permian): investigations in progress. In: I Workshop - Problems in the Western Gondwana Geology, South America - Africa correlations: du Toit revisited, 2007, Gramado. *Extended Abstracts*…Porto Alegre: UFRGS, 2007. p.151-157.

ROHN, R.; SIMÕES, M. G. Pelecypods of the basal Serrinha Member (Rio do Rasto Formation, Passa Dois Group, Upper Permian) at the Reserva-Cândido de Abreu region of the Paraná State. In: XV CONGRESSO BRASILEIRO DE PALEONTOLOGIA, 1997, São Pedro. *Boletim de Resumos*...São Pedro: Sociedade Brasileira de Paleontologia, 1997. p. 72.

ROHN, R.; MEGLHIORATTI, T.; CORDEIRO-SILVA, A. Tafonomia de bivalves em testemunhos de furos de sondagem das formações Serra Alta e Teresina (Permiano) no leste da Bacia do Paraná. In: XX Congresso Brasileiro de Paleontologia, 2007, Búzios. *Anais*...Rio de Janeiro: Sociedade Brasileira de Paleontologia, 2007. p.278-279.

RUNNEGAR, B. Evolutionary history of the bivalve Subclass Anomalodesmata. *Journal of Paleontology*, Tulsa, v.48, n.5, p. 904-939. 1974.

RUNNEGAR, B.; NEWELL, N.D. Caspian- like relict moluscan fauna in the South America Permian. *Bulletin of American Museum of Natural History*, Nova York, v.146, p.1-66. 1971.

SAVAZZI, E.; PEIYI, Y. Some morphological adaptations in freshwater bivalves. *Lethaia*, Oslo, v.25, p. 195-209. 1992.

SIMÕES, M.G.; KOWALEWSKI, M. Complex shell beds as paleoecological puzzles: A case study from the Upper Permian of the Paraná Basin, Brazil. *Facies*, Erlangen, v.38, p. 175-196. 1998.

SIMÕES, M.G.; TORELLO, F.F. Modelo de tafofácies para os moluscos bivalves do Grupo Passa Dois (Formações Serra Alta, Teresina e Corumbataí), Permiano Superior, Bacia do Paraná, Brasil. *Revista Brasileira de Geociências*, São Paulo, v.33, n.3, p. 1-10. 2003.

SIMÕES, M.G.; TORELLO, F.F.; ROCHA-CAMPOS, A.C. Gênese e Classificação da Coquina de Camaquã, Formação de Corumbataí (Neopermiano), na Região de Rio Claro, SP. *Anais da Academia Brasileira de Ciências*, Rio de Janeiro, v.68, n.4, p. 545-557. 1996.

SIMÕES, M.G.; ROCHA-CAMPOS, A.C.; ANELLI, L.E. Paleoecology and evolution of Permian pelecypod assemblages (Paraná Basin) from Brazil. In: JOHNSTON, P.A.; HAGGART, J.W. (Eds). *Bivalves- An eon of evolution: paleobiological studies honoring Norman D. Newell*. Calgary : University of Calgary Press, 1998. p.443-452.

SIMÕES, M.G.; ANELLI, L.E.; DAVID, J.M. *Othonella araguaiana* (Bivalvia, Megadesmidae) from the Corumbataí Formation (Midlle Permian), eastern margin of the Paraná Basin: systematical, evolutionary and biostratigraphical significances. *Revista do IG*, São Paulo, v. 10, p. 45-55. 2010.

SIMÕES, M.G.; MARQUES, A.C.; MELLO, L.H.C.; ANELLI, L.E. Phylogenetic analysis of the genera of the extinct Family Megadesmidae (Pelecypoda, Anomalodesmata), with remarks on its paleoecology and taxonomy. *Journal of Comparative Biology*, Ribeirão Preto, v.2, n.2, p. 75-90. 1997.

SIMÕES, M.G.; TORELLO, F.F.; MELLO, L.H.C.; GHILARDI, R.P. O conteúdo fossilífero de novos afloramentos do Grupo Passa Dois (Neopermiano), nas porções centro sul e nordeste do Estado de São Paulo: implicações bioestratigráficas e

paleoecológicas. *Acta Geológica Leopoldensia*, Porto Alegre, v.23, n.50, p.61-90. 2000.

STOLLHOFEN, H.; STANISTREET, I. G.; ROHN, R.; HOLZFOERSTER, F.; WANKE, A. The Gai-As lake system, northern Namibia and Brazil. In: GLERLOWSKI-KORDESCH, E. H.; KELTS, K. R. (Eds). *Lake basins through space and time*. Tulsa: AAPG Studies in Geology 46, 2000. p. 87-108.

WANKE, A. *Karoo- Etendeka Uncoformites in NW Namibia and their Tectonic Implications*. 2000. 114f. Dissertação (Doutorado), Universidade de Würzburg, Alemanha, 2000.

WASS, R.E. The anterior musculature of the Permian bivalve *Astartila* Dana. *Journal of Paleontology*, Tulsa, v.46, n.2, p. 231-322. 1972.

WESSELINGH, F.P. Long-lived lake molluscs as island faunas: a bivalve perspective. In*:* RENEMA, W. (Ed.). *Biogeography, time and place: distributions, barriers and islands*. Dordrecht: Springer, 2007. p.275-314.

