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ARQUIVOS DO MUSEU NACIONAL

Nunquam aliud natura, aliud sapientia dicit
Juvenal, 14, 321
In silvis academi quorere rerum,
Quamquam Socraticis madet sermonibus
Ladisl. Netto, ex Hor

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ARQUIVOS DO MUSEU NACIONAL



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TEORIA E MÉTODOS EM ANTRACOLOGIA. 2 - TÉCNICAS DE CAMPO E DE LABORATÓRIO ¹

(Com 4 figuras)

RITA SCHEEL-YBERT ²

RESUMO: Este artigo dá continuação a uma série de textos sobre a metodologia antracológica adaptada às regiões tropicais. São apresentadas as técnicas de trabalho de campo e de laboratório, em particular o modo de depósito dos carvões de origem arqueológica, amostragem antracológica, concentração do material, constituição de coleções de referência, utilização de bancos de dados antracológicos, determinação dos carvões e dimensão dos fragmentos identificados, assim como uma discussão sobre amostras flotadas, considerando os fragmentos que bóiam e o refugo de peneira.

Palavras-chave: antracologia, carvão, banco de dados, microscopia, flotação.

ABSTRACT: Theory and methods in anthracology. 2 - Field and laboratory techniques.

This paper presents a suite to a series of articles on the anthracological methodology in the tropics. We discuss here the techniques of field and laboratory work, especially the way archaeological charcoal is deposited, anthracological sampling, concentration of the material, constitution of reference collections, use of charcoal data-bases, charcoal determination, and dimension of charcoal pieces that can be identified, as well as a discussion on the flotation technique.

Key words: anthracology, archaeological charcoal, data-base, microscopy, flotation.

INTRODUÇÃO

A identificação de espécies a partir de material carbonizado é bastante antiga (HEER, 1866; PREJAWA, 1896; BREUIL, 1903), mas o método utilizado na época, a confecção e análise de lâminas finas, era lento e difícil, e as pesquisas não podiam almejar à reconstituição paleoambiental. A utilização da microscopia de luz refletida (WESTERN, 1963; VERNET, 1973) possibilitou a multiplicação das análises antracológicas, facilitando o estudo dos carvões e propiciando o desenvolvimento de abordagens paleoecológicas e paleoetnológicas, além de ensejar a realização de pesquisas metodológicas.

Este desenvolvimento levou os pesquisadores a aprimorar também os métodos de amostragem no campo, assim como a aprofundar uma série de questionamentos teóricos sobre a pertinência e a validade dos estudos antracológicos (cf. SCHEEL-YBERT, 2004). Ainda que a preocupação com a análise metodológica tenha se desenvolvido muito entre os antracólogos nas últimas décadas, a maior

parte dos trabalhos foi realizada em regiões mediterrâneas e temperadas da Europa (CHABAL, 1988, 1997; HEINZ, 1990; BADAL-GARCIA & HEINZ, 1991; THÉRY-PARISOT, 2001) e, em menor grau, nos Estados Unidos (SMART & HOFFMAN, 1988). Uma grande parte dos princípios estabelecidos por estes autores pode ser aplicada aos estudos de antracologia tropical, mas a definição de procedimentos metodológicos adaptados aos trópicos é muito importante, devido às especificidades de seus diversos ambientes.

A antracologia é uma disciplina relativamente nova no Brasil (SCHEEL, GASPAS & YBERT, 1996a, 1996b; SCHEEL-YBERT, 1998, 1999, 2000, 2001; SCHEEL-YBERT *et al.*, 2003), onde a necessidade de adaptação da metodologia de coleta de campo se fez sentir desde os primeiros trabalhos. Até hoje, ainda é raro que os arqueólogos brasileiros colem os carvões de modo sistemático, pois este material costuma ser considerado exclusivamente como uma possível fonte de datações radiocronológicas. Esta atitude, aliás, não é restrita à arqueologia brasileira, e foi observada também em Portugal

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(FIGUEIRAL, 1994) e na Itália (FIORENTINO, 1995), por exemplo.

Este artigo tem como objetivo ressaltar a importância da coleta sistemática dos carvões e apresentar aos arqueólogos e futuros antracólogos brasileiros uma metodologia adaptada.

TÉCNICAS DE CAMPO

1. MODO DE DEPÓSITO DOS CARVÕES

A metodologia de amostragem antracológica deve ser adaptada em função do modo de depósito dos carvões. A distinção entre os carvões concentrados nas estruturas de combustão e os carvões dispersos nas camadas arqueológicas é fundamental, pois estes dois tipos de depósito fornecem informações distintas e, em consequência, devem ser coletados separadamente. Os carvões concentrados são mais visíveis durante a escavação, mas as camadas arqueológicas em geral apresentam também uma grande quantidade de carvões dispersos no sedimento (CHABAL, 1988, 1997; HEINZ, 1990; BADAL-GARCIA & HEINZ, 1991), provenientes da dispersão dos fragmentos de queima ou da limpeza periódica de fogões ou fogueiras.

Os sedimentos da maior parte dos sítios arqueológicos brasileiros contêm uma grande quantidade de fragmentos de carvão dispersos. É provável que eles tenham sido originados pela queima de lenha doméstica, mas essa hipótese ainda deve ser confirmada na maioria dos casos. No caso de sambaquis do litoral brasileiro, foi demonstrado que os carvões dispersos provinham efetivamente da lenha coletada para uso doméstico, para a qual não havia seleção (SCHEEL-YBERT, 1999, 2001). A análise de fragmentos de carvão provenientes de várias coletas de madeira (lenha) sucessivas ao longo do período de ocupação, que representem uma boa amostragem da vegetação contemporânea, é uma premissa indispensável para uma boa interpretação paleoecológica baseada neste material (SCHEEL-YBERT, 2004).

Os carvões concentrados freqüentemente se originam de fogos, fogões ou fogueiras que tiveram uma curta utilização no tempo, ou representam apenas os restos da última queima neles realizada, o que implicaria numa amostra pouco significativa da vegetação como um todo. Eles podem também estar relacionados a atividades especializadas, por exemplo materiais de construção ou objetos manufaturados queimados acidentalmente, queima de cerâmica ou, em outras regiões do mundo, fornos de padaria, de metalurgia etc., que muitas vezes requerem um combustível

especial mas que podem ser reconhecidos no campo a partir de critérios arqueológicos. As estruturas contendo carvões concentrados sempre devem ser coletadas separadamente, pois seu estudo oferece importantes informações paleoetnológicas.

Em regiões temperadas, considera-se que as interpretações paleoecológicas devem ser baseadas exclusivamente nos fragmentos de carvões dispersos. Não só estes fragmentos recobrem um período de atividades mais longo, mas principalmente porque se considera que o estudo de carvões concentrados fornece resultados qualitativos e quantitativos incompletos e aberrantes do ponto de vista paleoecológico (HEINZ, 1990). Diversos autores observaram que as amostras de fogueiras (carvões concentrados) fornecem geralmente um número de *taxa* inferior àquele encontrado nos carvões dispersos nos sedimentos arqueológicos, e que eles são freqüentemente sub- ou super-representados (HEINZ 1990; BADAL GARCIA & HEINZ 1991; BADAL GARCIA 1992).

No entanto, CHABAL (1989a) e THIÉBAULT (1995) observaram que em certos casos os carvões de fogueiras fornecem informações bastante precisas sobre o paleoambiente vegetal; para isso, é necessário que a amostra apresente uma grande riqueza taxonômica, associada a um longo tempo de utilização. PERNAUD (1992) concorda que os carvões concentrados em certas estruturas podem fornecer uma imagem válida do ambiente vegetal, mas alerta que é somente a análise dos fragmentos dispersos que confirma, ou não, a validade das interpretações obtidas.

Na zona tropical, só existe até agora um estudo sobre esta questão (SCHEEL-YBERT, 1998). Diversas amostras de carvões concentrados de fogueiras de sambaquis foram analisadas no sudeste do Estado do Rio de Janeiro, demonstrando que eles em geral apresentam uma grande diversidade florística e permitem em todos os casos a dedução de um ambiente vegetal que é qualitativamente semelhante ao que é verificado pelo estudo dos carvões dispersos. Isso tende a mostrar que, em teoria, o estudo de carvões concentrados fornece, nos trópicos, informações paleoecológicas fiáveis, desde que se disponha de um grande número de fogueiras, contendo uma grande quantidade de fragmentos, em cada camada arqueológica. Na prática, esta condição é muito dificilmente preenchida, de modo que, em função do mínimo amostral, as análises paleoecológicas devem ser preferencialmente baseadas no estudo dos carvões dispersos.

2. AMOSTRAGEM ANTRACOLÓGICA

Uma análise antracológica qualitativa e quantitativa confiável só é possível a partir da análise de um grande número de carvões para cada estrato³, de modo que a superfície do sítio arqueológico deve ser amostrada o mais amplamente possível, para cada nível estratigráfico.

O ideal é que a amostragem antracológica seja feita concomitantemente à escavação arqueológica, a qual deve seguir o método de decapagem de camadas naturais em superfícies amplas, a fim de obter resultados que permitam boas interpretações paleoecológicas e paleoetnológicas e que levem em conta as eventuais heterogeneidades locais do sítio. O método geralmente preconizado para a amostragem concomitante à escavação consiste na amostragem sistemática do sítio seguindo uma malha de 1m². Deve-se coletar uma amostra em cada quadrícula, em cada decapagem. A superfície a ser

amostrada deve perfazer entre ¼ e a totalidade de cada metro quadrado, em função da riqueza da camada em carvões (CHABAL, 1988).

Este método pode ser adaptado, seja em razão de contingências da escavação arqueológica (SCHEEL-YBERT, 1998), seja devido à abundância de carvões no sítio (SCHEEL-YBERT & SOLARI, no prelo).

No caso do Sambaqui Ilha da Boa Vista I (Estado do Rio de Janeiro), por exemplo, cuja escavação foi feita pelo método de decapagem de superfícies amplas, a malha de quadriculamento adotada pelos arqueólogos foi de 2 metros de lado (BARBOSA, GASPAS & BARBOSA, 1994). A amostragem antracológica foi feita em quadrículas alternadas, coletando-se, em cada decapagem, um balde de 10 litros de sedimento em seções de 30 x 30cm situadas no ângulo nordeste de cada quadrícula (Fig.1). Este material foi peneirado a seco, no campo, com malha de 4 mm e reservado para flotação e triagem posterior.

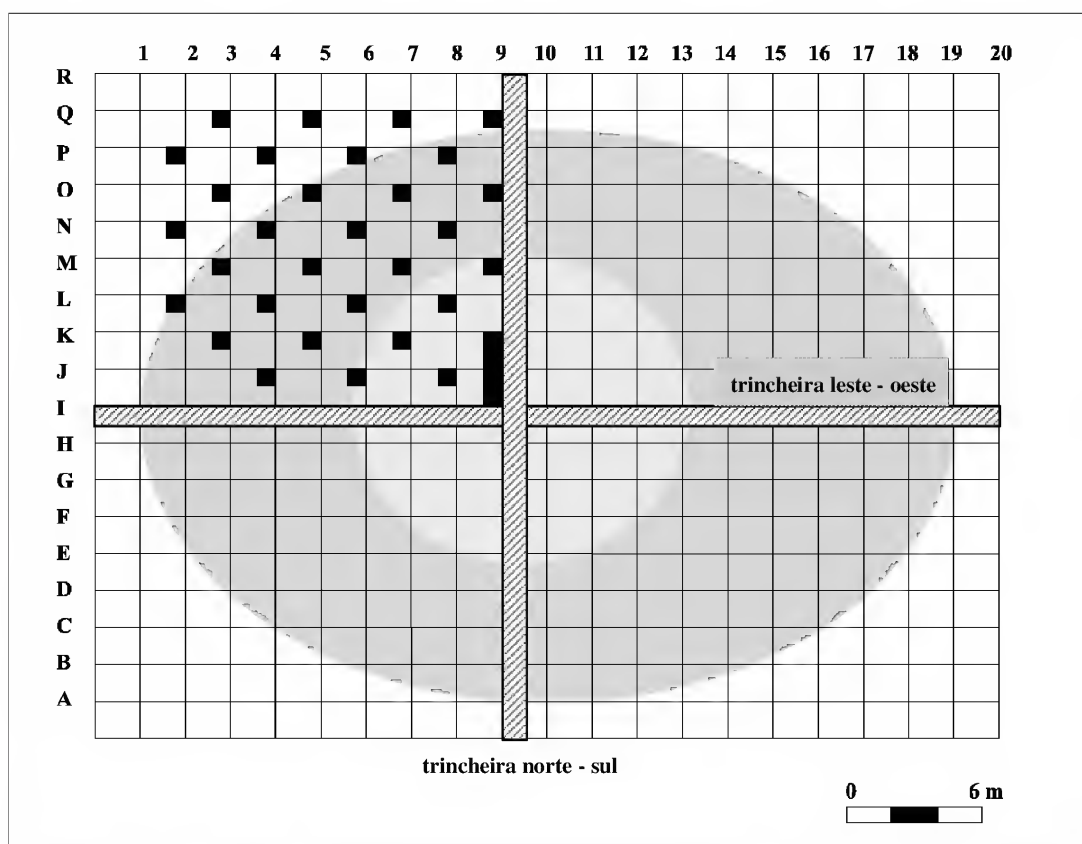


Fig.1- Esquema do quadriculamento do Sambaqui da Ilha da Boa Vista I, com localização das quadrículas amostradas e do perfil antracológico (■) em escala exagerada. A elipse cinza escuro representa a superfície do sítio; o círculo cinza claro representa a área de maior concentração dos vestígios de habitação (adaptado de BARBOSA, GASPAS & BARBOSA, 1994).

³ Uma discussão sobre o número mínimo de carvões da amostra antracológica e sobre a validade amostral será apresentada em um artigo posterior desta série.

No caso do Abrigo Santa Elina (Estado de Mato Grosso), sítio que se caracteriza pelo excelente estado de conservação dos macro-restos vegetais e pela grande abundância de carvões (SCHEEL-YBERT & SOLARI, no prelo), a malha definida durante a escavação arqueológica foi de 1 metro de lado. A amostragem antracológica foi inicialmente feita em todas as quadrículas, nas quais foi coletado sedimento em seções correspondentes a $\frac{1}{4}$ de cada metro quadrado, em cada decapagem. Este material foi peneirado a seco com malha de 4mm e os carvões foram recuperados por triagem manual diretamente no campo. A quantidade excessiva de carvões obtida levou a uma redução da amostragem em campanhas posteriores, que continuou sendo feita em seções de $\frac{1}{4}$ de metro quadrado, mas em quadrículas alternadas. Ainda assim, uma grande quantidade de carvões foi coletada.

Na arqueologia brasileira, limitações de tempo e dinheiro freqüentemente conduziram os arqueólogos a realizar escavações em pequenas trincheiras, baseadas em decapagens artificiais e com recuperação parcial dos vestígios. Embora esta tendência esteja sendo revertida, escavações em superfícies amplas ainda são relativamente raras, de modo que a amostragem antracológica deve sempre ser feita de acordo com o modo de escavação escolhido e as condições encontradas pela equipe que estuda o sítio. Nos casos em que uma amostragem por superfícies amplas não é possível, ou em sítios nos quais as escavações tenham sido realizadas previamente, sem recuperação dos carvões, pode-se proceder à amostragem antracológica pelo método de perfis. Este método também pode ser utilizado em associação ao método de amostragem sistemática.

No caso de amostragem de solos, a coleta é feita exclusivamente ao longo de perfis, por decapagem de camadas sucessivas em níveis artificiais.

A amostragem em perfil padronizada por nossa equipe segue seções de 2m de largura por 50cm de profundidade (ou seja, 1m²); a decapagem é feita em níveis artificiais de 10cm de espessura. Nos casos em que a estratificação natural da camada arqueológica estiver em discordância com os níveis artificiais, é importante sempre proceder de modo a não misturar o material proveniente de sedimentos diferentes. Deve-se também sempre coletar as amostras de carvões concentrados separadamente.

Freqüentemente é difícil manter-se constantes a horizontalidade e a espessura dos níveis artificiais

neste tipo de amostragem. Por isso, foi concebido um “guia de amostragem”, muito simples de construção e de utilização, que facilita a realização das amostragens em níveis regulares (YBERT, SCHEEL & GASPAR, 1997).

Por outro lado, deve-se sempre evitar “raspar” o sedimento com a colher durante a coleta para amostragem antracológica, a fim de não esmagar os carvões. Preferencialmente, deve-se retirar pequenos blocos de sedimento e colocá-los no balde. O mesmo deve ser observado durante a peneiragem; a utilização da pazinha para “ajudar” o sedimento a passar pela peneira destrói os carvões e impossibilita sua análise, ainda mais quando o sedimento está molhado. Deve-se evitar inclusive esmagar o sedimento contra a peneira, mesmo com as mãos, a fim de não destruir os carvões que se pretende analisar.

3. CONCENTRAÇÃO DO MATERIAL

De um modo geral, três métodos de recuperação dos carvões podem ser utilizados: coleta manual, peneiragem ou flotação (BADAL *et al.*, 1989; FIGUEIRAL, 1992).

A coleta manual dos carvões só é indicada para os carvões concentrados. Ela é útil no caso da identificação de estruturas no campo, por exemplo fogueiras ou estacas queimadas, para dar informações sobre a associação de restos botânicos com outros tipos de vestígios, e também para datação. No entanto, este método não deve ser utilizado como único modo de amostragem antracológica, pois geralmente só leva em conta os fragmentos maiores, resultando inevitavelmente numa amostra distorcida.

A utilização da peneira garante uma melhor amostragem, sendo importante para revelar os carvões dispersos contidos no sedimento arqueológico. No entanto, é fundamental que todos os fragmentos de carvão retidos pela peneira sejam coletados, pois a seleção das peças maiores ou mais bem conservadas introduz um elemento de escolha subjetiva que acarretará erros de interpretação.

Em regiões tropicais, a concentração do material arqueológico deve ser feita utilizando-se peneiras de malha de 4mm (*vide “Dimensão dos fragmentos identificados”*). Podem-se usar peneiras de malha inferior, mas nunca superior.

Tanto no caso de amostragem sistemática em superfícies amplas, quanto de coletas em perfil, o sedimento deve ser coletado em baldes. Deve-se sempre anotar a quantidade de baldes retirada em

cada unidade, a fim de se ter uma estimativa mais precisa do volume de sedimento amostrado. Sempre que possível, deve-se pesar o sedimento contido nos baldes. Estes dados são importantes para se comparar a abundância relativa de carvões entre as diversas camadas de um sítio ou entre sítios diferentes, o que só é possível quando se conhece o tamanho exato da amostra (superfície amostrada, volume, peso do sedimento amostrado etc.).

A peneiragem a seco, relativamente fácil, pois normalmente faz parte da cadeia operatória da escavação arqueológica, em geral é insuficiente para uma concentração eficaz da amostra antracológica. Embora o ideal seja peneirar o sedimento uma única vez, isto nem sempre é possível, devido a limitações técnicas. Por isso pode-se, por exemplo, peneirar o sedimento a seco no campo, a fim de diminuir a quantidade a ser transportada, e fazer a flotação posteriormente.

A peneiragem com água pode ser feita por imersão parcial das peneiras num tanque, piscina ou equivalente, ou lavando-se o sedimento da peneira com uma mangueira. A peneiragem com mangueira, muito útil para outras disciplinas, principalmente a zooarqueologia, costuma ser inadequada para a recuperação dos restos vegetais, que podem ser pulverizados pelo jato de água ou pelos instrumentos utilizados para revolver o material.

O maior problema envolvido na utilização de peneiras para a amostragem antracológica decorre do enorme volume de material a ser triado, em particular para os níveis ricos em conchas (no caso de sambaquis) ou em cascalho, tornando este método, em geral, lento e pouco produtivo.

A flotação é o método ideal para recuperação dos restos vegetais, pois implica em menor esforço metodológico e maior eficiência, além de ser o menos agressivo para o material. A flotação permite a recuperação de material botânico de todas as classes de tamanho preservadas no sedimento. Os fragmentos de carvão sendo de pequenas dimensões e muito leves, sua capacidade de flutuação pode ser aproveitada para separá-los do material mais pesado. Além disso, na medida em que uma parte do material flutua e a outra permanece retida pela peneira da célula de flotação, este método facilita a separação de numerosos outros restos, úteis a outras disciplinas (sementes, moluscos, ossos de peixe, cerâmica, fauna etc.).

O princípio de funcionamento de uma “célula de flotação” é bastante simples. Consiste em lavar o sedimento, depositado em uma peneira submersa

numa cuba, em uma corrente de água turbilhonante. Os carvões, liberados do sedimento, são levados à superfície da água e em direção à periferia da cuba, caindo sobre uma peneira de malha fina onde os elementos sólidos são recuperados (YBERT, SCHEEL & GASPAR, 1997; PEARSALL, 2000). Esta técnica é baseada na diferença de densidade dos resíduos orgânicos e inorgânicos. Fragmentos carbonizados de madeira, sementes ou tubérculos em geral flutuam, enquanto restos de moluscos, ossos e cerâmica, são depositados na peneira.

Existem vários modelos de células de flotação, desde o artesanal, baseado na imersão de um balde numa cuba maior contendo água, até os mais elaborados, com assistência mecânica. O modelo de uma célula de flotação desenvolvido no Brasil foi apresentado por YBERT, SCHEEL & GASPAR (1997); vários modelos utilizados nos Estados Unidos e na Europa foram apresentados por PEARSALL (2000).

Se existir uma fonte de água nas proximidades do sítio, a flotação pode ser feita diretamente no campo. Quando possível, deve-se esvaziar sistematicamente a cuba da célula de flotação após o tratamento de cada amostra, a fim de evitar contaminação entre amostras diferentes, especialmente quando existe a possibilidade de se fazer uma datação radiocarbônica posterior (*vide “Análise e identificação dos carvões”*). No campo ou no laboratório, o sedimento que permanece sobre a peneira (refugo de peneira) deve ser sistematicamente triado, a fim de recuperar os fragmentos de carvão que não flutuaram (*vide “Amostras flotadas: fragmentos flutuantes e refugo de peneira”*).

O material peneirado com água ou submetido a flotação deve ser seco longe de uma fonte de calor intensa para evitar sua fragmentação e deterioração da estrutura anatômica. A utilização de cones de papel jornal é muito prática para secar os fragmentos, que em seguida devem ser acondicionados em sacos plásticos, mas deve ser evitada quando se intenciona fazer a datação dos carvões. Os carvões não devem ser manipulados até sua secagem completa, a fim de evitar uma quebra acidental.

4. AMOSTRAS FLOTADAS: FRAGMENTOS FLUTUANTES E REFUGO DE PENEIRA

Num estudo feito em diferentes frações resultantes da flotação de uma amostra do sítio de Lattara, na região mediterrânea da França, foi observado que

o refugio da peneira contém tantos fragmentos quanto a fração flotada (que bôia), mas que a riqueza taxonômica é muito mais elevada nesta última (CHABAL, 1989b, 1997). A autora considera esse fato como uma regra geral, e acredita que a flotação provoque uma triagem desigual em função do peso dos fragmentos: apenas os maiores fragmentos seriam retidos na peneira (o que explicaria a menor riqueza taxonômica do refugio da peneira) e somente eles sofreriam uma refragmentação posterior (o que explicaria o mesmo número de fragmentos nas duas frações).

No estudo antracológico do Sambaqui do Forte (Cabo Frio, Estado do Rio de Janeiro), a fração flotada e o refugio da peneira de 32 amostras foram coletados e analisados separadamente (SCHEEL-YBERT, 1998). A quantidade de fragmentos em cada uma destas frações é muito variável de um nível a outro, mas os carvões flotados são em geral predominantes. No plano qualitativo, observou-se que certos *taxa* se encontram sempre preferencialmente no refugio da peneira (p.ex. *Condalia* sp) ou nos carvões flotados (p.ex. *Maytenus* sp, *Pachystroma* sp), enquanto outros podem ser, de acordo com as amostras, mais abundantes em uma fração ou em outra (p.ex. Myrtaceae tipo 1 e tipo 5). A riqueza taxonômica das duas frações é, em geral, comparável (Fig.2). Além disso, não foi notada nenhuma diferença de repartição de tamanho entre os carvões flotados e os que permaneceram na peneira, e nós consideramos que não existe nenhuma razão que possa explicar que uma refragmentação posterior afete os fragmentos de somente uma das duas frações.

A melhor forma de explicar as variações observadas são as diferenças de características físicas entre os *taxa*, especialmente a densidade, mas também a presença eventual de impregnações calcárias, que tendem a aumentar a densidade dos fragmentos e, logo, a impedi-los de flutuar. Nos casos em que o sedimento arqueológico está molhado, os carvões também ficam encharcados, o que aumenta sua densidade e impede a flutuação. Por outro lado, é provável que o fenômeno de vitrificação⁴ também esteja relacionado. De fato, os fragmentos de *Condalia* sp, encontrados principalmente na fração não-flotada, estavam sempre vitrificados. Durante

a flotação de amostras de fornos de carvoeiros, os fragmentos vitrificados afundam sistematicamente, ao contrário dos não vitrificados (P. OGÉREAU, com. pes., 1998). A vitrificação, que provoca a fusão das paredes celulares, diminui os espaços vazios no interior do carvão, o que resulta num aumento de densidade do carvão.

Apesar de discordar de suas hipóteses, há concordância com CHABAL (1989b, 1997) quanto à necessidade de se triar sistematicamente o refugio de peneira após a flotação e de se analisar os fragmentos das duas frações, a fim de obter uma imagem mais representativa da composição taxonômica da amostra antracológica.

TÉCNICAS DE LABORATÓRIO

1. ANÁLISE E IDENTIFICAÇÃO DOS CARVÕES

A determinação taxonômica dos carvões fósseis é feita pela comparação de sua estrutura anatômica, que se conserva perfeitamente após carbonização, com aquela do lenho de espécies atuais conhecidas, seja diretamente a partir de amostras carbonizadas contidas numa coleção de referência, seja através de descrições e/ou fotografias de obras da literatura.

Existe um grande número de atlas de anatomia da madeira relativos às espécies mediterrâneas e temperadas (GREGUSS, 1959; SCHWEINGRUBER, 1978, 1990; VERNET *et al.*, 2001 etc.), mas eles são raros nas zonas tropicais e, quando existentes, se referem mais especificamente à região amazônica (DÉTIENNE & JACQUET, 1983; DECHAMPS, 1979, 1980, 1985), ou são especializados em madeiras comerciais (MAINIERI & CHIMELO, 1989), com raras exceções (BARROS & CALLADO, 1997). Existem também livros gerais de anatomia que, embora bastante completos, não têm vocação para "atlas" (METCALFE & CHALK, 1950).

Uma importante série de trabalhos referentes às madeiras americanas foi publicada por RECORD e HESS (RECORD, 1942, 1943a, b, 1944a, b, c, d, e; HESS, 1946, 1948; RECORD & HESS, 1943, entre outros). Suas chaves de determinação são muito úteis, mas a raridade das ilustrações torna difícil a utilização destes trabalhos para a determinação antracológica. Este é o caso também das obras de

⁴ Fenômeno de fusão e de homogeneização das paredes celulares do carvão, que adquire um aspecto vitrificado e muito refringente. Apesar do nome, este fenômeno não tem relação com a fusão do silício, que só ocorre em temperaturas muito altas (ca. 1300 a 1400°C). Corpos silicosos intactos são freqüentemente encontrados no interior de células carbonizadas, e servem como critério de determinação.

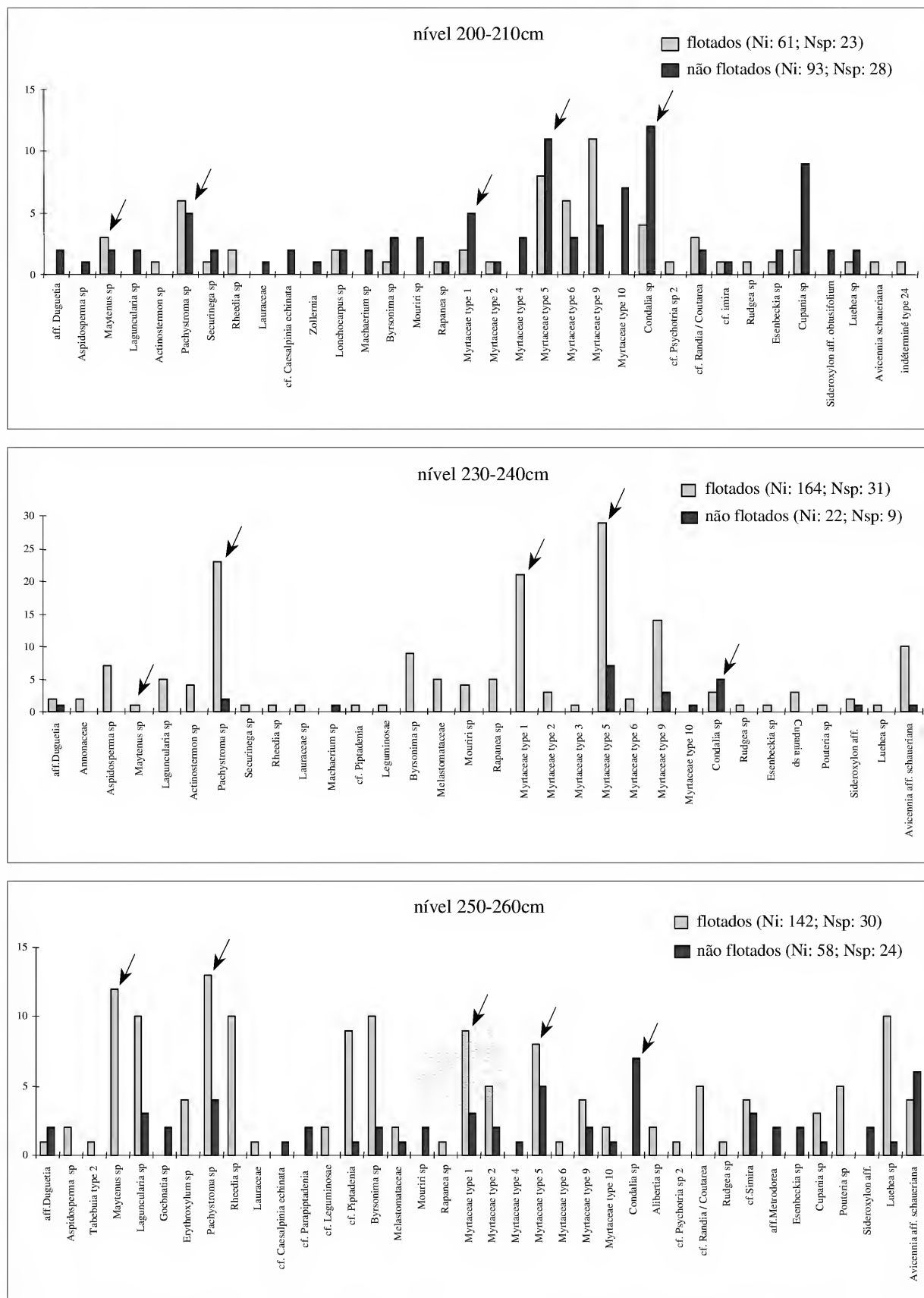


Fig.2- Proporção entre carvões flotados e não flotados em três níveis diferentes do Sambaqui do Forte (RJ), em número de fragmentos; (→) taxa mencionados no texto.

DECHAMPS (1979, 1980, 1985). Pode-se utilizar também um grande número de artigos especializados na anatomia de espécies atuais, que é impossível citar por extenso. Para uma excelente compilação das referências bibliográficas sobre a anatomia sistemática da madeira de espécies atuais publicadas de 1900 até 1993, ver GREGORY (1994).