ANEXOS

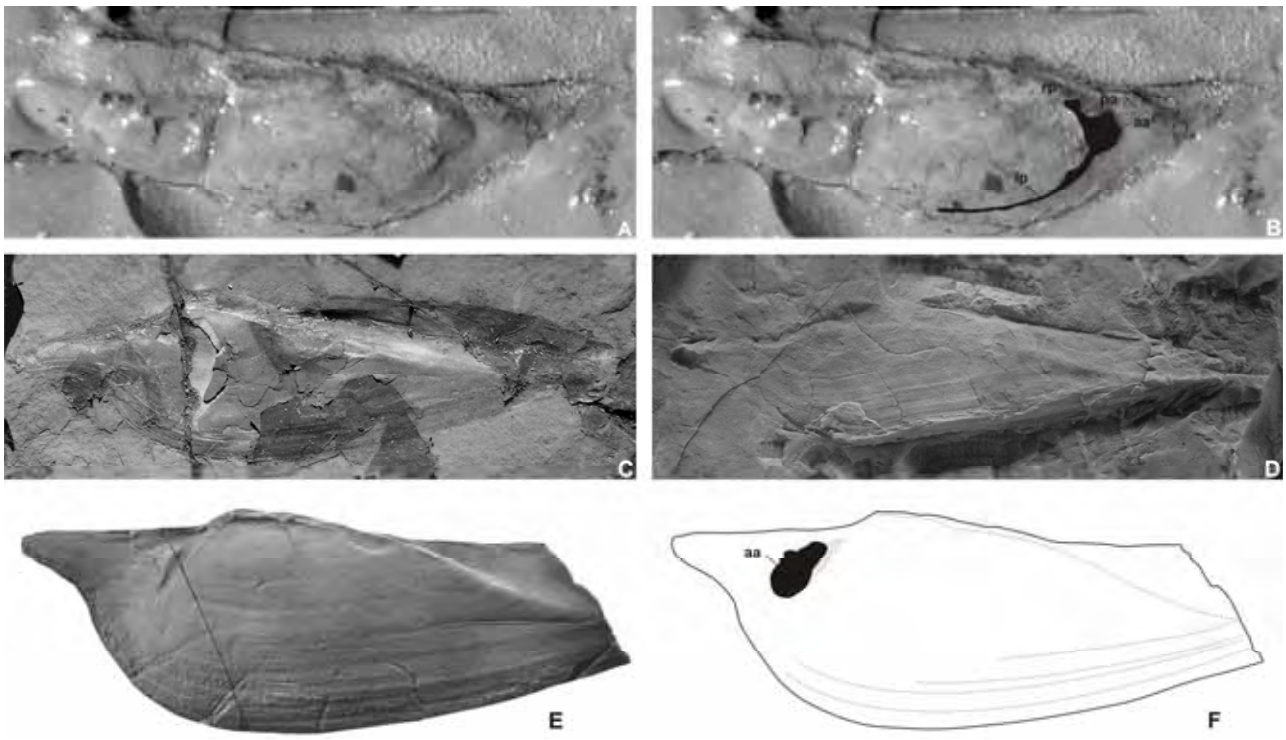

Figura 1 - Espécimes do gênero *Anhembia*. A-D, *Anhembia froesi*; E-F, *Anhembia gigantea*; A, molde interno, valva direita, IG/SMA-744-I, x 2.7; B, representação artística destacando a musculatura, IG/SMA-744-I, x 2.7; C, molde interno, valva esquerda, IG/SMA-611-I, x 1.2; D, molde interno, valva esquerda, DGP-7-90, x 0.9; E, molde interno, valva esquerda, DGP-7-91, x 0.9; F, representação artística destacando a musculatura, DGP-7-91, x 0.9. (aa, adutor anterior; pa, protator anterior; rp, retrator pedial; lp, linha palial).

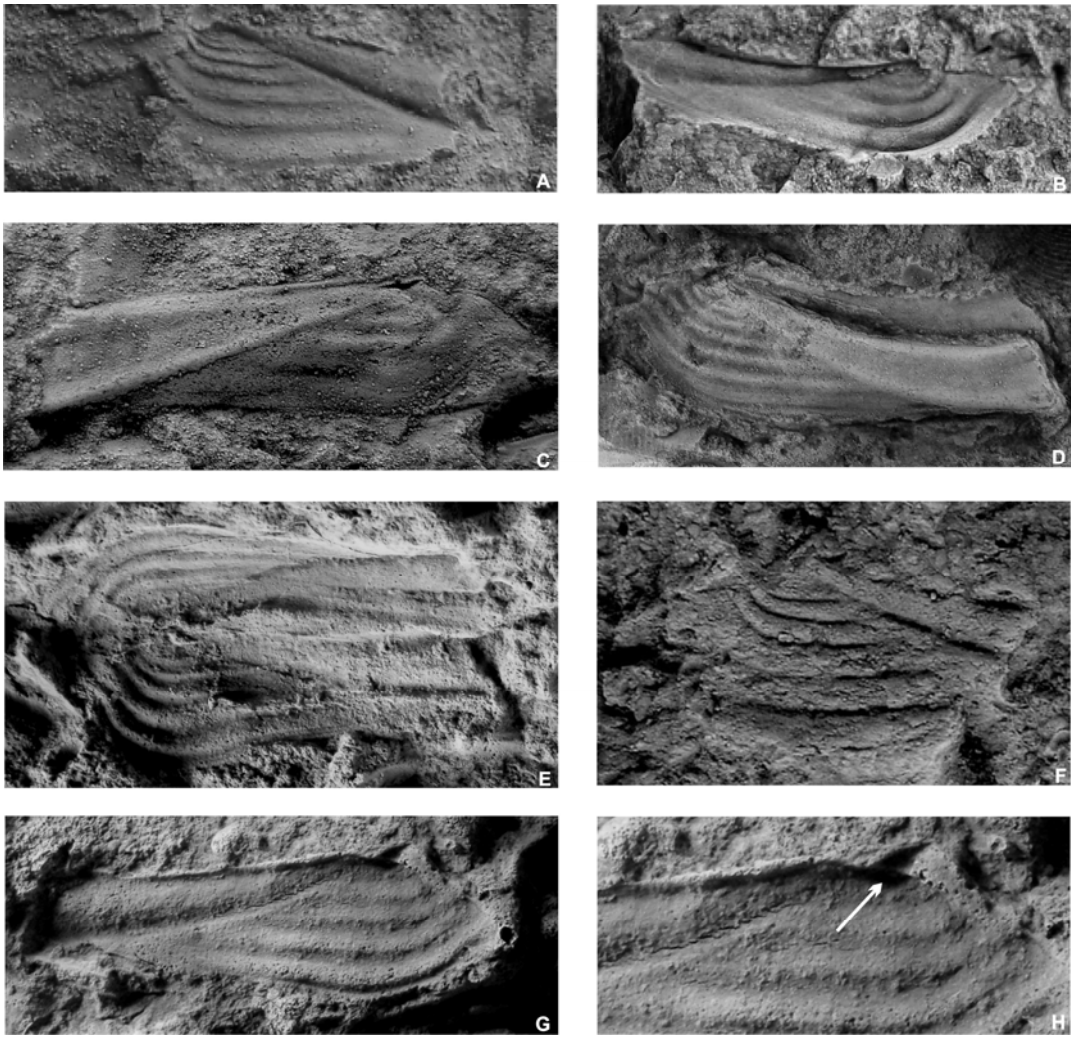

Figura 2 – Espécimes de *Leinzia similis*. A, molde externo, valva direita, DGP 7-86, x 3,6; B, molde externo, valva esquerda, DGP 7-85, x 2,2; C, molde interno, valva direita, DGP 7-88, x 3,2; D, molde interno, valva esquerda, DGP 7-86, x 1,9; E, molde interno, valvas conjugadas, DGP 7-88, x 2,7; F, molde externo, valva esquerda, URC MB 319, x 6,5; G, molde de látex do molde interno, valva esquerda, DGP, 7-88, x 2,6; H, molde de látex do molde interno, valva esquerda, a seta indica a fosseta triangular, DGP, 7-88, x 3,1.