A análise dos fragmentos de carvão a serem identificados é feita em microscópio óptico de luz refletida com campo claro e campo escuro, a partir da quebra manual dos fragmentos segundo os três planos fundamentais da madeira: transversal, longitudinal tangencial e longitudinal radial (Fig.3). Para as identificações, uma grande importância deve ser dada aos caracteres qualitativos (disposição dos poros e do parênquima, seriação dos raios, ornamento das pontuações intervasculares, tamanho e forma das pontuações radiovasculares, presença de canais, corpos silicosos etc.), mas deve-se levar em conta também as medidas dos caracteres anatômicos. Informações sobre o estudo da anatomia da madeira podem ser encontradas na literatura especializada (BURGER & RICHTER, 1991; IAWA COMMITTEE, 1989; METCALFE & CHALK, 1950; etc.).

A utilização de técnicas de microscopia mais avançadas, como por exemplo o contraste interferencial (DIC), pode ser muito útil para uma melhor visualização dos caracteres anatômicos, em particular detalhes observados em maior aumento, como por exemplo as características das pontuações. Observações em microscopia eletrônica de varredura (MEV) também podem ser feitas, a fim de confirmar as determinações ou para representação fotográfica das amostras. Embora BLANKENHORN, JENKINS & KLINE (1972) e CUTTER, CUMBIE & MCGINNES (1980) façam referência à boa condutividade dos carvões, que tornaria inútil qualquer preparação antes da observação em MEV, nós obtivemos melhores resultados com uma metalização prévia com platina.

Note que, como nenhum tratamento químico é efetuado, é possível obter-se, após a determinação anatômica no microscópio óptico, uma datação de ^{14}C no mesmo fragmento (VERNET, BAZILE & EVIN, 1979), o que é muito interessante quando a quantidade de carvões coletada é pequena.

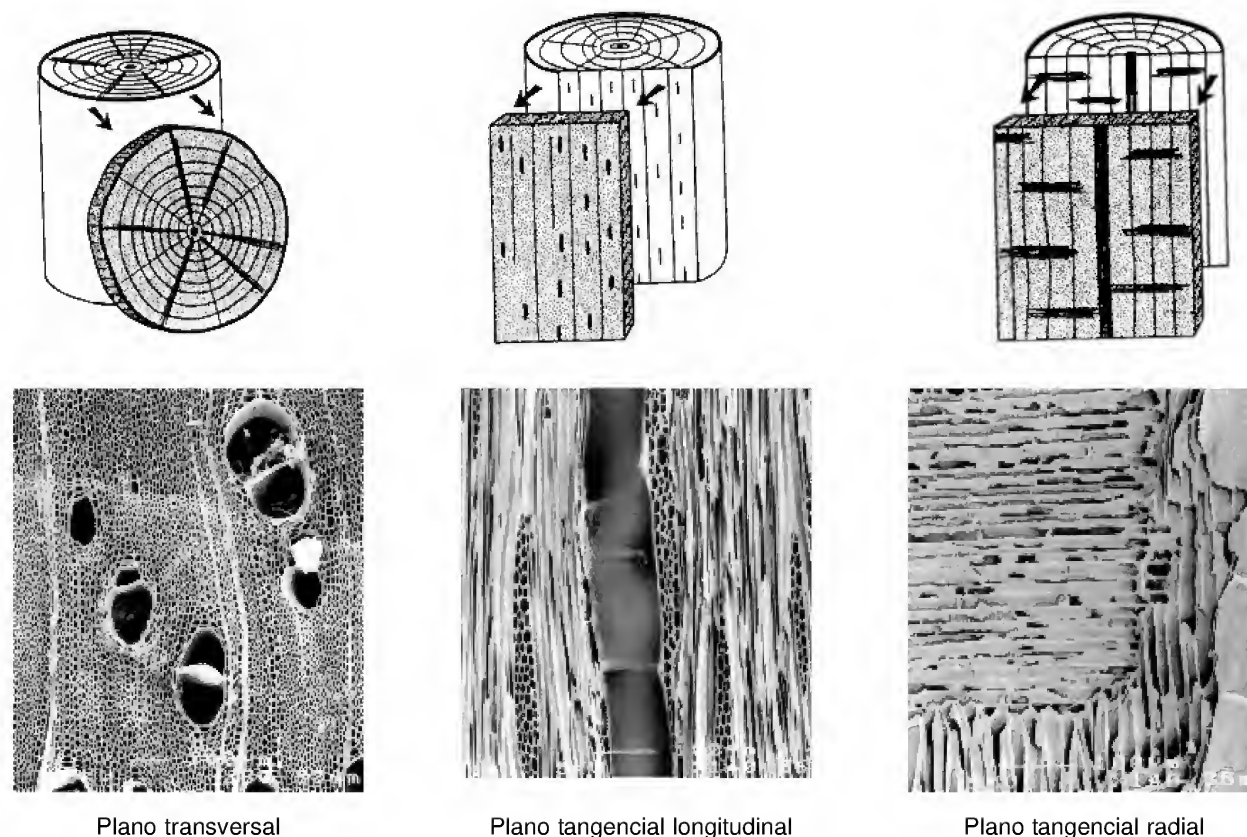


Fig.3- Os três planos fundamentais da madeira: relação com o eixo do lenho e imagens em microscopia eletrônica de varredura (Leguminosae Caesalpinoideae: *Cassia speciosa* Schrad.).

2. DIMENSÃO DOS FRAGMENTOS IDENTIFICADOS

Fragmentos de carvão de apenas 0,5mm de lado podem ser identificados, especialmente no caso das gimnospermas de regiões temperadas (VERNET, BAZILE & EVIN, 1979), mas em fragmentos tão pequenos a determinação é em geral longa, difícil e imprecisa (CHABAL, 1988; SCHEEL-YBERT, 2000). Quanto menor o fragmento, mais difícil será sua determinação, e mais elevado será o nível taxonômico alcançado. O estudo de fragmentos muito pequenos, além de aumentar o esforço de determinação, tem como consequência diminuir a precisão da determinação taxonômica.

Em regiões tropicais, fragmentos cujo lado maior é inferior a 4mm são muito dificilmente identificáveis, pois eles não costumam reunir um conjunto de caracteres anatômicos suficientemente amplo para permitir sua determinação, sequer no nível de família (SCHEEL-YBERT, 2000, 2001).

A precisão de determinação possível em regiões onde a diversidade florística é menor não será provavelmente jamais alcançada em estudos nos trópicos. Contudo, uma diminuição no grau de incerteza das determinações pode ser obtida levando-se em consideração sistematicamente um grande número de caracteres anatômicos em cada amostra, o que impõe um tamanho mínimo para os fragmentos estudados e torna necessária a utilização de um máximo de dados da literatura, de uma boa coleção de referência e de um banco de dados o mais completo possível.

3. CONSTITUIÇÃO DE UMA COLEÇÃO DE REFERÊNCIA

De modo geral, a anatomia de madeiras tropicais é muito pouco conhecida, especialmente no Brasil. Na maioria dos casos, os trabalhos existentes na literatura são insuficientes para a determinação da maioria das espécies lenhosas encontradas nas análises antracológicas. Em consequência, a elaboração de coleções de referência de madeiras e de carvões atuais para as diferentes associações vegetais encontradas na região de estudo é indispensável.

As amostras podem ser obtidas a partir de coletas de campo ou de doações de xilotecas. Quando se faz amostragem no campo, é indispensável coletar também material fértil (flores e frutos), a fim de produzir exsiccatas que permitam a identificação taxonômica do material por especialistas.

Todas as amostras de madeira atual obtidas devem ser, na medida do possível, divididas em duas partes: uma parte deve ser conservada intacta e a

outra deve ser carbonizada visando sua inclusão na coleção de referência. As amostras carbonizadas não devem medir menos de 1cm de lado.

Idealmente, a carbonização é feita em um forno a mufla, no qual as amostras são carbonizadas a 400°C durante 40 minutos. Cada amostra de madeira deve ser embrulhada em papel alumínio, com o número de referência escrito a lápis, na madeira, e com caneta permanente, no papel alumínio.

Quando não se dispõe de um forno, as amostras de madeira podem ser queimadas em uma fogueira (G.WILLCOX, com.pes., 1996), embrulhadas em papel alumínio e com as referências de cada amostra marcadas, por exemplo, em etiquetas de alumínio escritas em baixo-relevo. Embora o grafite seja resistente à queima, não se deve confiar exclusivamente na referência escrita a lápis sobre a madeira, pois pode ocorrer uma deposição de óleos e graxas que cobre a superfície da amostra.

Após carbonização, as amostras devem ser organizadas de forma a facilitar seu acesso e consulta. A melhor solução que encontramos é a utilização de organizadores com pequenas gavetas (Fig.4). Cada gaveta é etiquetada com o nome da espécie e o número de referência, mas um arquivo completo contendo todas as informações de coleta também deve ser feito.

4. CARACTERÍSTICAS DA MADEIRA CARBONIZADA

A constituição de coleções de referência de madeira carbonizada é fundamental, em particular devido às eventuais modificações estruturais do lenho após combustão.

Embora não afete a organização dos tecidos do lenho, o processo de carbonização pode resultar em variações dos caracteres morfométricos (tamanho das células), as quais são devidas a uma importante reorganização estrutural da madeira submetida a fortes temperaturas. O aumento da temperatura provoca a degradação da celulose e da hemicelulose e o rearranjo do carbono numa estrutura semelhante à grafite, acompanhados da destruição da estrutura microfibrilar da madeira (MCGINNES, KANDEEL & SZOPA, 1971). Experimentos de carbonização de amostras de *Quercus alba* mostraram que as alterações mais significativas concernem as dimensões das amostras, com uma retração que variou de cerca de -12% a -25% e que é mais elevada no plano tangencial longitudinal (MCGINNES, KANDEEL & SZOPA, 1971).



Fig.4- Aspecto dos organizadores contendo a coleção de referência de madeiras carbonizadas (antracoteca) do Laboratório de Antracologia do Museu Nacional.

A análise das respostas à carbonização de seis espécies africanas pertencentes a diversas famílias demonstrou que a natureza e a magnitude das modificações são muito variáveis, e em grande parte dependentes da natureza das fibras da madeira (PRIOR & GASSON, 1993). As variações nos caracteres morfológicos e anatômicos medidos são tão mais importantes quanto a temperatura de carbonização é mais elevada. Segundo estes resultados houve, após carbonização, uma dilatação das células de parênquima axial e uma diminuição significativa da altura dos raios lenhosos em todas as espécies, enquanto que as variações do diâmetro tangencial dos poros variou entre uma diminuição de -41% até uma dilatação de +28%.

Em consequência, tanto que nosso conhecimento dos processos de carbonização e das mudanças anatômicas que intervêm em sua estrutura durante sua transformação em carvão não serão completas,

deveremos utilizar os dados anatômicos quantitativos com muita prudência, especialmente quando compararmos carvões a amostras de madeira não-carbonizadas. Em todo caso, o grau de incerteza nas determinações será sempre minimizado pela utilização de uma coleção de referência de amostras carbonizadas.

5. BANCO DE DADOS ANTRACOLÓGICO

A imensa riqueza da vegetação brasileira tem por consequência uma maior dificuldade de identificação das espécies que no caso de regiões onde a diversidade florística é menor. Para facilitar o processo de determinação dos fragmentos antracológicos, foi elaborado um programa que permitiu a constituição de um banco de dados informatizado (SCHEEL-YBERT, SCHEEL & YBERT, 1998). Esse programa funciona em Windows, foi escrito em Microsoft Access 2.0 e

posteriormente atualizado para Access 2000 (SCHEEL-YBERT, SCHEEL & YBERT, 2002). Os caracteres anatômicos utilizados foram baseados na lista-padrão proposta pela Associação Internacional de Anatomistas da Madeira (IAWA COMMITTEE, 1989).

Este programa permite a entrada de dados anatômicos referentes a carvões atuais (ou eventualmente a madeiras não carbonizadas), aos carvões fósseis e aos dados da literatura. Ele permite a realização de pesquisas baseadas em um ou mais caracteres, eventualmente com uma margem de erro que é estabelecida durante a consulta, isto é, um número definido de características das fichas-resultado que podem ser diferentes daquelas estabelecidas na ficha-consulta; as características discordantes aparecem marcadas em vermelho. Os resultados da pesquisa são apresentados por ordem de família e de espécie, mas podem ser ordenados de outra forma.

Pode-se imprimir relatórios sob a forma de fac-símile das fichas, ou de descrições anatômicas padronizadas. Neste último caso, o resultado da pesquisa é gravado sob forma de um arquivo-texto que pode ser lido por qualquer editor de texto. Até seis imagens podem ser associadas a cada ficha anatômica, e estas também podem ser impressas. Além disso, o programa é trilingue, e todas as opções podem ser lidas em português, francês ou inglês.

Os dados anatômicos de todas as amostras da coleção de referência foram incluídos no banco de dados, assim como tipos anatômicos encontrados em amostras arqueológicas. Informações sobre a ecologia e a área de distribuição geográfica das espécies foram incluídas para a maior parte dos *taxa*, a partir dos dados de coleta ou de informações obtidas na literatura.

O banco de dados se mostrou extremamente útil para a determinação de fragmentos fósseis, pois é possível utilizá-lo como chave de determinação. O principal interesse deste programa, além de sua eficácia e simplicidade de uso, é o fato de ter sido especialmente concebido para a identificação antracológica. De fato, se a maior parte dos caracteres qualitativos da madeira se conservam nos carvões (com exceção dos caracteres organolépticos, como cor, cheiro, densidade etc.), os parâmetros morfométricos, especialmente o tamanho das células, a espessura das paredes, o diâmetro dos poros e das pontuações, etc., podem variar (*vide* “*Características da madeira carbonizada*”). Por isso, a identificação taxonômica

não pode se basear exclusivamente na comparação das medidas dos caracteres anatômicos de um fragmento de carvão fóssil com aqueles de uma amostra de madeira atual não carbonizada.

CONCLUSÃO

Os estudos antracológicos fornecem, a partir das mesmas amostras, informações importantes tanto no domínio das variações paleoambientais e paleoclimáticas quanto em aspectos paleoetnológicos. Estes dois temas interpretativos não são incompatíveis e podem ser abordados a partir do mesmo material, desde que se conheça a origem de cada amostra no contexto arqueológico. A intervenção do homem pré-histórico no transporte da madeira até o sítio arqueológico não invalida as reconstituições da vegetação passada baseadas na antracologia (SCHEEL-YBERT, 1998, 2000). Por outro lado, o uso da antracologia para as reconstituições paleoambientais não deve ofuscar as informações paleoetnológicas contidas na mesma amostra (SCHEEL-YBERT, 2001).

A amostragem de carvões com objetivos paleoecológicos deve obedecer a dois requisitos básicos: eles devem provir de uma utilização doméstica para combustível, e corresponder aos resíduos de uma atividade que tenha tido uma duração temporal suficientemente longa (CHABAL, 1992). O primeiro aspecto deve-se ao caráter pouco seletivo da coleta de madeira para lenha doméstica, ao contrário do que ocorre com a utilização da madeira para finalidades específicas (material de construção, fabricação de artefatos ou combustíveis especializados). O segundo, ao fato de que existe uma correlação direta entre o tempo de duração da coleta de lenha e a superfície da área de captação de recursos, cuja vegetação será certamente mais bem representada a partir de várias coletas de lenha durante o tempo de ocupação do sítio. Por isso, as análises paleoecológicas devem ser preferencialmente baseadas nos carvões dispersos, enquanto os carvões concentrados fornecem principalmente informações paleoetnológicas.

A imensa riqueza da vegetação tropical traz alguns problemas para a determinação taxonômica das espécies em fragmentos de carvões. A precisão da determinação é sensivelmente diminuída em relação às regiões temperadas, onde a diversidade florística é menor, e onde as determinações ao nível de espécie são bastante comuns. Apesar disso, os resultados obtidos até o momento mostram que os estudos antracológicos são perfeitamente aplicáveis a regiões

tropicais. Reconstituições paleoambientais muito satisfatórias podem ser obtidas mesmo com identificações taxonômicas limitadas ao gênero, e a abrangência das informações paleoetnológicas que podem ser obtidas é incalculável.

O desenvolvimento da antracologia no Brasil deve se acompanhar de um aprofundamento dos estudos metodológicos e tafonômicos e de um enriquecimento das coleções de referência. Estas pesquisas poderão contribuir, posteriormente, com estudos de modelização do ecossistema que levem em conta a atividade humana.

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ESTUDO POLÍNICO DE ESPÉCIES DE AESCHYNOMENEAE E PHASEOLEAE (PAPILIONOIDEAE - LEGUMINOSAE JUSS.) OCORRENTES NAS RESTINGAS DO ESTADO DO RIO DE JANEIRO ¹

(Com 40 figuras)

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RESUMO: Foram analisados os grãos de pólen de espécies encontradas nas restingas do Estado do Rio de Janeiro, pertencentes às tribos: Aeschynomeneae (Benth.) Hutch. [*Aeschynomene fluminensis* Vell., *Stylosanthes guianensis* (Aubl.) Sw., *S. viscosa* (L.) Sw., *Zornia latifolia* Sm.] e Phaseoleae DC. [*Canavalia maritima* (Aubl.) Thouras, *Centrosema virginianum* (L.) Benth. e *Macroptilium bracteatum* (Nees & Mart.) Maréchal & Baudet.]. Pretende-se, com este trabalho, oferecer subsídios palinológicos que auxiliem à Taxonomia, à Aeropalinologia, à Melissopalínologia, bem como, contribuir para a formação do catálogo polínico da flora das restingas do Estado do Rio de Janeiro. Os resultados polínicos obtidos sobre as espécies das duas tribos estudadas permitiram separá-las dentro das tribos. Os resultados obtidos mostram que as espécies da tribo Aeschynomeneae apresentaram grãos de pólen parassincolpados ou colpados e parassincolporados; os grãos de pólen da tribo Phaseoleae foram descritos como colporados e o tamanho, a forma dos grãos de pólen e a ornamentação da sexina diferiram entre as espécies. Conclui-se que dentro dos gêneros existe uma certa homogeneidade nas características polínicas, contudo, os gêneros são, morfopolinicamente, distintos. Assim, as espécies puderam ser separadas dentro das tribos.

Palavras-chave: Palinologia, Papilionoideae-Leguminosae, Aeschynomeneae, Phaseoleae, Restinga.

ABSTRACT: Pollinic study of some species of Aeschynomeneae e Phaseoleae (Papilionoideae - Leguminosae Juss.) occurring in "restingas" of Rio de Janeiro State.

In the present paper were analysed the pollen grains of the family Leguminosae Juss. (Papilionidae) occurring in the flora of coastal strand vegetation ("restingas") from Rio de Janeiro state belonging to the following tribes: Aeschynomeneae (Benth.) Hutch. [*Aeschynomene fluminensis* Vell., *Stylosanthes guianensis* (Aubl.) Sw., *S. viscosa* (L.) Sw., *Zornia latifolia* Sm.] and Phaseoleae DC. [*Canavalia maritima* (Aubl.) Thouras, *Centrosema virginianum* (L.) Benth. and *Macroptilium bracteatum* (Nees & Mart.) Marechal & Baudet.]. It was aimed to offer palynological data to Taxonomy, Aeropalynology, Melissopalynology as well as contribute to organize a pollinic catalog of the "restingas" of the Rio de Janeiro state. The obtained results demonstrated that: the species of tribe Aeschynomeneae were organized by presence of parassincolpate pollen grains or colpate and parassincolporate ones; the pollen grains of species of the tribe *Phaseolae* were colporate, with size, shape and ornamentation of the sexine of pollen grains different among species. We conclude that inside the each genus exist some homogeneity in the pollinic characteristics; however, the genera are morphopolinical distinct.

Key words: Palynology, Papilionoideae-Leguminosae, Aeschynomeneae, Phaseoleae, "Restinga"

INTRODUÇÃO

Em continuidade ao estudo da família Leguminosae Juss. (Papilionoideae) ocorrentes nas restingas do Estado do Rio de Janeiro

(GONÇALVES-ESTEVEES & CRESPO, 1994) apresenta-se, no momento, a palinologia de espécies pertencentes às tribos: Aeschynomeneae (Benth.) Hutch. [*Aeschynomene fluminensis* Vell., *Stylosanthes guianensis* (Aubl.) Sw., *Stylosanthes*

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viscosa (L.) Sw., *Zornia latifolia* Sm.] e Phaseoleae DC. [*Canavalia maritima* (Aubl.) Thouras, *Centrosema virginianum* (L.) Benth. e *Macroptilium bracteatum* (Nees & Mart.) Maréchal & Baudet.]. Espécies dessas tribos já foram objeto de estudos palinológicos desenvolvidos por VISHNU-MITRE & SHARMA, 1962; BARTH, 1964; MELHEM, 1971; PIRE, 1974; MAKINO, 1978; TEWARI & NAIR, 1979; GUINET, 1981; FERGUSON & SKVARLA 1981, 1983, 1988; GONÇALVES-ESTEVES & CRESPO, 1994 e SILVESTRE-CAPELATO & MELHEM, 1997. Todos esses autores evidenciaram a variedade morfológica das espécies. Pretende-se, com este trabalho, oferecer subsídios palinológicos que auxiliem à taxonomia, à Aeropalinologia, à Melissopalínologia, bem como, contribuir para a formação do catálogo polínico da flora das restingas do Estado do Rio de Janeiro.

MATERIAL E MÉTODOS

O material polínico foram retiradas anteras férteis de flores em antese e/ou botões florais bem desenvolvidos. O material foi obtido de exsicatas depositadas nos herbários do Museu Nacional Rio de Janeiro (R) e da Fundação Estadual de Engenharia do Meio Ambiente Alberto Castellanos (GUA). As siglas seguem HOLMGREN, HOLMGREN & BAINETT (1990).

Material utilizado – BRASIL.

Aschynomeneae – *Aschynomene fluminensis* - RIO DE JANEIRO: Jacarepaguá, D.Sucre 6549 e outros (GUA*); ESPÍRITO SANTO: Vitória, I. Weiter 575 (R). *Stylosanthes guianensis* – MACAË: Cabiúnas, V.Esteves 609 e outros (R*). MINAS GERAIS: Alto Paraíso, H.S.Irwin s/n, 19/III/71 (RB256252); RIO DE JANEIRO: Jacarepaguá, restinga, Vaunce s/n, s/data (RB181901). *S. viscosa* – RIO DE JANEIRO: Saquarema, Restinga de Ipitangas, D.Araújo 9127 (GUA*); Cabo Frio, A.P.Viegas e H.P.Krug s/n, 16/X/1938 (RB112866). *Zornia latifolia* – RIO DE JANEIRO: Angra dos Reis, A.Castellanos 2585 (GUA*); Angra dos Reis, Ilha Grande, L.C.Giordano e outros 282 (RB); Rio de Janeiro, C.Cauvelli s/n, 17/II/1944 (RB49117).

Phaseoleae – *Canavalia maritima* – RIO DE JANEIRO: Maricá, Barra de Maricá, D.Araújo 4819 (GUA*); Praia Grande, C.Rizzini s/n, s/data (RB342818); Arraial do Cabo, T.Kajita e outros

s/n, 10/XII/1999 (RB268085). *Centrosema virginianum* – RIO DE JANEIRO: Jacarepaguá, H.M.Chaves s/n, 22/X/1963 (GUA03693*); Restinga de Jacarepaguá, Rizzo s/n, s/data (RB163958). *Macroptilium bracteatum* – RIO DE JANEIRO: Jacarepaguá, H.E.Strang s/n, 14/VIII/1978 (GUA00169); MACAË: Cabiúnas, R.M.Harley 16169 (RB*).

Sempre que possível, procurou-se analisar os grãos de pólen de três espécimes de uma mesma espécie sendo um destes escolhido como padrão (indicado no material examinado por um asterisco), para as mensurações, descrições e ilustrações polínicas. Para o estudo sob microscópio de luz o material polínico foi preparado segundo o método acetolítico de ERDTMAN (1952) enquanto que para a obtenção das eletromicrografias em microscopia eletrônica de varredura (Zeiss DSM 960), utilizou-se material polínico não acetolisado. Os grãos de pólen foram espalhados sobre suportes metálicos previamente recobertos por fita de carbono e, em seguida, receberam uma fina camada de ouro paládio por cerca de três minutos. Do material padrão foram mensurados 25 grãos de pólen dos diâmetros polar (DP) e equatorial (DE), em vista equatorial (em *Aschynomene fluminensis* e em *Canavalia maritima* não foram obtidas 25 medidas devido à posição preferencial de queda, em vista polar, dos grãos de pólen na lâmina). Com os resultados obtidos, foram efetuados tratamentos estatísticos calculando-se a média aritmética (\bar{x}), o desvio-padrão da amostra (s); o desvio padrão da média ($s_{\bar{x}}$); o coeficiente de variabilidade (CV%) e o intervalo de confiança a 95% (IC 95%). Para as medidas dos demais caracteres, como as do diâmetro equatorial em vista polar (DEVP), do lado do apocolpo (LA), das aberturas e camadas da exina foi calculada a média aritmética a partir de 10 medidas, o mesmo ocorrendo para as medidas dos diâmetros dos grãos de pólen dos espécimes de comparação.

A terminologia adotada e as descrições polínicas seguiram os critérios de BARTH & MELHEM (1988), MELHEM *et al.* (2003) e PUNT *et al.* (1999), levando-se em consideração o tamanho, a forma, o número de aberturas e o padrão de ornamentação da sexina. A denominação da área polar e o tamanho da abertura estão de acordo com a classificação estabelecida por FAEGRI & IVERSEN (1966) para o índice da área polar.

RESULTADOS

Tribo Aeschynomeneae

Aeschynomene fluminensis (Figs.1-6)

Grãos de pólen pequenos (Tabs.1-2), isopolares, subprolatos, âmbito subtriangular, sem área polar, 3-parassincolporados (Figs.1, 4), trilobados, exina microrreticulada (Figs.2-3).

Os colpos são longos, largos (Fig.5), com opérculo e membrana ornamentada, endoabertura circular (Tab.3).

A exina apresenta microrretículos conspícuos no mesocólporo (Fig.6) e menores no pólo e próximo das aberturas (Figs.4, 6); a sexina é simplescolumelada e mais espessa que a nexina.

Stylosanthes

(Figs.7-16)

Espécies estudadas – *Stylosanthes guianensis* – (Figs.7-13); *S. viscosa* – (Figs.14-16).

Grãos de pólen médios (Tabs.1-2), isopolares, prolatos, âmbito subcircular, sem área polar, 3-parassincolpados (Fig.10), exina microrreticulada.

Os colpos são longos, largos (Tab.3), com opérculo e membrana ornamentada (Figs.11-12, 14). Em MEV, pode-se observar que a membrana apresenta dois tipos definidos de granulação: um menos conspícuo localizado no contorno do colpo e outro, mais conspícuo, sobre o colpo (Figs.10, 13, 15).

A exina apresenta microrretículos com muros estreitos e perfurações esparsas (Figs.8-9, 13, 16); a sexina é simplescolumelada e mais espessa que a nexina.

Zornia latifolia

(Figs.17-23)

Grãos de pólen médios (Tabs.1-2), isopolares, prolatos, âmbito subcircular, área polar pequena, 3-colpados, exina microrreticulada.

Os colpos são longos, largos (Tab.3), com opérculo e membrana ornamentada (Figs.22-23). Em MEV, pode-se observar que a membrana apresenta dois tipos definidos de granulação: um menos conspícuo localizado no contorno do colpo e outro mais conspícuo, sobre o opérculo (Fig.23).

A exina possui microrretículos cujos lumens apresentam formas e tamanhos variados, sem

redução do diâmetro próximo das aberturas (Figs.18-20); a sexina é simplescolumelada e mais espessa do que a nexina.

Tribo Phaseoleae

Canavalia maritima

(Figs.24-26)

Grãos de pólen grandes (Tab.1), isopolares, suboblatos, âmbito triangular, área polar pequena (Tab.2), 3-colporados, exina perfurada/rugulada.

Os colpos são longos, com endoabertura lalongada e recobertos por membrana ornamentada (Fig.25). Os grãos de pólen caem na lâmina, preferencialmente, em vista polar.

A exina é perfurada no mesocólporo e rugulada na região polar (Figs.24, 26). A sexina é simplescolumelada e o teto é espesso na região do mesocólporo, tornando-se mais fino próximo da abertura (Fig.24). Os pólos apresentam uma concavidade quando observados sob MEV (Fig.25).

Centrosema virginianum

(Fig.27-34)

Grãos de pólen grandes, isopolares, prolato-esferoidais (Tab.1), âmbito triangular, área polar pequena (Tab.2), 3-colporados, exina heterobrocada.

Os colpos são longos, largos, cobertos por membrana ornamentada (Figs.30, 32, 34) e apresentam uma margem com retículos menores (Fig.31), a endoabertura é lalongada e muito ampla (Figs.33-34).

A exina apresenta muros largos e baixos, com perfurações esparsas, lumens amplos, com báculos no interior (Fig.31).

Macroptilium bracteatum

(Fig.35-40)

Grãos de pólen médios (Tab.1), isopolares, oblato-esferoidais, âmbito subcircular, área polar pequena (Tab.2), 3-colporados, exina microrreticulada.

Os colpos são longos, largos, com margem ornamentada (Figs.38-39), endoabertura aproximadamente circular (Fig.39).

Exina com muros largos, baixos com elevações nos pontos de interseção das malhas (Fig.37), sexina mais espessa do que a nexina.

CHAVE POLÍNICA ARTIFICIAL PARA SEPARAÇÃO DAS ESPÉCIES ESTUDADAS

- 1 . Grãos de pólen parassincolpados ou parassincolporados
- 2 . Grãos de pólen pequenos, subprolatos, parassincolporados *Aeschynomene fluminensis*
- 2'. Grãos de pólen médios, prolatos, parassincolpados *Stylosanthes guianensis*;
..... *S. viscosa*
- 1'. Grãos de pólen colpados ou colporados
- 3 . Grãos de pólen 3-colpados, prolatos *Zornia latifolia*
- 3'. Grãos de pólen 3-colporados, não prolatos
- 4 . Grãos de pólen médios, oblato-esferoidais, endoabertura aproximadamente circular
..... *Macroptilium bracteatum*
- 4'. Grãos de pólen grandes, suboblato ou prolato-esferoidais, endoabertura lalongada
- 5 . Grãos de pólen suboblato, exina perfurada/rugulada *Canavalia maritima*
- 5'. Grãos de pólen prolato-esferoidais, exina heterobrocada, com báculos no interior dos lumens
..... *Centrosema virginianum*

Tabela 1. Medidas (em μm) dos diâmetros dos grãos de pólen, em vista equatorial, de espécies das tribos Aeschynomeneae e Phaseoleae (n=25).

ESPÉCIES	FAIXA DE VARIÇÃO	DP		FAIXA DE VARIÇÃO	DE	
		$\bar{x} \pm s_x$	IC 95%		$\bar{x} \pm s_x$	IC 95%
Tribo Aeschynomeneae						
<i>Aeschynomene fluminensis</i>	23,2-24,8	23,9	-	20,0-21,8	20,5	-
<i>Stylosanthes guianensis</i>	40,0-43,8	41,5 \pm 0,2	41,1-41,9	27,5-31,2	29,6 \pm 0,3	29,0-30,2
<i>Stylosanthes viscosa</i>	29,8-32,0	30,7 \pm 0,1	30,5-30,9	22,5-25,0	23,7 \pm 0,2	23,3-24,1
<i>Zornia latifolia</i>	30,0-35,0	33,1 \pm 0,4	32,3-33,8	21,2-26,2	23,2 \pm 0,3	22,6-23,8
Tribo Phaseoleae						
<i>Canavalia maritima</i>	38,8-50,0	44,3	-	57,5-62,5	60,0	-
<i>Centrosema virginianum</i>	46,7-57,5	51,7 \pm 0,7	50,2-53,1	42,5-55,0	48,0 \pm 0,7	46,6-49,4
<i>Macroptilium bracteatum</i>	32,5-38,5	36,1 \pm 0,4	35,3-36,8	32,0-37,5	35,4 \pm 0,3	34,7-36,1

(DP) diâmetro polar, (DE) diâmetro equatorial, (\bar{x}) média aritmética, (s_x) desvio-padrão da média, (IC) intervalo de confiança.