A NEW PERMIAN BIVALVE (MEGADESMIDAE, PLESIOCYPRINELLINAE) FROM THE SERRINHA MEMBER, RIO DO RASTO FORMATION, PARANÁ BASIN, BRAZIL

Um Novo Bivalve Permiano (Megadesmidae, Plesiocyprinellinae) do Membro Serrinha (Formação Rio do Rasto), Bacia do Paraná, Brasil

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RESUMO

Durante recente organização das coleções paleontológicas do Laboratório de Paleontologia Sistemática do Instituto de Geociências, Universidade de São Paulo, foram localizados alguns espécimes de moluscos bivalves, ainda não descritos, que chamaram nossa atenção pelas seguintes razões: a- todos os espécimes são moldes internos de valvas conjugadas, articuladas fechadas, alguns destes com restos da concha silicificada; b- todos os moldes internos têm a mesma forma geral e características internas, representando espécimes de um mesmo táxon; c- os moldes internos e as valvas silicificadas estão bem preservadas, e incluem estruturas frágeis de difícil preservação, tais como o molde interno do ligamento externo e também as cicatrizes musculares; d- e igualmente importante, todos os espécimes estão registrados como provenientes das rochas do Grupo Passa Dois (Permiano), Membro Serrinha, da Formação Rio do Rasto. Embora não existam informações sobre o autor da coleta e localização geográfica dos espécimes, o estudo detalhado da morfologia desses fósseis evidencia tratar-se de um gênero de bivalve distinto dos já descritos para a fauna endêmica do Grupo Passa Dois. Fundamentado na forma geral da concha, estrutura da charneira e cicatrizes musculares, o novo táxon é atribuído à Família Megadesmidae Vokes, 1967, a mais diversificada dentre aquelas do Permiano da Bacia do Paraná. Os espécimes são aqui designados como *Beurlenella elongatella* gênero e espécie novos. A forma geral dos espécimes, bem como o modo de preservação, indica que se trata de um bivalve escavador raso ativo, rápido, suspensívoro, que foi provavelmente preservado *in situ*, em depósitos gerados por sedimentação episódica.

Palavras-chave: Bivalvia; Megadesmidae; Permiano; Bacia do Paraná; Membro Serrinha; Formação Rio do Rasto.

ABSTRACT

During a recent inspection in the Paleontological Collection of the Institute of Geosciences, University of São Paulo, we have identified some specimens of undescribed mollusk bivalves. These called our attention for the following reasons: a- all specimens are internal molds of conjugated and closed articulated valves, some of them presenting fragments of silicified shells; b- all internal molds have similar general shape and internal characters, representing specimens of the same taxon; c- the internal molds and silicified valves are well preserved, including fragile structures, which are hardly preserved, such as the internal mold of the external ligament and muscle scars; d- and equally important**,** according to the labels of all specimens, they were collected from rocks of the Passa Dois Group (Permian), Serrinha Member of the Rio do Rasto Formation. Although who collected the shells and the precise geographic location of the specimens are still unknown, the detailed study of these fossils brings us to the conclusion that they are morphologically distinct from any heretofore published genus of the endemic fauna of bivalves from Passa Dois Group. Based in its general shape, hinge structure and muscles scars, the new form can be classified under the Family Megadesmidae Vokes, 1967, the most diverse group of Permian bivalves of the Paraná Basin. The specimens are referred as *Beurlenella elongatella* new gen. and sp. The shell shape and taphonomy indicate that this bivalve was a shallow, rapid, active burrower, suspension feeder, probably preserved in situ, in event deposits.

Keywords: Bivalvia; Megadesmidae; Permian; Paraná Basin; Serrinha Member; Rio do Rasto Formation.

INTRODUCTION

The classical endemic, Permian molluscan fauna of the Passa Dois Group, Paraná Basin (Mendes, 1952; Runnegar and Newell, 1971; Simões, Rocha-Campos, Anelli, 1998) includes, according to the present knowledge, the following biozones (Rohn, 1994) in stratigraphic succession: *Anhembia froesi* (Serra Alta and Corumbataí formations), *Pinzonella illusa* (Teresina and Corumbataí formations), *Pinzonella neotropica* (Teresina and Corumbataí formations), *Leinzia similis* (Rio do Rasto Formation, Serrinha Member), and *Palaeomutela*? *platinensis* (Rio do Rasto Formation, Morro Pelado Member). Most of the previous studies have dealt with the systematics, paleoecology and taphonomy of bivalves of the *Pinzonella illusa* and *Pinzonella neotropica* biozones, where the shells are usually silicified and well preserved (Torello and Simões, 1994; Simões and Anelli, 1995; Simões, Torello, Rocha-Campos, 1996; Simões et al., 1997; Simões, Rocha-Campos, Anelli, 1998; Simões and Kowalewski, 1998; Ghilardi, 1999; Mello, 1999; Kowalewski et al., 2000; Ghilardi and Simões, 2002; Simões et al., 2000; Simões and Torello, 2003). Less well known are the faunas of the Serra Alta Formation (*Anhembia froesi* Biozone, Maranhão and Petri, 1996), and Serrinha (*Leinzia similis* Biozone) and Morro Pelado (*Palaeomutela*? *platinensis* Biozone) members, of the Rio do Rasto Formation. Actually, despite the exhaustive studies of Rohn (1985, 1988, 1994), and a short note in Rohn and Simões (1997), the bivalves of the Serrinha Member of the Rio do Rasto Formation are still poorly studied, described and drawn (Mendes, 1954; Rohn, 1994; Rohn and Simões, 1997).

Several lines of evidences suggest that the bivalve fauna of the Serrinha Member is more diverse than previously reported in the literature (see, for example, Rohn, 1994; Rohn and Simões, 1997). In fact, during a recent examination of the bivalve collection of the Institute of Geosciences, University of São Paulo a considerable number of forgotten, and undescribed bivalve specimens of the Serrinha Member were found.

These specimens were donated to Professor Josué Camargo Mendes (Institute of Geosciences, University of São Paulo) in the seventies, when he immediately recognized the importance of those specimens, due to their good preservation (A.C. Rocha-Campos, personal communication, 2009). However, for unknown reasons, J.C. Mendes was not able to study those bivalves, and since then, they have been forgotten. In the present study, we describe these bivalves with the following purposes: first, to add new systematic information about the bivalve fauna of the Serrinha Member; second, to show that the examination of this interval harbors bivalves could provide relevant taphonomical and paleoecological information, and finally, to call attention of geologists and paleontologists working with the Rio do Rasto Formation to the possible occurrence of unknown fossil material.