Tabela 2. Medidas (em μm) dos diâmetros dos grãos de pólen, em vista polar, de espécies das tribos Aeschynomeneae e Phaseoleae (n=25).

ESPÉCIES	DEVP		LA	
	FAIXA DE VARIACÃO	\bar{x}	FAIXA DE VARIACÃO	\bar{x}
Tribo Aeschynomeneae				
<i>Aeschynomene fluminensis</i>	17,5-22,0	19,6	-	-
<i>Stylosanthes guianensis</i>	30,0-34,5	31,9	-	-
<i>S. viscosa</i>	22,5-28,8	25,8	-	-
<i>Zornia latifolia</i>	25,0-27,5	26,4	5,0-7,0	5,9
Tribo Phaseoleae				
<i>Canavalia maritima</i>	58,7-63,7	62,0	18,5-21,2	19,9
<i>Centrosema virginianum</i>	45,0-52,5	49,0	13,8-15,0	14,5
<i>Macroptilium bracteatum</i>	31,2-39,5	35,9	10,0-12,6	10,9

(DEVP) diâmetro equatorial em vista polar, (LA) lado do apocolpo, (\bar{x}) média aritmética.

Tabela 3. Média (em μm) das medidas das aberturas e das camadas da exina dos grãos de pólen de espécies das tribos Aeschynomeneae e Phaseoleae (n=10).

ESPÉCIES	ABERTURA				EXINA		
	COLPO		ENDOABERTURA		total	sexina	nexina
	compr.	larg.	compr.	larg.			
Tribo Aeschynomeneae							
<i>Aeschynomene fluminensis</i>	15,5	1,4	5,5	5,5	2,0	1,1	0,9
<i>Stylosanthes guianensis</i>	39,1	2,7	-	-	1,9	1,1	0,8
<i>S. viscosa</i>	26,9	2,2	-	-	1,2	0,8	0,4
<i>Zornia latifolia</i>	24,6	5,4	-	-	1,8	1,0	0,8
Tribo Phaseoleae							
<i>Canavalia maritima</i>	25,0	2,5	11,0	20,0	4,2	3,4	0,8
<i>Centrosema virginianum</i>	40,1	8,1	17,6	19,7	4,0	3,0	1,0
<i>Macroptilium bracteatum</i>	25,8	4,9	7,3	7,6	3,3	2,3	1,0

(compr.) comprimento, (larg.) largura.

Tabela 4. Média (em μm) dos diâmetros polar (DP) e equatorial (DE) em vista equatorial e sua relação (P/E) em grãos de pólen de espécimes de comparação de Aeschynomeneae e Phaseoleae (n=10).

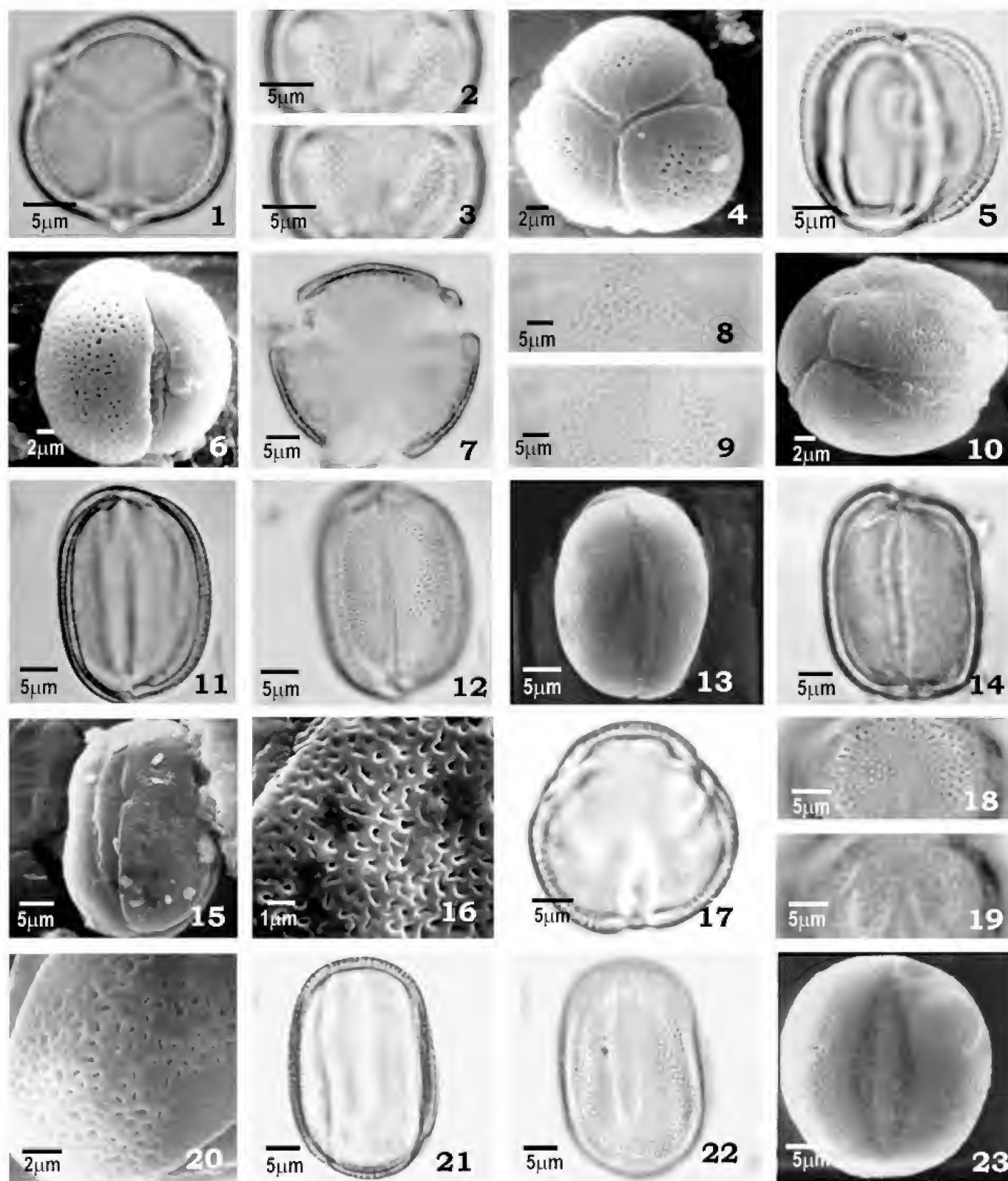
ESPÉCIES	DP	DE	P/E
Tribo Aeschynomeneae			
<i>Aeschynomene fluminensis</i>			
R194398	27,0	18,3	1,5
<i>Stylosanthes guianensis</i>			
RB181901	36,6	23,5	1,5
RB 256252	37,8	25,5	1,5
<i>S. viscosa</i>			
RB 112866	36,8	18,3	2,0
<i>Zornia latifolia</i>			
RB49117	35,6	22,4	1,6
RB 280594	34,8	24,4	1,4
Tribo Phaseoleae			
<i>Canavalia maritima</i>			
R268085	69,3	42,3	1,6
RB 342818	63,8	38,8	1,6
<i>Centrosema virginianum</i>			
RB 163958	48,7	49,3	1,0
<i>Macroptilium bracteatum</i>			
RB 196397	75,0	75,7	1,0

DISCUSSÃO E CONCLUSÃO

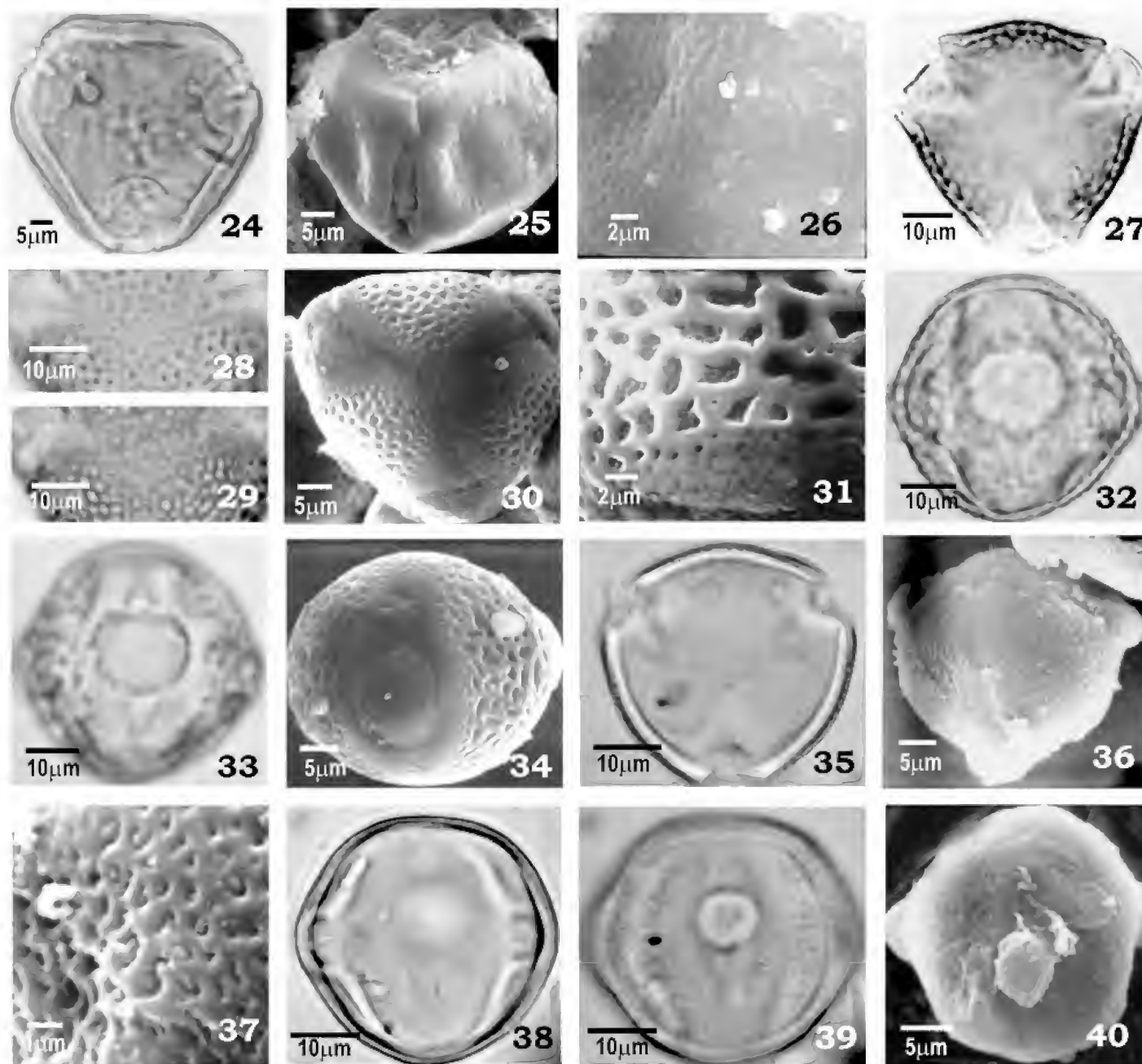
As espécies estudadas apresentaram características que permitiram separá-las dentro das tribos. Assim, as espécies da tribo Aeschynomeneae foram separadas, na chave polínica, das espécies da tribo Phaseoleae, pela presença de grãos de pólen parassincolpados ou parassincolporados e colpados (na primeira tribo), enquanto que os grãos de pólen das espécies da tribo Phaseoleae caracterizaram-se por serem colpados, diferindo entre si, principalmente, pelo tamanho e pela forma dos grãos de pólen, bem como, pela ornamentação da exina.

Dentre os trabalhos consultados que trataram da palinologia de espécies de Aeschynomeneae, apenas SILVESTRE-CAPELATO & MELHEM (1997) analisaram os grãos de pólen de *Aeschynomene elegans* Sch. & Cham. que, para estas autoras, caracterizaram-se por serem

subprolatos, 3-colporados, com endoabertura lalongada e exina microrreticulada. Os resultados aqui obtidos diferem pela presença de parassincólporos mostrando, portanto, a existência de variabilidade no tipo de abertura entre as espécies. As duas espécies de *Stylosanthes* aqui estudadas também o foram por MELHEM (1971) que descreveu *S. guianensis* para o cerrado; PIRE (1974) e SILVESTRE-CAPELATO & MELHEM (1997). Estes autores concordaram que o gênero é estenopolínico e os resultados encontrados por eles foram muito semelhantes. SILVESTRE-CAPELATO & MELHEM (1997) comentaram que, em trabalho anterior realizado por SILVESTRE-CAPELATO (1993), foi verificada a sincolpia mas que em 1997, elas reconheceram ser isto uma consequência da ruptura dos colpos, muito longos. No presente estudo, foi observada a parassincolpia e confirmada em análise de microscopia eletrônica de varredura.



Fotomicrografias e eletromicrografias dos grãos de pólen de espécies da Tribo Aeschynomeneae – *Aeschynomene fluminensis*, vista polar: fig.1- corte óptico, figs.2-3- análise de L.O., fig.4- vista geral (MEV); vista equatorial: fig.5- corte óptico, fig.6- abertura. *Stylosanthes guianensis*, vista polar: fig.7- corte óptico, figs.8-9- análise de L.O., fig.10- vista geral (MEV); vista equatorial: fig.11- corte óptico, fig.12, fig.13- abertura e superfície. *Stylosanthes viscosa*, vista equatorial: fig.14- corte óptico, fig.15- abertura, fig.16- superfície. *Zornia latifolia*, vista polar: fig.17- corte óptico, figs.18-19 análise de L.O., fig.20- superfície; vista equatorial: fig.21- corte óptico, fig.22- superfície, fig.23- abertura (MEV)



Fotomicrografias e eletromicrografias dos grãos de pólen de espécies de Tribo Phaseoleae – *Canavalia maritima*, vista polar: fig.24- corte óptico; vista equatorial: fig.25- abertura, fig.26 - superfície. *Centrosema virginianum*, vista polar: fig.27- corte óptico, figs.28-29- análise de L.O, fig.30- vista geral (MEV), fig.31- superfície; vista equatorial: fig.32- corte óptico, figs.33-34- abertura e superfície. *Macroptilium bracteatum*, vista polar: fig.35- corte óptico, fig.36- vista geral (MEV), fig.37- superfície (MEV); vista equatorial: fig.38- corte óptico, figs.39-40- abertura e superfície.

Quatro espécies de *Zornia* foram estudadas, palinologicamente, por SILVESTRE-CAPELATO & MELHEM (1997) e, dentre elas, *Z. latifolia*. PIRE (1974), também analisou os grãos de pólen de *Z. latifolia*. Os resultados encontrados por estes autores foram semelhantes aos do presente estudo. Com relação à tribo Phaseoleae, os grãos de pólen

de espécies dos gêneros *Canavalia*, *Centrosema* e *Macroptilium* foram analisados por SILVESTRE-CAPELATO & MELHEM (1997). As referidas autoras descreveram os grãos de pólen de *Canavalia picta* Mart. ex Benth. como oblatos, 3-colporados, exina microrreticulada. Para MAKINO (1978), KAVANAGH & FERGUSON (1981), FERGUSON &

SKVARLA (1981), os grãos de pólen eram heteropolares com exina psilada. No presente estudo, a espécie *Canavalia maritima* foi descrita como possuindo grãos de pólen suboblato, isopolares, com exina perfurado-rugulada, caracterizando, assim, uma grande variação nas características polínicas nas espécies de *Canavalia*. Para SILVESTRE-CAPELATO & MELHEM (1997), os grãos de pólen de *Centrosema grandiflorum* Benth. eram subprolatos (acetolisados) ou oblato (não acetolisados), 3-colporados, endoabertura lolongada, operculada, exina reticulada, com muros sinuosos e lúmens menores junto das aberturas. No presente estudo, *C. virginianum* foi descrita como possuindo características polínicas semelhantes às citadas pelas autoras no que se refere ao tamanho do grão de pólen, quanto ao tipo de abertura e à ornamentação da sexina. A endoabertura, no entanto, foi considerada lalongada, ampla, os colpos apresentaram-se recobertos por membrana ornamentada e apresentaram uma margem com reticulação menor. A exina foi descrita como heteroreticulada, apresentando muros largos e baixos com perfurações esparsas, lúmens amplos, com báculos no interior. Os grãos de pólen de *Macroptilium erythroloma* (Benth.) Urban foram descritos por SILVESTRE-CAPELATO & MELHEM (1997) como prolato-esferoidais, 3-colporados, circundados por área psilada, endoabertura lolongada e exina microrreticulada. As características encontradas no presente estudo para *M. bracteatum* mostraram ser semelhantes àquelas de *M. erythroloma* diferindo, apenas, na forma dos grãos de pólen, na presença de margem ornamentada sobre os colpos, nas dimensões da endoabertura (aproximadamente circular) e na presença de muros largos, baixos com elevações nos pontos de interseção das malhas. Embora o número de espécies estudadas de cada gênero, pertencentes as duas tribos, não tenha sido grande, foi possível concluir que os táxons de *Stylosanthes* apresentaram certa homogeneidade nas características polínicas. Os caracteres intergenéricos e intragenéricos, no entanto, mostraram-se, polinicamente, distintos.

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PASSIFLORACEAE DA MATA DE ENCOSTA DO JARDIM BOTÂNICO DO RIO DE JANEIRO E ARREDORES, RIO DE JANEIRO, RJ ¹

(Com 3 figuras)

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MARIA DA CONCEIÇÃO VALENTE ⁴

RESUMO: As Passifloraceae da mata de encosta do Jardim Botânico do Rio de Janeiro e arredores estão representadas por cinco táxons: *Passiflora amethystina* Mikan, *P. capsularis* L., *P. racemosa* Brot., *P. sidaefolia* M. Roemer e *P. truncata* Regel. Para identificação das espécies apresenta-se uma chave analítica, seguida de descrições morfológicas, citação do material examinado, distribuição geográfica, nomes populares, dados fenológicos e do hábitat, comentários e ilustrações.

Palavras-chave: Passifloraceae, *Passiflora*, taxonomia, Rio de Janeiro.

ABSTRACT: Passifloraceae in the Rio de Janeiro Botanical Garden hillside forest and surroundings, Rio de Janeiro, RJ.

The inventory of the Passifloraceae family in the Rio de Janeiro Botanical Garden hillside forest and surroundings was realized and five taxa was found: *Passiflora amethystina* Mikan, *P. capsularis* L., *P. racemosa* Brot., *P. sidaefolia* M. Roemer and *P. truncata* Regel. A key for identification of the species, with their morphological descriptions, examined material, geographic distribution, popular names, phenology, habitats, taxonomic comments and illustrations are presented.

Key words: Passifloraceae, *Passiflora*, taxonomy, Rio de Janeiro.

INTRODUÇÃO

A família Passifloraceae está representada por 17 gêneros (BRUMMITT, 1992; MABBERLEY, 1997) e aproximadamente 630 espécies (HOLM-NIELSEN, JØRGENSEN & LAWESSON, 1988; DEGINANI, 1999), com distribuição tropical pelas Américas e África (METCALFE & CHALK, 1965; JOLY, 1993). A maioria está subordinada ao gênero *Passiflora* L. (KILLIP, 1938; PURI, 1947; BARROSO *et al.*, 1978), que possui cerca de 400 espécies (BRIZICKY, 1961; SACCO, 1980; CERVI, 1986; ESCOBAR, 1988; DEGINANI, 1999).

A família é facilmente reconhecida por apresentar hábito escandente, folhas alternas com gavinhas axilares, pecíolo geralmente com glândulas e flores com coroa e androginóforo.

A área investigada compreende 147,06ha referente à mata de encosta do Jardim Botânico do Rio de Janeiro e Horto Florestal, e 34,8ha do Parque Lage, composta por floresta ombrófila densa submontana alterada, com regiões de

afloramentos rochosos, fazendo parte da Serra Carioca e limitando-se com o Parque Nacional da Tijuca.

O estudo desta flora vascular iniciou-se com as coletas de Kuhlmann que, em 1927, apresentou um mapa fitogeográfico assinalando as espécies arbóreas do Horto Florestal (MARQUETE *et al.*, 1994).

O presente estudo faz parte do Projeto “Vegetação das áreas do entorno do Jardim Botânico do Rio de Janeiro, Parque Lage e Horto Florestal”, desenvolvido pela equipe do Projeto “Avanços Taxonômicos e Coleções Botânicas (Programa Diversidade Taxonômica – PROTAXON)”, do Instituto de Pesquisas Jardim Botânico do Rio de Janeiro. Ao dar-se continuidade à divulgação, atualização e complementação da listagem de espécies, objetiva-se contribuir para a publicação de dados mais abrangentes sobre a flora local e, conseqüentemente, para o conhecimento da diversidade das espécies no Estado do Rio de Janeiro, e conseqüentemente, do Brasil.

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MATERIAL E MÉTODOS

Foram realizadas excursões mensais na área em estudo, de 1991 a 1999, pelo "Projeto vegetação das áreas do entorno do Jardim Botânico do Rio de Janeiro, Parque Lage e Horto Florestal", procurando complementar as coletas realizadas antes da implantação do mesmo.

Foi utilizado material adicional, de áreas próximas à estudada, para completar a descrição das espécies, quando estas se encontravam sem flor ou fruto.

Dados sobre a distribuição geográfica, floração e frutificação, além de outras informações importantes, como nome vulgar e características das espécies no hábitat natural, foram obtidos nas etiquetas das exsicatas dos herbários consultados (siglas de acordo com HOLMGREN, KEUKEN & SCHOFIELD, 1990): GUA, HB, R, RB e RFA e acrescidos de dados descritos na bibliografia especializada. A caracterização da vegetação está de acordo com a classificação de VELOSO, RANGEL FILHO & LIMA (1991).

RESULTADOS E DISCUSSÃO

Passiflora L., Sp. Pl. 1: 955. 1753.

Trepadeiras herbáceas com gavinhas axilares. Folhas alternas, pecíolos com ou sem glândulas, lâminas membranáceas a cartáceas, simples, lobadas a levemente lobadas para o ápice, margem inteira a levemente serrada, 3-5 nervuras saindo da base. Estípulas foliáceas ou linear-subuladas. Brácteas 3, ovadas a lanceoladas, ou ausentes. Flores hermafroditas, axilares, isoladas ou aos pares; pedicelo articulado; tubo do cálice curto-cilíndrico a campanulado; 5 sépalas membranáceas, oblongas a lanceoladas; 5 pétalas membranáceas, oblongas a lanceoladas; corona filamentosa, com 1-5 séries; opérculo membranoso; límen anular, cupuliforme ou ausente; androceu com 5 estames livres aderidos ao ginóforo, formando o androginóforo, anteras dorsifixas; gineceu com 3 estiletos, estigmas capitados. Frutos bagas ou cápsulas; sementes comprimidas, numerosas, com testa endurecida, costada, foveolada, reticulada ou sulcada transversalmente.

CHAVE PARA IDENTIFICAÇÃO DAS ESPÉCIES DE *PASSIFLORA*

DA MATA DE ENCOSTA DO JARDIM BOTÂNICO DO RIO DE JANEIRO E ARREDORES

1. Pecíolos sem glândulas; coronas com 1 série de filamentos; brácteas ausentes; frutos cápsulas *Passiflora capsularis*
- 1'. Pecíolos com glândulas; coronas com 2-5 séries de filamentos; brácteas presentes; frutos bagas 2
2. Lâminas com ápice truncado a obtuso, glândulas entre as nervuras laterais, 3 nervuras saindo da base; estípulas linear-subuladas; testas das sementes irregularmente sulcadas *Passiflora truncata*
- 2'. Lâminas com ápice agudo a obtuso, glândulas nos bordos entre os lobos, 5 nervuras saindo da base; estípulas ovadas, oblíquas ou assimétricas ovadas, foliáceas; testas das sementes costadas, foveoladas ou reticuladas 3
3. Inflorescências racemosas; sépalas corniculadas no ápice, límens ausentes *Passiflora racemosa*
- 3'. Flores solitárias; sépalas com carena no ápice ou não, límens cupuliformes 4
4. Lâminas nitidamente 3-lobadas, 5-8 glândulas nos pecíolos; sépalas com carena no ápice; coronas com 4 séries de filamentos; frutos elípticos; testas das sementes costadas *Passiflora amethystina*
- 4'. Lâminas levemente 3-lobadas no ápice, 2 pares de glândulas nos pecíolos; sépalas sem carena no ápice; coronas com 5 séries de filamentos; frutos globosos; testas das sementes reticuladas *Passiflora sidaefolia*

1. *Passiflora amethystina* Mikan, *Delect. Fl. et Faun. Bras.* 39. 1820. (Fig.1 a-e)

Descrição – Caule cilíndrico, tricomas esparsos. Folhas com pecíolos 2,0-6,5cm compr., 5-8 glândulas curto-estipitadas, tricomas esparsos; lâminas membranáceas, 3-lobadas, 2,8-9,4cm compr. na nervura média, 2,5-7,5cm compr. na nervura lateral, 4,1-12,7cm larg., ápice de agudo a obtuso, apiculado, base subcordada a subpeltada, margem inteira a levemente serreada, glândulas nos bordos entre os lobos, 5 nervuras saindo da base, glabras em ambas as faces. Estípulas 1,5-2,7 x 0,4-1,5cm, foliáceas, ovado-assimétricas, ápice apiculado, base oblíqua. Brácteas 0,6-3,0 x 0,3-1,3cm, lanceoladas, caducas. Flores azuis, lilâses, púrpuras ou alvas, axilares, solitárias; pedicelos 7,0-11,0cm compr., glabros; sépalas 1,6-2,6 x 0,4-0,5cm, oblongo-lanceoladas, ápice obtuso, carena dorsal aristada 0,4-0,7cm compr., glabras; pétalas 1,8-2,7 x 0,3-0,4cm, oblongas, ápice obtuso; corona com 4 séries, 2 externas ca. 2,0cm compr., filamentos liguliformes, 2 internas ca. 1,2cm compr., filamentos filiformes; opérculo plicado; límen cupuliforme; androginóforo 2,0-3,0cm compr., estames 0,5-0,8cm compr., anteras 0,6-0,8 x 0,1-0,3cm; ovário 0,4-0,6 x 0,2-0,3cm, oblongo, viloso, ferrugíneo-tomentoso, estilete 0,8-1,0cm compr. Frutos 4,0-6,2 x 1,0-2,3cm, bagas, elípticos; sementes ca. 0,5 x 0,3cm, ovadas, testa costada.

Material examinado – BRASIL, RIO DE JANEIRO, município do Rio de Janeiro, encosta do Jardim Botânico do Rio de Janeiro, Lagoinha, fl., RB23561, A.Ducke e J.G.Kuhlmann s.n., 20/III/1922.

Material adicional – BRASIL, RIO DE JANEIRO, município do Rio de Janeiro, estrada da Vista Chinesa, fr, RB, J.A.Jesus 1608, 30/V/1972; fl, RB, V.G.L.Klein e M.L.Pereira 1065, 09/V/1991.

Distribuição geográfica – Bolívia, Brasil e Paraguai. No Brasil: Goiás, Distrito Federal, Bahia e nas regiões Sudeste e Sul.

Nome popular – Maracujá-azul, maracujá-de-cobra, maracujá.

Dados fenológicos – É encontrada, ocasionalmente, em flor e fruto o ano todo.

Hábitat – Floresta Ombrófila Densa e Savana. Espécie heliófila a semi-heliófila, ocorrendo principalmente em beira de estrada e em clareiras da mata.

Comentários – *Passiflora amethystina* é uma espécie bem distinta das outras estudadas, principalmente

por apresentar lâminas nitidamente 3-lobadas, 5-8 glândulas no pecíolo, carena no ápice das sépalas, corona com quatro séries de filamentos e semente com testa costada. SACCO (1980) caracteriza a espécie pelas folhas escurecidas quando submetidas à secagem, flores azul-purpúreas e ovário em geral ferrugíneo-viloso-tomentoso. Pertence ao subgênero *Passiflora* L. série *Lobatae* Killip.

2. *Passiflora capsularis* L., *Sp. Pl.* 1: 957. 1753. (Fig.1f-j)

Descrição – Caule anguloso, pubescente. Folhas com pecíolos 0,5-3,0cm compr., glândulas ausentes, pubescentes; lâminas membranáceas, 2-lobadas, raro 3-lobadas, 1,0-8,0cm compr. na nervura média, 2,0-10,6cm compr. na nervura lateral, 2,5-8,3cm larg., ápice agudo, apiculado, base cordada, margem inteira, 3 nervuras saindo da base, pubescente em ambas as faces. Estípulas 0,4-0,7cm compr, linear-subuladas, levemente falcadas. Brácteas ausentes. Flores alvas ou cremes, axilares, solitárias ou aos pares; pedicelos 1,0-5,0cm compr., pubescentes; sépalas 1,5-2,7 x 0,3-0,4cm, linear-lanceoladas, ápice agudo, sem carena, pubescentes, 3 nervuras proeminentes na face dorsal; pétalas 1,0-1,5 x 0,2cm, oblongo-lanceoladas, ápice obtuso; corona com 1 série, ca. 1,2cm compr., filamentos filiformes, unidos na base por membrana delgada; opérculo plicado; límen anelar; androginóforo 0,7-1,5cm compr., estames 0,3-0,5cm compr., anteras ca. 0,4 x 0,1cm, ovário 0,3-0,5 x 0,2-0,4cm, obovóide, levemente pubérulo, estilete 0,4-0,6cm compr. Frutos 2,3-8,5 x 0,7-4,5cm, capsulares-loculicidas, elipsoidais ou fusiformes, violáceos; sementes ca. 0,4 x 0,2cm, elípticas, testa sulcada transversalmente.

Material examinado – BRASIL, RIO DE JANEIRO, município do Rio de Janeiro, estrada para o Horto do Instituto Brasileiro de Desenvolvimento Florestal, fl., RB340717, s.col., s.n., sem data.

Material adicional – BRASIL, RIO DE JANEIRO, município do Rio de Janeiro, Tijuca, Exclesior, fr., HB, E.Pereira 66, 21/XII/1940.

Distribuição geográfica – América Central; Colômbia, Equador, Brasil, Paraguai e Uruguai. No Brasil: Pará, Mato Grosso, Goiás, Piauí, Ceará e nas regiões Sudeste e Sul.

Nome popular – Maracujá-branco-miúdo, maracujá-branco, maracujá-mirim, maracujazinho, maracujá.

Dados fenológicos – Foi encontrada em flor nos meses de janeiro a maio, e outubro a dezembro, e em fruto em janeiro, março a maio, novembro e dezembro.

Habitat – Floresta Ombrófila Densa, Vegetação de Influência Marítima, Savana e Estágio Sucessional Secundário. É uma espécie heliófila a semi-helíofila, e tem preferência por capoeiras e orla de florestas, em terrenos com boa drenagem, raramente encontrada no interior da floresta (CERVI, 1981;1992), sendo uma planta de formação secundária que sofre intensa herbivoria. Comentários – *Passiflora capsularis* distingue-se das demais espécies estudadas principalmente pela ausência de glândulas no pecíolo e de brácteas,

flores com corona unisseriada e frutos capsulares. Suas folhas são geralmente bilobadas, podendo ser encontrado um curto lobo central em alguns espécimes. Pertence ao subgênero *Decaloba* (DC.) Rchb. seção *Xeroga* (Raf.) Killip. Esta espécie pode apresentar uma segunda série de filamentos da corona de 3,0 mm compr., de coloração violeta (CERVI, 1986). Suas folhas são abortivas e suas raízes são suspeitas de prejudiciais ao gado e hemenogogas (PIO-CORRÊA, 1984).