MATERIAL AND METHODS

As mentioned above, all specimens herein described are housed in the Scientific Collection of the Institute of Geosciences, University of São Paulo, São Paulo, under the code GP/1E. Although the specimens had been extracted from the rock matrix prior to their addition to that collection, the internal molds are made of grayish mudstone, which is the same matrix infilling of the closed articulated silicified shells. The type of preservation and lithology of the internal molds seem to be similar to that of bivalve-rich horizons found in the basal portion of Serrinha Member (see Rohn, 1994; Warren et al., 2008). However, the specimens were labeled only as placed in Passa Dois Group, Serrinha Member. Hence, the exact location and stratigraphic horizon where the specimens were collected are still unknown.

In total, ten bivalve specimens were studied and all of them are internal molds of conjugated valves of closed articulated shells. This set of specimens consists of three internal molds with silicified shell remains, six internal molds (two are almost

completely preserved internal molds and four have the posterior end of the shell missing) and one deformed internal mold (dorso-ventrally compressed). Plasticine casts and impregnation with magnesium show internal anatomical characters of the examined specimens, including muscle scars and hinge features. Finally, the suprageneric systematics is based on Morris, Dickins and Astafieva-Urbaitis (1991), and, at the family level, on Runnegar and Newell (1971), Runnegar (1974), and Simões et al. (1997). Shell obesity and elongation indexes were calculated according to Stanley (1970).

SYSTEMATIC PALEONTOLOGY

Subclass HETEROCONCHIA Hertwig, 1895

Superorder ANOMALODESMATA Dall, 1899

Order PHOLADOMYOIDA Newell, 1965

Superfamily PHOLADOMYOIDEA (King, 1844) Gray, 1847

Family MEGADESMIDAE Vokes, 1967

Subfamily PLESIOCYPRINELLINAE Simões et al., 1997

Comments. Runnegar and Newell (1971) assigned to Megadesmidae Vokes, 1967 the bivalves that yield robust and nacreous shells, with short siphons, a stout external ligament, lacking teeth or with a blunt tooth in the right or both valves. Simões et al. (1997) performed a cladistic analysis on the monophyly of the Family Megadesmidae and found it supported only by the blunt tooth of the right valve. The bivalve shells from the Serrinha Member have short and distinct nymph and a well marked blunt tooth in the right valve. These features suggest that the specimens belong to the Family Megadesmidae Vokes (1967). The absence of the accessory muscle scars (a, b, ava, see

Runnegar, 1966, 1974) suggests affinities to the Subfamily Plesiocyprinellinae (Simões et al., 1997).

Genus *Beurlenella* new genus

Figures 1, 2, Table 1

Type-species. *Beurlenella elongatella* n. gen. and sp.

Diagnosis. Megadesmid very elongate posteriorly; anterior margin rounded and expanded. Umbonal ridge well defined, slightly curved, located very close to posterior dorsal margin. A well developed blunt tooth is present in the right valve.

Etymology. It is named *Beurlenella* in honor of the eminent German geologist Karl Beurlen (1901-1985), in recognition of his contribution to the knowledge of the paleontology and stratigraphy of the Gondwana sequence of the Paraná Basin (states of Paraná, Santa Catarina and Rio Grande do Sul), Brazil. Data gathered by K. Beurlen during the fifties provided some clues to understating of the evolution of the endemic molluscan fauna of the Passa Dois Group, Permian.

Remarks. The new genus *Beurlenella* has several characters that make it very distinct from other endemic bivalve species from the Permian Paraná Basin. Actually, the shells of *Beurlenella* share a set of common characters that, isolated, can be seen in distinct megadesmids of the Passa Dois Group. For example, the shells of *Beurlenella* are elongated; a feature also noted in *Jacquesia* Mendes, 1944, *Favalia* Mendes 1962, and *Houdhausiella* Mendes 1952, but, on the other hand, these shells are edentulous or have a poorly developed megadesmid blunt tooth in the right valve. Carinate, elongated shells are also found in *Leinzia* (Holdhaus, 1918) and *Anhembia* (Mendes, 1949), but a

remarkable rostrum, which is absent in *Beurlenella,* is present in the anterior extremity of these shells. Although *Plesiocyprinella* Holdhaus, 1918, and *Ferrazia* Reed, 1932 have a well developed megadesmid tooth in the right valve, just like *Beurlenella* does, those shells are not elongate. In addition to that, *Ferrazia* has a completely distinct ornamentation.

Beurlenella elongatella new species

Figures 1A-K, 1M-N, 2

Holotype. GP/1E 4816.

Comments: The holotype specimen GP/1E 4816 (Figures 1A-E) is an internal mold, which comprises a preserved and nearly complete silicified right valve, showing the expanded anterior region of shell, the umbonal carina located close to the posterior dorsal margin and the internal mold of the parivincular ligament.

Paratypes. GP/1E 4815, 4817, 4818, 4919, 4920, 4021, 4022, 4823, 4825.

Comments. Plasticine casts of hinge area of paratypes GP/1E 4815 (Figures 1G-I) and GP/1E 4825 (Figures 1J-K) clearly show the presence of megadesmid blunt in their right valves (arrows).

Diagnosis. As for the genus (see above).

Etymology: *elongatella*, referring to the posteriorly elongated nature of *Beurlenella* shells.

Stratigraphy. Passa Dois Group, Serrinha Member (?), Rio do Rasto Formation, eastern margin of the Paraná Basin.

Locality. Unknown.

Age. Permian, Guadalupian to Early Lopingian.

Description. Megadesmid shell of medium size, varying in length from 44 – 49 mm for incomplete specimens (see Table 1), thick, equivalve, inequilateral, very elongate posteriorly, moderate inflated, non-gaped anteriorly. Posterior end of the shell unknown. Umbones low, slightly prosogyrous; postero-umbonal ridge, slightly curved, well defined but slender, located very close to posterior dorsal margin. Lunule absent; escutcheon very narrow. Ligament short, opisthodetic, parivincular, external, attached to a very slender nymph placed deep on the anterior portion of the escutcheon. Anterior margin expanded androunded; ventral margin anteriorly convex and straight posteriorly; dorsal margin straight. Surface ornament of well-marked, irregularly spaced comarginal growth lines of varying width. Hinge of right valve with a well defined blunt tooth; left valve with a well defined socket. Posterior adductor and pedal retractor scars well defined, not connected to the adductor. Anterior adductor muscle scars and pallial line not observed.

Discussion. The new species from Paraná Basin here described presents robust valves and a blunt tooth in the right valve, features that properly include them in the Family Megadesmidae. The elongated nature of their shells is also observed in other elements of the endemic fauna of the Passa Dois Group, such as *Holdhausiella* (Holdhaus) and

Jacquesia (Reed). However, in these genera, the hinge is edentulous (*Holdhausiella*) or with a poorly developed megadesmid tooth in the right valve (Jacquesia). These hinge characteristics are in remarkable contrast with those shown by *Beurlenella elongatella*, where the megadesmid tooth is well developed. *B. elongatella* resembles *Favalia arcuata* in general shell shape (see Runnegar and Newell, 1971, p. 43, fig. 17b, e), but its shells are thicker and its obesity index is higher. In addition, the shells of *F. arcuata* are edentelous. Finally, the size and position of the opistodetic ligament in *B. elongatella* are very similar to that observed in *Plesiocyprinella* (see Figures 1D, 1L).

TAPHONOMY, PALEOECOLOGY AND FACIES ASSOCIATION

As demonstrated by Stanley (1970, 1972), Kondo (1987, 1989) and Ghilardi and Simões (2000), the biostratinomy and functional anatomy of infaunal bivalves are potential sedimentological tools for stratigraphical analyzes. In this context, the mode of preservation and the paleoautoecology of the shells of *Beurlenella elongatella* can provide several clues about the kind of strata where they were preserved, despite the fact this information is missing.

Beurlenella elongatella is a very elongated, compressed to moderately inflated, non-gaped shell, with a broad anterior margin that may have accommodated a large foot, during life. Hence, the anatomy of *B. elongatella* indicates that this species was an active, rapid, suspension-feeder and shallow burrower (see Stanley, 1970). In this context, the life habit of *B. elongatella* was similar to that of other megadesmids with posteriorly elongated shells, such as *Myonia*, *Holdhausiella* and *Jacquesia*, except, perhaps, by the fact that the new species was a rapid burrower. As suggested by Stanley (1970), recent bivalves with very elongated valves use very little or no rocking movement (see also Rocha-Campos and Simões, 1993) and the foot of these bivalves normally emerges in a direction parallel to the long axis of the shell. In this way, the

mode of life of *B. elongatella* was probably with its shell positioned with the main axes nearly perpendicular to bedding. It was inferred that the mode of life of Late Paleozoic megadesmids was similar (see Rocha-Campos and Simões, 1993). Since the shells keep the same position when burrowing into the sediment (Stanley, 1970), bivalves with very elongated shells are preserved *in situ*, within the substrate, in the same position (see Anelli, Simões, Rocha-Campos, 1998). In other words, erosional and rapid depositional events can be identified based only on the preserved position of the infaunal bivalve shells (Ghilardi and Simões, 2000). Finally, like other megadesmids, *B. elongatella* was probably a suspension-feeder bivalve, indicating that food resources were dominantly in suspension in the water.

The taphonomy and functional morphology of Paleozoic marine bivalves are well known from a number of papers (see a review in Ghilardi, 1999). Most of shell-rich beds from Paleozoic epeiric seas (see, for example, Brett and Baird, 1986), as was the case of Paraná Basin during the Mid Permian, were formed under the influence of storms (see Torello and Simões, 1994; Simões, Torello, Rocha-Campos, 1996, Simões et al., 2000; Simões and Kowalewski, 1998; Simões and Torello, 2003). As discussed by Kondo (1997), storm process may be erosional or depositional, depending on the environment and severity of the storm. In shallow water (well above storm wave base), or in very shallow seas (as it was the case of Paraná Basin), a large amount of sediment may be removed during storms, causing infaunal disruption. On the middle to lower shelf (well below the normal wave base), however, there may be rapid deposition of suspended muddy blankets after a storm, without significant erosion or substrate disruption. Thus, the sedimentological and taphonomical record of bivalve shells within a storm-dominated succession will differ greatly, depending on the position with respect to water depth or storm wave base (see Rodrigues, Simões, Leme, 2003, for a similar pattern with Paleozoic cnidarians).

As demonstrated by various authors (Seilacher, 1982; Seilacher, Reif and Westphal, 1985; Brett and Baird, 1986; Brett, 1990; Brett and Seilacher, 1991; Anelli, Simões and Rocha-Campos, 1998; Simões and Kowalewski, 1998), infaunal bivalves preserved *in situ* are invariably associated to storm events, especially obrution deposits. The shells of *B. elongatella* are conjoined and pristine. Although the original position in the rock matrix is missing, the fact that the shells are closed articulated, without signs of abrasion, fragmentation, and encrustation, indicates that those shells were not exposed to the sediment/water interface. In summary, there are no signs that *B. elongatella* shells were repeatedly washed out and transported, which ultimately indicates that the shells were probably preserved in deposits generated just in and/or below storm wave base, probably in distal tempestites (obrution deposits).

Hummocky and swaley cross-stratification, which have often been pointed out as sedimentary structures characteristic of storm events, are in fact the unique sedimentary structures originated during storm sedimentation. Therefore we may search in the stratigraphical record of the Rio do Rasto Formation for the most plausible interval where storm sedimentation prevails. These intervals are likely to preserve bivalve shells with similar taphonomic signatures, as those found in the shells of *B. elongatella*. According to Warren et al. (2008), the lower portion of the Rio do Rasto Formation is characterized by beds that were deposited in offshore environments subjected to storm action (see also Rohn, 1994). These rocks are part of storm-dominated facies, where sandstones with hummocky cross-stratification and heterolitic mudstones are common (Warren et al., 2008). This lower portion of the Rio do Rasto Formation is part of the interval of the Serrinha Member, the same assigned in the label of our examined specimens. According to Rohn (1994) and Rohn and Simões (1997), the base of the Serrinha Member is, in part, the interval of the *Leinzia similis* Biozone, but when considering the examined collection, typical members of this biozone are missing.

However, Rohn and Simões (1997) have defined a distinct (unnamed) bivalve biozone in the basal portion of the Serrinha Member, which is a little older than the typical *Leinzia similis* Biozone. The bivalves from this interval are commonly preserved as molds in green-yellowish shale, as articulated valves, either closed or butterflied, some probably preserved *in situ* (Rohn and Simões, 1997). Hence, the taphonomical conditions of the bivalve shells present in this basal interval are similar to that of the specimens herein described. Alternatively, however, it should be remembered that the fact that the studied shells are close articulated does not exclude *per se* the possibility of an occurrence of these shells in the strata of the Morro Pelado Member of the Rio do Rasto Formation. This is explained by the fact that some shells of the *Palaeomutela*? *platinensis* Biozone (above the Serrinha Member) were also found articulated (Rohn, 1994), indicating they were abruptly buried by sediments associated to turbulent hyperpycnal flows, such as at river mouths in lakes (R. Rohn, personal communication, 2009). Unfortunately, only further research can confirm or refute the assertion above mentioned, named the identification of bivalve shells preserved *in situ* in storm deposits in the basal portion of the Rio do Rasto Formation (Serrinha Member), or otherwise in marginal lacustrine to fluvial deposits in the mid portion of this unit (Morro Pelado Member). Since the studied specimens were labeled as “Serrinha Member”, the first option seems to be the most plausible in light of the information available.