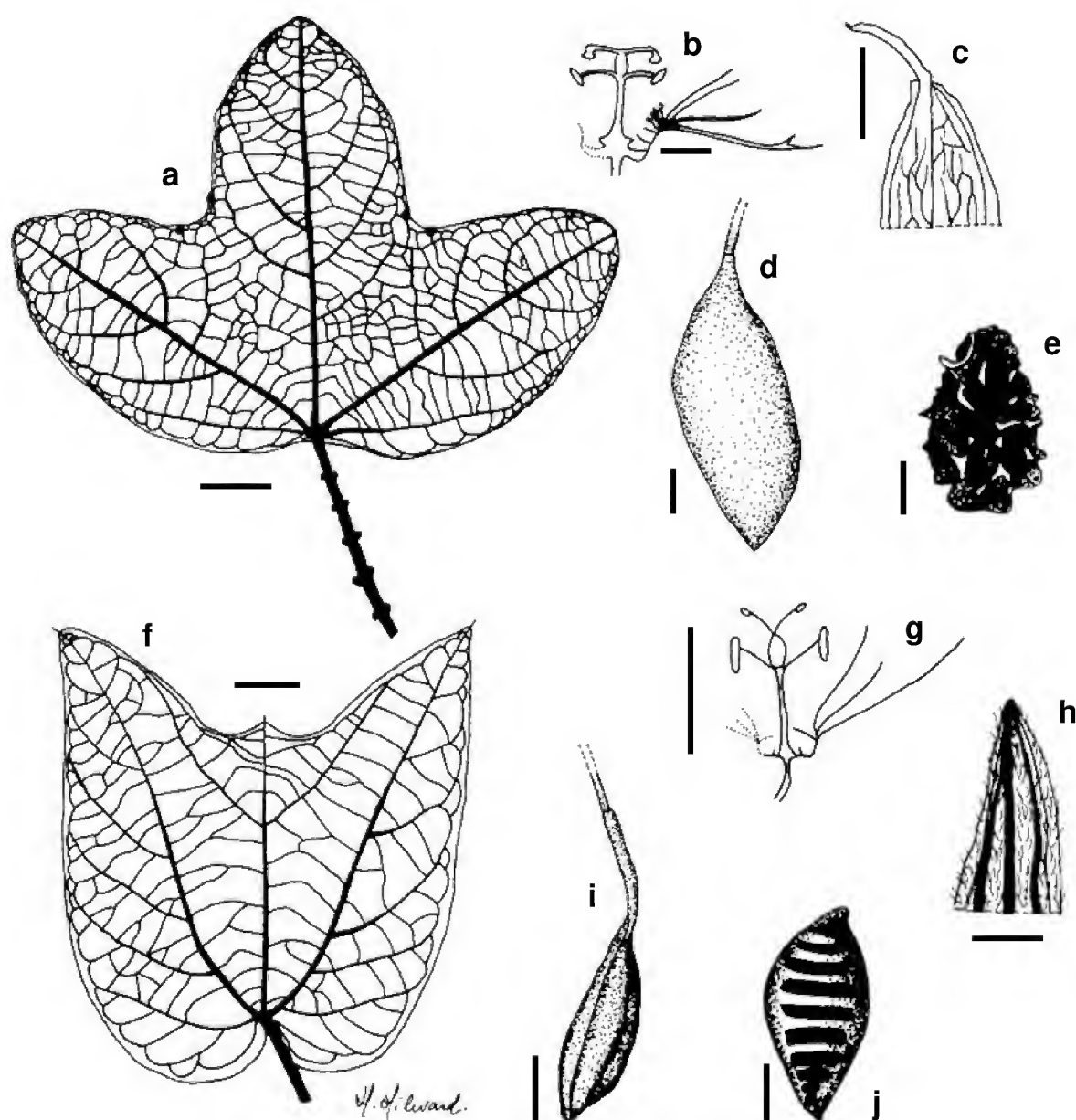


Fig.1- *Passiflora amethystina*: (a) forma da folha e aspecto geral da nervação, (b) esquema geral da flor, (c) ápice da sépala, (d) fruto, (e) semente; *Passiflora capsularis*: (f) forma da folha e aspecto geral da nervação, (g) esquema geral da flor, (h) ápice da sépala, (i) fruto, (j) semente. Escalas: a, b, d, f, i = 1cm; c, e, h, j = 1mm; g = 2cm.

3. *Passiflora racemosa* Brot., *Trans. Linn. Soc.* 12: 71. 1817. (Fig.2 a-f)

Descrição – Caule cilíndrico, glabro. Folhas com pecíolos 0,8-6,0cm compr., 2 pares de glândulas sésseis, glabros; lâminas membranáceas a cartáceas, polimorfas, ovadas quando inteiras, assimétricas quando lobadas de um só lado, ou simetricamente 3-lobadas como na forma adulta com 4,0-10,5cm compr. na nervura média, 3,5-9,0cm compr. na nervura lateral, 5,5-14,6cm larg., lobos oblongos 1,1-4,5cm larg., ápice agudo, base subpeltada ou cordada, margem inteira, glândulas nos bordos entre os lobos, 5 nervuras saindo da base, glabras em ambas as faces. Estípulas 1,2-2,0 x 0,8-1,3cm, foliáceas, ovadas, oblíquas, ápice apiculado, base obtusa. Brácteas 0,8-1,0 x 0,5-0,6cm, ovadas, ápice agudo, base obtusa, róseas a vinosas. Inflorescências axilares, racemosas. Flores alvas, rosas ou vermelhas, solitárias ou aos pares; pedicelos 1,5-2,0cm compr., glabros; sépalas 3,5-4,0 x 0,8-0,9cm, oblongas, ápice corniculado, sem carena, glabras; pétalas 2,0-2,5 x 0,4-0,5cm, oblongas, ápice obtuso; corona filamentosa até a base com 3 séries, ca. 0,4cm compr.; opérculo divergindo horizontalmente, denticulado; límen ausente; androginóforo 3,5-4,8cm compr., estames 0,7-1,2cm compr., anteras 0,6-0,8 x 0,1-0,2cm; ovário 0,6-0,7 x ca.0,2cm, oblongo, glabro, estilete 0,6-0,8cm compr. Frutos 5,0-7,0 x 2,0-3,0cm, bagas, oblongos; sementes 0,5-0,6 x 0,3-0,4cm, elípticas, testa foveolada.

Material examinado – BRASIL, RIO DE JANEIRO, município do Rio de Janeiro, matas do Jardim Botânico do Rio de Janeiro, RB, A.P.Duarte 140, 04/VII/1946; fl., RB, Miguel e outros 4, 06/III/1963; Pedra do Marinheiro, fl., GUA, M.Santos e outros 37, 24/V/1979; fl., fr., RB, N.M.F.Silva e outros 274, 02/VI/1992; fl., RB, R.Marquete e outros 1996, 24/VIII/1994; fl., RB, P.Botelho e outros 60, 29/VIII/1995; RB, M.Milward e R.Marquete 32, 20/X/1999; Grotão, Pedra d'água, fl., RB, G.Martinelli 2829, 01/VIII/1977.

Distribuição geográfica – Brasil: Espírito Santo e Rio de Janeiro. Introduzida na horticultura européia (KILLIP, 1938).

Nome popular – Maracujá-mirim, maracujá.

Dados fenológicos – Foi encontrada em flor nos meses de março a dezembro e em fruto em maio a junho, agosto a dezembro.

Hábitat – Floresta Ombrófila Densa e Vegetação de Influência Marítima. Espécie ombrófila a heliófila, ocorrendo em bordas de florestas e clareiras.

Comentários – *Passiflora racemosa* caracteriza-se

principalmente pelas inflorescências racemosas, flores com os ápices das sépalas corniculados, ausência de límen e três séries de filamentos da corona, e testa das sementes foveoladas. As lâminas são polimorfas, apresentando-se desde inteiras até 3-lobadas, alguns exemplares desta espécie são encontrados somente com lâminas inteiras, ou seja, um indivíduo jovem, geralmente, este tipo de material pode dificultar a identificação. Pertence ao subgênero *Calopanthus* (Harms) Killip, que antes nomeava uma seção, devido à forma de seu opérculo. Sendo uma das mais vistosas passifloras, tem sido muito introduzida no cultivo, produzido extensamente na hibridação artificial (PIO-CORREIA, 1984). *Passiflora racemosa* é conhecida também sob o nome de *P. princeps* Lodd., ambos os nomes foram propostos em 1817 (KILLIP, 1938). Comestível, medicinal e ornamental, sendo própria para pergolados de jardins residenciais (FUKS *et al.*, 1999).

4. *Passiflora sidaefolia* M. Roemer, *Fam. Nat. Syn.* 2: 173. 1846. (Fig.2 g-l)

Descrição – Caule cilíndrico, glabro. Folhas com pecíolos 0,8-3,1cm compr., 2 pares de glândulas sésseis, glabros; lâminas membranáceas a cartáceas, levemente 3-lobadas para o ápice, 3,2-8,6cm compr. na nervura média, 2,8-6,5cm compr. na nervura lateral, 2,4-7,1cm larg., ápice agudo a obtuso, base arredondada, subtruncada ou subpeltada, margem inteira, glândulas nos bordos entre os lobos, 5 nervuras saindo da base, glabras em ambas as faces. Estípulas 1,3-3,0 x 0,5-1,8cm, foliáceas, assimétrico-ovadas, ápice apiculado a aristado, base oblíqua. Brácteas 3,5-6,0 x 1,8-3,5cm, lanceolado-ovadas, imbricadas, ápice apiculado, base auriculada. Flores azuis, alvas ou alva-esverdeadas, axilares, solitárias; pedicelos ca. 2,5cm compr., glabros; sépalas 2,5-3,0 x 1,0-1,2cm, oblongo-lanceoladas, ápice agudo, sem carena, glabros; pétalas 2,5-3,0 x 1,0-1,3cm, oblongo-lanceoladas, ápice agudo; corona com 5 séries, 2 externas, 2,5-3,0cm compr., filamentos ligulados, 3 internas com filamentos filiformes; opérculo membranoso, encurvado, crenado na margem; límen cupuliforme; androginóforo ca. 4,0cm compr., estames ca. 1,0cm compr., anteras ca.0,6 x 0,2cm; ovário ca.0,6 x 0,3cm, ovóide, glabro, estilete ca.1,2cm compr. Frutos 2,5-4,5 x 2,1-3,8cm, bagas, globosos; sementes 0,5-0,6 x 0,3-0,4cm, obovadas, testa reticulada.

Material examinado – BRASIL, RIO DE JANEIRO, município do Rio de Janeiro, entorno do Jardim Botânico do Rio de Janeiro, Lagoinha, fl., RB21315, D.Constantino s.n., 07/XI/1925.

Material adicional – BRASIL, RIO DE JANEIRO, município do Rio de Janeiro, Vista Chinesa, fr., RB, R.Marquete e outros 2171, 23/VI/1995; estrada das Paineiras, fl., fr., RB, J.P.Fontella e outros 405, 20/I/1970; estrada do Redentor, fl., RB, A.P.Duarte 347, 08/X/1946; fl., RB, A.P.Duarte 8743, X/1964; morro do Corcovado, fl., fr., RB, R.Marquete e outros 228, 04/X/1989; fr., RB298876, L.C.S.Silva s.n., 28/VII/1992.

Distribuição geográfica – Brasil: Minas Gerais, Rio de Janeiro e São Paulo.

Nome popular – Maracujzinho.

Dados fenológicos – Foi encontrada em flor nos meses de janeiro, e outubro a dezembro, e fruto em janeiro, junho, julho, outubro e dezembro.

Habitat – Floresta Ombrófila Densa. Espécie heliófila, ocorrendo em orla de floresta e beira de estrada.

Comentários – As principais características diagnósticas para *P. sidaefolia* são as lâminas levemente 3-lobadas para o ápice, flores com cinco séries de filamentos na coroa e testa da semente reticulada. De acordo com MASTERS (1872), as brácteas são um atributo de fácil reconhecimento. Pertence ao subgênero *Passiflora* L. série *Imbricatae* Killip.

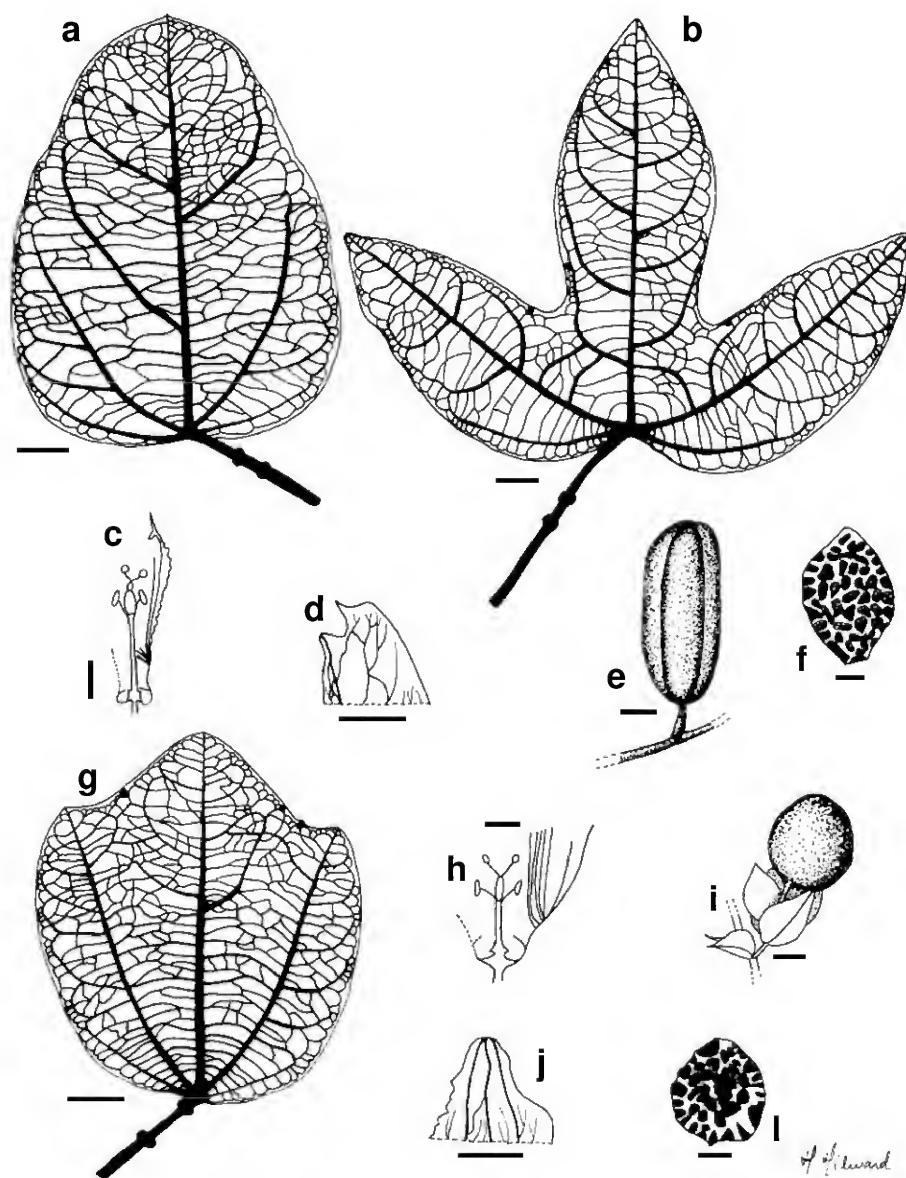


Fig.2- *Passiflora racemosa*: (a) forma da folha jovem e aspecto geral da nervação, (b) forma da folha adulta e aspecto geral da nervação, (c) esquema geral da flor, (d) ápice da sépala, (e) fruto, (f) semente. *Passiflora sidaefolia*: (g) forma da folha e aspecto geral da nervação, (h) esquema geral da flor, (i) detalhe do ramo frutífero, (j) ápice da sépala, (l) semente. Escalas: a-c, e, g-i = 1cm; f, j, l = 1mm; d = 5mm.