FINAL REMARKS

All the examined specimens were referred to the new megadesmid genus and species *Beurlenella elongatella*. It is not a surprise that the small assemblage studied here is dominated by megadesmid bivalves, since this group was the most diverse and abundant in the Paraná Basin during Permian times. Hence, our data is not only another indication of the dominance of Megadesmidae in the Passa Dois Group fossil record,

but also a remarkable evidence of the morphological disparity showed in this group of Permian bivalves of the Paraná Basin. Therefore, we assign this new element to the Serrinha Member molluscan fauna.

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REFERENCES

ANELLI, L. E.; SIMÕES, M. G.; ROCHA-CAMPOS, A. C. Life mode of some Brazilian Upper Paleozoic anomalodesmatans. In: JOHNSTON, P. A; HAGGART, J. W. *Bivalves: An Eon of evolution - Paleobiological Studies in Honoring of Norman D. Newell*. Calgary: University of Calgary Press, 1998. p. 65-74.

BRETT, C. E. Obrution deposits. In: BRIGGS, D. E. G.; CROWTHER, P. R. *Palaeobiology, a Synthesis*. Oxford: Blackwell, 1990. p. 239-243.

BRETT, C.; BAIRD, G. C. Comparative taphonomy: a key to paleoenvironmental interpretation based on fossil preservation. *Palaios*, v. 1, p. 207-227, 1986.

BRETT, C. E.; SEILACHER, A. Fossil Lagerstatten: a taphonomic consequence of event sedimentation. In: EINSELE, G. et al., *Cycles and Events in Stratigraphy*. Berlin: Springer, 1991. p. 283-297.

GHILARDI, R. P. *Paleoautoecologia dos bivalves do Grupo Passa Dois (Neopermiano), no Estado de São Paulo: bivalves fósseis como indicadores da dinâmica sedimentar*. 1999. 160 f. Dissertação (Mestrado) - Instituto de Geociências, Universidade São Paulo, São Paulo, 1999.

GHILARDI, R. P.; SIMÕES, M. G. Bivalves fósseis como indicadores da dinâmica sedimentar: um estudo de casos do Permiano da Bacia do Paraná, Brasil. *Acta Geologica Leopoldensia*, v. 23, n. 51, p. 3-20, 2000.

GHILARDI, R. P.; SIMÕES, M. G. Foram os bivalves do Grupo Passa Dois (Exclusive Formação Rio do Rasto), Neopermiano, invertebrados tipicamente dulcícolas? *Pesquisas em Geociências*, v. 29, p. 91-99, 2002.

HOLDHAUS, K. Sobre alguns lamelibranchios fósseis do sul do Brasil. *Serviço Geológico e Mineralógico, Monografia* 2, 1918. p. 1-24.

KONDO, Y. Burrowing depth of infaunal bivalves- observation of living species and its relation to shell morphology. *Transactions and Proceedings of the Palaeontological Society of Japan*, v. 148, p. 306-323, 1987.

KONDO, Y. A method of analysing mode of occurrence of bivalve fossils-comparison of position and orientation of living and fossil bivalves. *Benthos Research*, v. 37, p. 73-82, 1989.

KONDO, Y. Inferred bivalve response to rapid burial in a Pleistocene shallow-marine deposit from New Zealand. *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 128, p. 87-100, 1997.

KOWALEWSKI, M.; SIMOES, M. G.; TORELLO, F. F.; MELLO, L. H. C ; GHILARDI, R. P.Drill holes in shells of Permian benthic invertebrates. *Journal of Paleontology*, v. 74, p. 532-543, 2000.

MARANHÃO, M. S. A. S.; PETRI, S. Novas ocorrências de fósseis nas formações Corumbataí e Estrada Nova do Estado de São Paulo e considerações preliminares sobre seus significados paleontológicos e bioestratigráfico. *Revista do Instituto Geológico, São Paulo*, v. 17, p. 33-54, 1996.

MELLO, L. H. C. *Análise cladística dos bivalves do Grupo Passa Dois (Neopermiano), Bacia do Paraná, Brasil*: implicações taxonômicas, evolutivas e paleobiogeográficas. 1999. 160 f. Dissertação (Mestrado) - Instituto de Geociências, Universidade São Paulo, São Paulo, 1999.

MENDES, J. C. Lamelibrânquios triássicos de Rio Claro. *Boletim da Faculdade de Filosofia Ciências e Letras.* Série Geologia, v. 45, v. 1, p. 41-75, 1944.

MENDES, J. C. Novos lamelibrânquios fósseis da Série Passa Dois, Sul do Brasil. *Boletim da Divisão de Geologia e Mineralogia*, DNPM, v. 133, p. 1-40, 1949.

MENDES, J. C. A Formação Corumbataí na região do Rio Corumbataí (estratigrafia e descrição dos lamelibrânquios). *Boletim da Faculdade de Filosofia Ciências e Letras*. Série Geologia, v. 145, p. 1-119, 1952.

MENDES, J. C. Contribuição à estratigrafia da Série Passa Dois no Estado do Paraná. *Boletim da Faculdade de Filosofia Ciências e Letras* Série Geologia, v. 175, p. 1-119, 1954.

MENDES, J. C. Lamelibrânquios permianos do oólito de Angatuba, estado de São Paulo (Formação Corumbataí). *Boletim da Sociedade Brasileira de Geologia*, v. 11, n. 1, p. 37-56, 1962.

MORRIS N. J.; DICKINS, J. M.; ASTAFIEVA-URBAITIS, K. Upper Paleozoic Anomalodesmatan Bivalvia. *Bulletin of the British Museum of Natural History (Geology)*, v. 47, p. 51-100, 1991.

PETRI, S.; FÚLFARO, V. J. Sobre a geologia das cidades balizadas pelas cidades de Barra do Garça e Guiratinga, Mato grosso e Jataí Amorinópolis, Goiás. *Boletim da Sociedade Brasileira de Geologia*, v. 15, n. 3, p. 59-80, 1966.

ROCHA-CAMPOS, A. C.; SIMÕES, M. G. *Australomya sinuosa* sp.n., um novo Megadesmídeo (Mollusca, Pelecypoda) da Formação Rio Bonito (Permiano), Bacia do Paraná, Brasil. *Anais da Academia Brasileira de Ciências*, v. 65, n. 1, p. 29-39, 1993.

RODRIGUES, S. C.; SIMÕES,M. G.; LEME, J. M. Tafonomia comparada dos Conulate (Cnidária), Formação Ponta Grossa (Devoniano), Bacia do Paraná, Estado do Paraná. *Revista Brasileira de Geociências*, v. 33, n. 4, p. 381-390, 2003.

ROHN, R. Bivalves da Formação Rio do Rasto (Permiano Superior) no Estado do Paraná. In: CONGRESSO BRASILEIRO DE PALEONTOLOGIA, 9., 1985, Fortaleza. *Resumos*... Rio de Janeiro: Sociedade Brasileira de Paleontologia, 1985. v. 1, p. 134.

ROHN, R. *Bioestratigrafia e paleoambientes da Formação Rio do Rasto na borda leste da Bacia do Paraná (Permiano Superior, estado do Paraná).* 1988. 2v. Dissertação (Mestrado) - Instituto de Geociências, Universidade São Paulo, São Paulo, 1988.

ROHN, R. *Evolução ambiental da Bacia do Paraná durante o Neopermiano no leste de Santa Catarina e do Paraná*. 1994. 2v. Tese (Doutorado)- Instituto de Geociências, Universidade São Paulo, São Paulo, 1994.

ROHN, R.; SIMOES, M. G. Pelecypods of the basal Serrinha Member (Rio do Rasto Formation, Passa Dois Group, Upper Permian) at the Reserva-Cândido de Abreu region of the Paraná State. In: CONGRESSO BRASILEIRO DE PALEONTOLOGIA, 15, 1997, São Pedro. *Boletim de Resumos*...São Pedro: SBG, 1997, p. 72.

RUNNEGAR, B. Systematic and biology of some desmodont bivalves from the Australian Permian. *Journal of Geological Society of Australia*, v. 13, n. 2, p. 373-386, 1966.

RUNNEGAR, B. Evolutionary history of the bivalve Subclass Anomalodesmata. *Journal of Paleontology*, v. 48, p. 904-939, 1974.

RUNNEGAR, B.; NEWELL, N. D. Caspian-like relict molluscan fauna in South American Permian. *Bulletin of the American Museum of Natural History,* v. 146, p. 1-66, 1971.

SEILACHER, A. General remarks about event deposits. In: EINSELE, G.; SEILACHER, A. *Cyclic and Event Stratification*. Berlin: Springer, 1982. p. 16l-174.

SEILACHER, A.; REIF, W. E.; WESTPHAL, F. Sedimentological, ecological and temporal patterns of fossil Lagerstatten. *Philosophical Transactions Royal Society London B*, v. 311, p. 5- 23, 1985.

SIMÕES, M. G.; ANELLI, L. E. *Runnegariella*, um novo gênero de Megadesmidae (Pelecypoda) da Formação Corumbataí (Neopermiano), Bacia do Paraná, Brasil. *Revista Geociências,* v. 14, p. 161-173, 1995.

SIMÕES, M. G.; KOWALEWSKI, M. Shell beds as paleoecological puzzles: a case study from the Upper Permian of the Paraná Basin, Brazil. *Facies,* v. 38, p. 175-196, 1998.

SIMOES, M. G.; TORELLO, F. F. Modelo de tafofácies para os moluscos bivalves do Grupo Passa Dois (Formações Serra Alta, Teresina e Corumbataí), Permiano Superior, Bacia do Paraná, Brasil. *Revista Brasileira de Geociências,* v. 33, p. 1-10, 2003.

SIMÕES, M. G.; TORELLO, F. F.; ROCHA-CAMPOS, A. C. Gênese e classificação da coquina de Camaquã, Formação Corumbataí (Neopermiano), na Região de Rio Claro, SP. *Anais da Academia Brasileira de Ciências*, v. 68, p. 545-557, 1996.

SIMÕES, M. G.; ROCHA-CAMPOS, A. C.; ANELLI, L. E. Paleoecology and evolution of Permian pelecypod assemblages (Paraná Basin) from Brazil. In*:* JOHNSTON, P. A.; HAGGART, J. W. (Ed.) *Bivalves - An Eon of evolution: paleobiological studies honoring Norman D. Newell*. Calgary: University of Calgary Press, 1998. p. 443-452.

SIMÕES, M. G.; KOWALEWSKI, M.; TORELLO, F. F.; GHILARDI, R. P.; MELLO, L. H. C. Early onset of Modern-Style shell beds in the Permian sequences of the Paraná basin: implications for the Phanerozoic trend in bioclastic accumulations. *Revista Brasileira de Geociências*, v. 30, p. 499-503, 2000.

SIMÕES, M. G.; MARQUES, A. C.; MELLO, L. H. C.; ANELLI, L. E. Philogenetic analysis of the genera of the extinct family Megadesmidae (Pelecypoda, Anomalodesmata), with remarks on its paleoecology and taxonomy. *Journal of Comparative Biology,* v. 2, p. 75-90, 1997.

STANLEY, S. M. Relation of shell form to life habitats of the Bivalvia (Mollusca). *Memoir of the Geological Society of America*, v. 125, p. 1-296, 1970.

STANLEY, S. M. Functional morphology and evolution of byssally attached bivalve mollusks. *Journal of Paleontology*, v. 46, n. 2, p. 165-212, 1972.

TORELLO, F. F.; SIMÕES, M. G. Características tafonômicas da assembléia de *Pinzonella illusa* Reed, Formação Corumbataí (Neopermiano), Bacia do Paraná, Brasil. *Acta Geologica Leopoldensia*, v. 39, p. 159-173, 1994.

WARREN, L. V.; ALMEIDA, R. P.; HACHIRO, J.; MACHADO, R.; ROLDAN, L. F.; STEINER, S. S.; CHAMANI, M. A. C. Evolução sedimentar da Formação Rio do Rastro (Permo-Triássico da Bacia do Paraná) na porção centro sul do estado de Santa Catarina, Brasil. *Revista Brasileira de Geociências*, v. 38, n. 2, p. 213-227, 2008.

Legends

Figure 1. A-K, M-N, *Beurlenella elongatella* new gen. and sp., Passa Dois Group, Serrinha Member, Paraná Basin, Permian. All specimens x1.3. A, incomplete silicified internal mold with silicified shell remains, right valve view, GP/1E 4816; B, internal mold with fragments of silicified shell, left valve view, same specimen; C, anterior view, same specimen; D, dorsal view, same specimen, with the internal mold of the ligament preserved (arrow); E, drawing representation of the dorsal view, same specimen; F, incomplete internal mold, left side view, GP/1E 4815; G, ventral view, same specimen; H, dorsal view, same specimen showing hinge region; I, plasticine mold, internal view of articulated hinge region, showing the blunt tooth of right valve (arrow), based on the same specimen; J, internal mold showing the posterior part of shell covered with silicified shell, dorsal view, GP/1E 4825; K, plasticine mold, internal view of articulated hinge region, showing the blunt tooth of right valve (arrow), based on the same specimen; L, *Plesiocyprinella carinata* (Holdhaus) 1918, Corumbataí Formation, Upper Permian; silicified articulated shell, dorsal view showing the silicified ligament (arrow), DZP-681; M, almost dorsoventraly compressed internal mold, right side view, GP/1E 4822; N, dorsal view, same specimen.

Figure 2. *Beurlenella elongatella* new gen. and sp., Passa Dois Group, Serrinha Member, Paraná Basin, Upper Permian. All specimens x1.3. A, fragmentary internal mold with silicified shell remains, left side view, GP/1E 4819; B, muscle scars based in the same specimen; C, fragmentary internal mold, right side view, GP/1E 4815; D, muscle scars based on the same specimen. Muscles scar, (ppr, posterior pedal retractor; pa, posterior adductor).

Table 1. Measurements (mm) of *Beurlenella elongatella* new gen. and sp.

Table 1.

Specimen Code	Valve	Length	Height	Width	Elongation L/H	Obesity H/W
GP/1T 4818	R/L	49.68	25.88	---	1.92	---
GP/1T 4816	R/L	44.20	26.51	15.19	1.67	1.74
GP/1T 4825	R/L	---	27.74	17.74	---	1.56
GP/1T 4815	R/L	---	28.72	17.76	---	1.62
GP/1T 4817	R/L	---	24.03	14.33	---	1,68
GP/1T 4920	R/L	---	27.42	---	---	---

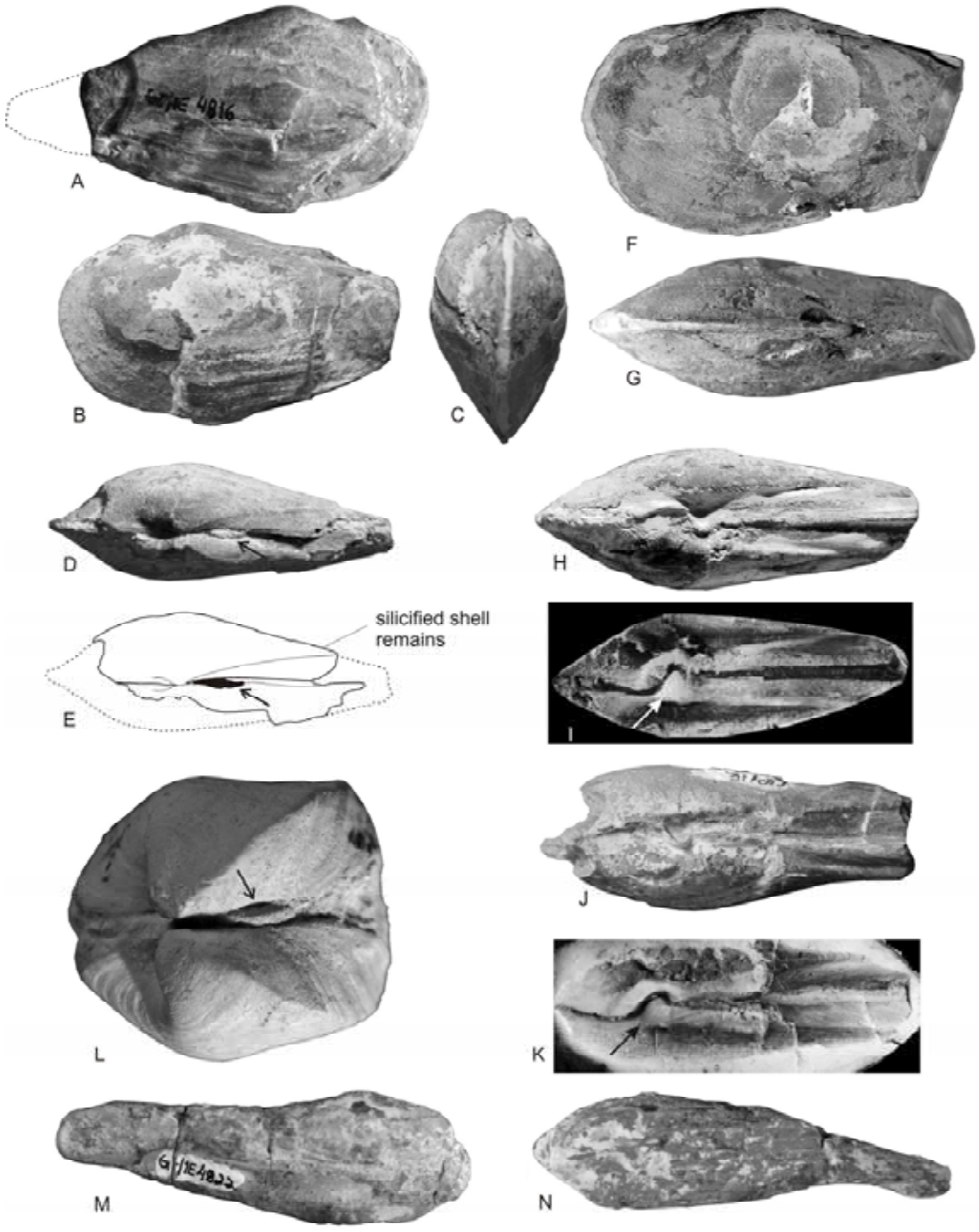

Figure 1

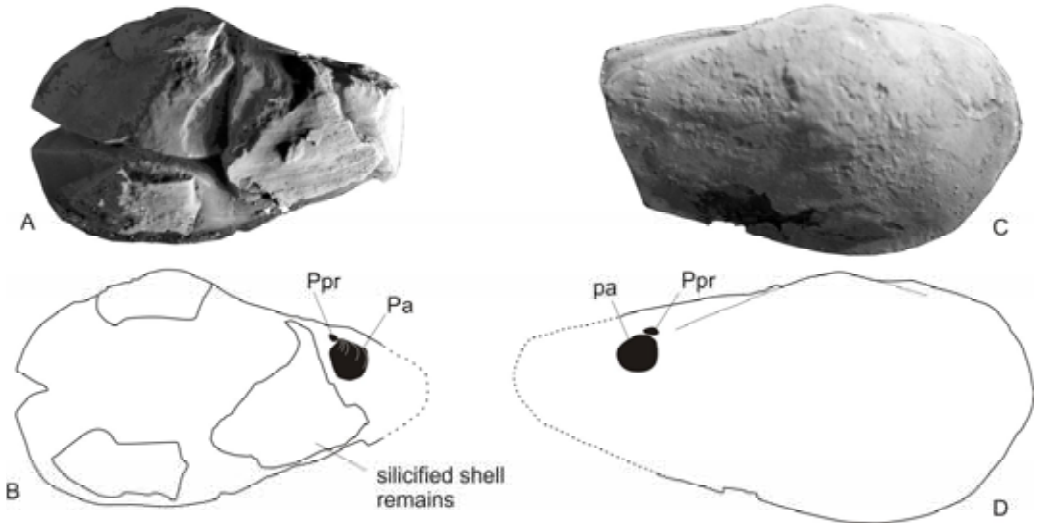

Figure 2