5. *Passiflora truncata* Regel, *Gartenflora* 8: 356, est. 276. 1858. (Fig.3 a-e)

Descrição – Caule triangular, glabrescente. Folhas com pecíolos 0,5-2,8cm compr., 1 par de glândulas sésseis, glabrescente; lâminas membranáceas, levemente 3-lobadas para o ápice, 3,0-6,4cm compr. na nervura média, 3,9-7,0cm compr. na nervura lateral, 4,4-8,1cm larg., ápice truncado a obtuso, apiculado, base obtusa, margem inteira, 1-5 glândulas entre as nervuras laterais, 3 nervuras saindo da base, glabrescente em ambas as faces. Estípulas ca. 0,3cm compr, linear-subuladas. Brácteas ca. 0,1 x 0,05cm, linear-subuladas. Flores alvas, esverdeadas ou amareladas, axilares, solitárias ou aos pares; pedicelos 0,4-2,0cm compr.; sépalas 0,5-0,7 x 0,2 x 0,4cm, lanceoladas, ápice agudo a obtuso, sem carena, glabrescente; pétalas 0,3-0,4 x 0,1cm, espatulada, ápice obtuso; corona com 2 séries, a externa 0,2-0,4cm compr., filamentos falciformes, a interna ca. 0,1cm compr., filamentos filiformes; opérculo plicado, ápice curvo; límen anelar; androginóforo ca. 0,5cm compr., estames ca. 0,2cm compr., anteras ca. 0,2 x 0,1cm, ovário 0,1-0,2 x 0,1cm, elíptico, glabrescente, estilete ca. 0,3cm compr. Frutos 1,6-3,0 x 1,6-3,0cm, bagas, globosos; sementes ca. 0,5 x 0,3cm, elípticas, testa irregularmente sulcada.

Material examinado – BRASIL, RIO DE JANEIRO,

município do Rio de Janeiro, Parque Lage, bt., fr., RB, B.Kurtz e outros 166, 27/II/1991.

Material adicional – BRASIL, RIO DE JANEIRO, município do Rio de Janeiro, Vista Chinesa, bt., fl., R, A.C.Brade 10624, 01/III/1931; bt., fl., HB, RFA, E.Pereira 4264, 29/I/1959; bt., RB, V.F.Ferreira 3356, 04/V/1984; Mesa do Imperador, fl., R90277, A.C.Brade s.n., 22/I/1932; Caminho do Pico da Tijuca, bt., fl., fr., RB55798, Altamiro e outros s.n., 06/II/1946.

Distribuição geográfica – Brasil: Rio de Janeiro, São Paulo, Paraná e Santa Catarina.

Nome popular – Maracujá.

Dados fenológicos – Foi encontrada em flor nos meses de outubro a abril, e em fruto de fevereiro a abril e outubro a dezembro.

Habitat – Floresta Ombrófila Densa. Espécie ciófila, ocorrendo principalmente no interior de mata e raramente em sua orla (SACCO, 1980).

Comentários – *Passiflora truncata* distingue-se das demais espécies estudadas principalmente pelas lâminas levemente truncadas no ápice, glândulas laminares entre as nervuras laterais, flores com duas séries de filamentos na corona e testa da semente irregularmente sulcada. Pertence ao subgênero *Decaloba* (DC.) Rchb. seção *Cieca* (Medik.) DC.

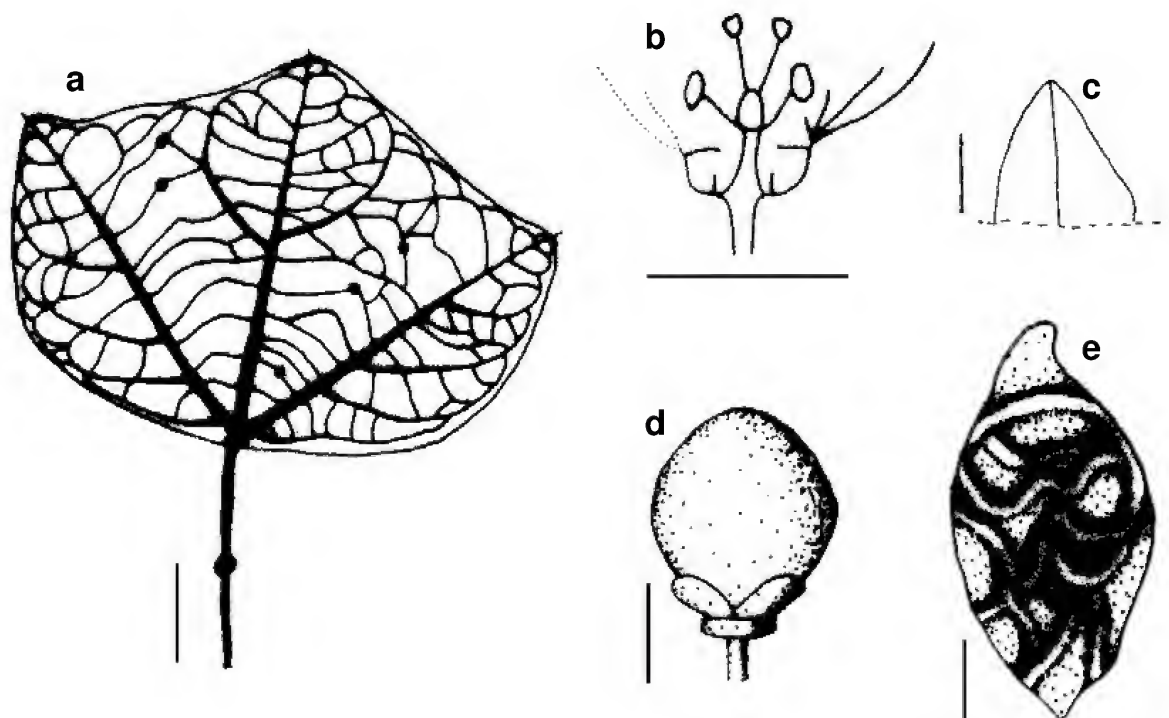


Fig.3- *Passiflora truncata*: (a) forma da folha e aspecto geral da nervação, (b) esquema geral da flor, (c) ápice da sépala, (d) fruto, (e) semente. Escalas: a, b, d = 1cm; c, e = 1mm.

CONCLUSÃO

De acordo com os levantamentos feitos nos herbários citados e excursões realizadas na mata de encosta do Jardim Botânico do Rio de Janeiro e arredores, foram encontradas para a família Passifloraceae as seguintes cinco espécies *Passiflora amethystina*, *P. capsularis*, *P. racemosa*, *P. sidaefolia* e *P. truncata*. As espécies distinguem-se pelo formato das folhas, estípulas, brácteas, fruto, testa da semente e pela disposição e número de glândulas na lâmina e pecíolo, além do número e formato das séries da corona.

Os táxons estudados ocorrem, preferencialmente, em beira de estradas, orla de florestas ou em clareiras, sendo raramente encontrados no interior da mata e sofrendo intensa herbivoria. *Passiflora racemosa*, *P. sidaefolia* e *P. truncata* apresentam distribuição restrita no Brasil ocorrendo, até o momento, na região Sudeste e a última sendo também encontrada na região Sul. *Passiflora amethystina* ocorre em toda região Sudeste e Sul, além dos Estados da Bahia e Goiás, enquanto que *P. capsularis* apresenta ampla distribuição por quase todo o país.

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NEW DATA ON SOUTH AMERICAN SPECIES OF *CHORDODES* (NEMATOMORPHA) ¹

(With 7 figures)

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ANDREAS SCHMIDT-RHAESA ³

ABSTRACT: Taxonomic characters of both male and female horse-hair worms *Chordodes brasiliensis*, and *C. nobilii* (Nematomorpha) and female of *C. carmelitanus* are re-described by scanning electron microscopy. Sexual dimorphism was found in the cuticular pattern of *C. brasiliensis*, the male has three different areolar types but the female shows five different areolar types that includes all three types of areoles as in the males, but along the ventral and dorsal midline, two further types of areoles are present.

The female cuticle of *C. carmelitanus* is characterized by three types of areoles, the crown areoles always occur in pairs on both sides along the ventral midline. Male of *C. nobilii* has two types of areoles, type 1 are slightly oval or circular in shape with minute projections on the apical surface. Type 2 areoles occur individually or in clusters and carry on their apical surface projections that can be short or longer. The female of this species has three types of areoles. Areoles of types 1 and 2 are very similar to each other. Crowned areoles (type 3) have quite long apical filaments and occur only along the ventral and the dorsal midline. A neotype of *nobilii* is erected as the original material cannot be traced. Host data of *C. brasiliensis* and new distribution records of *C. brasiliensis* and *C. nobilii* are reported.

Key words: Nematomorpha, Gordiida, *Chordodes*, South America, scanning electron microscopy.

RESUMO: Novos dados sobre espécies sul-americanas de *Chordodes* (Nematomorpha).

Neste trabalho estão sendo redescritas com microscopia de varredura, três espécies de *Chordodes*, *C. brasiliensis*, *C. carmelitanus* e *C. nobilii*. Macho do *C. brasiliensis*, com cutícula provida com três tipos de aréolas, as fêmeas apresentam dimorfismo sexual com cinco tipos de aréolas, dois tipos das quais encontram-se na linha ventral do corpo. A fêmea de *C. carmelitanus* com cutícula com aréolas de três tipos, apresentam na região ventral, longitudinalmente, uma faixa tendo aréolas coroadas pares no meio das quais saem tufo de prologamentos muito longos. O macho de *C. nobilii* com dois tipos de aréolas, tipo 1 de forma oval ou arredondadas tendo no ápice finos e curtos prolongamentos. Aréolas do tipo 2 apresentam-se isoladas, aos pares ou em grupos tendo no ápice prologamentos curtos ou longos. As fêmeas de *C. nobilii* com três tipos de aréolas. Nas aréolas do tipos 1 e 2 são semelhantes. O tipo 3 (aréolas coroadas) na linha ventral do corpo, apresentam no ápice prolongamentos longos. Outorga-se informações sobre hospedeiros do *C. brasiliensis* e novos dados da distribuição geográfica do *C. brasiliensis* e de *C. nobilii*.

Palavras-chave: Nematomorpha, Gordiida, *Chordodes*, América do Sul, microscópio de varredura.

INTRODUCTION

The biodiversity of horsehair worms (Nematomorpha) from southern South America, in particular Argentina, is comparatively well known (see, among many publications, MIRALLES & DE-VILLALOBOS, 1993). However, still several species from Argentina and more from the remaining South America are insufficiently known. Scanning Electron Microscopy has become the standard method in nematomorph taxonomy, because the

fine cuticular characters can be documented reliably with this method. We investigated here representatives of the genus *Chordodes* from different museum collections. *Chordodes* contains about 90 species and is the largest genus in Nematomorpha. The cuticular structure is usually very diverse, with several types of elevations called areoles. Characteristic for *Chordodes* are the so-called crowned areoles which are elevated above the surface and have an apical ring ("crown") of shorter or longer filaments.

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One of the best known species from South America is *Chordodes brasiliensis* Janda, 1894, but descriptions of this species, differ slightly between different specimens. JANDA (1894), in his original description mentions three types of areoles, an abundant flat one, a highly elevated one with fine apical filaments and irregularly distributed solid spines. The first two types were confirmed by subsequent descriptions, whereas the spines probably represent so-called tubercle areoles in which a fingerlike projection arises from a flat areole (MIRALLES, 1969). CAMERANO (1897a) described crowned areoles with very long filaments next to the dorsal and ventral midline in the female, a fact that was repeated in later descriptions (MIRALLES, 1976), but not confirmed by independent investigations (CARVALHO, 1946a, 1946b; CARVALHO & FEIO, 1950; MIRALLES & CAMINO, 1983; MIRALLES, 1993).

We additionally reinvestigated the holotype of *Chordodes carmelitanus* Carvalho & Feio, 1950. Scanning Electron Microscopical observations were already available from new recorded specimens (MIRALLES, 1989), but the investigation of the holotype could add new details. Finally, several specimens from the collection of the Museo de Ciencias Naturales in La Plata, Argentina, correspond to description of *Chordodes nobilii* Camerano, 1901. Because the holotype could not be located, we describe a neotype for this species.

MATERIAL AND METHODS

Preserved specimens from the following museums were investigated: Museo de Ciencias Naturales de La Plata (MLP), Museum für Naturkunde, Berlin, Germany (MNB), Museu Nacional of Rio de Janeiro, Brazil (MNRJ), Museo Regionale di Scienze Naturali, Torino (MZUT) and Natural History Museum, London, UK (NHML). All the preserved specimens were fixed in ethanol. In the present study we investigated twenty nine specimens of *Chordodes brasiliensis*, one of *C. carmelitanus* and twenty of *C. nobilii* and we report new records of *Chordodes brasiliensis* and *C. nobilii*. In order to optimize the traditional observation technique, we followed the new protocol propoused by SCHMIDT-RHAESA (2002a). Body measurements were made with outstretched worms using a ruler. Diameters were measured under dissecting microscope using a caliper ruler. Fragments of worms (anterior end, mid-body and posterior end) were dehydrated in an increasing ethanol series, critical point-dried,

mounted on bronze blocks and gold-sputter coated. Observations were performed using a JEOL SLM 1000 scanning electron microscope.

RESULTS

Chordodes brasiliensis Janda, 1894 (Figs.1-2)

1894 *Chordodes brasiliensis* Janda – Zool. Jahrb. Syst. Geogr. Tiere, 7:608, pls:19-20.

Holotype (no examined) – One male from Brazil (no further precision of locality) (JANDA, 1894).

Material examined – SEM. Midbody from: 1♂ (Córdoba: Alta Gracia, Argentina, MLP 3575); 1♂ (Corrientes, Capital, Argentina, MLP 5049); 1♀ (Corrientes, Capital, Argentina, MLP 5052); 10♂, 2♀ (Salta: Tala, Argentina, MZUT G2, G42); 1♀ (Salta Capital, Argentina, MLP 5052); 1♂ (Rio Noro, Humboldt, Station Catherina, NHML 1921.12.13.23-24); 1♂ (San Luis: El Reparito, Estancia Grande, Argentina, MLP 3574); 1♀ (Jujuy: San Lorenzo, Argentina, MZUT G46); 1♂, 2♀ (Tucumán: Las Tipas river, Argentina, MLP 3578); 1♂ (Misiones, Parque Nacional Iguazú, Base Yawi, Argentina, MLP 4903); 1♀ (Misiones: Cuña Pirú stream, Argentina, MLP 5050); 1♂ (Rio de Janeiro, Brazil, MNRJ 5348); 1♂ (Niterói, Brazil, MNRJ, no accession number); 1♀ (Japuhiba, Brazil, MNRJ no accession number); 1♀ (Viçosa, Brazil, MNRJ no accession number); 1♀ (Santa Teresa, Brazil, MNRJ no accession number). SEM from terminal end: 1♂ (Salta: Tala, Argentina, MZUT G2), 1♂ (Rio Noro, Humboldt, Station Catherina, NHML 1921.12.13.23-24), 1♀ (Corrientes, Capital, Argentina, MLP 5052). LM of midbody from 25♂ (Salta: Tala, Argentina, MZUT G2).

Host – MANTODEA: *Stagmatoptera hyaloptera* (see CAMERANO, 1897b), *Stagmatoptera* sp. (see CARVALHO, 1946a), *Stagmatoptera precaria* (see CARVALHO, 1946b), undetermined mantid (see CARVALHO, 1946b), probably *Phyllovates* sp. (see SCHMIDT-RHAESA & EHRMANN, 2001).

♂ – Color of body varies between light brown to dark brown. Posterior end of males (Fig.1A) is not bilobed. The cloacal opening is oval and surrounded by slender spines (circumcloacal spines). Around the cloacal opening the cuticle is smooth with minute bristles. Anterolateral of the cloacal opening are two straight and narrow rows of bristles. They reach up to 250µm in length.

The cuticle shows three types of areoles (Fig.1C-F). Type 1 areoles are the most abundant, they are oval

with an irregular shape and a roughly structured surface (Fig.1C-F). Scattered among these areoles are areoles of type 2 (tubercle areoles) with a long (15.7µm) fingerlike projection (tubercle) which is in an excentric position on the areole (Fig.1D, E). Both areolar types are transversal to the longitudinal axis of the body. Areoles of type 3 are distinctly elevated over the other areoles (up to 21.5µm). They occur abundantly, but individualized and are scattered between the areoles of type 1 (Fig.1C, F). Rarely they form loose clusters of up to four areoles (Fig.1F). The apical surface of these areoles differ between specimens, is rugged (MLP 4903) (Fig.1F) or with very fine processes (MNRJ 5348) (Fig.1D).

♀ – Color of body as in males, it varies between light brown to dark brown. The posterior end (Fig.2A) is rounded and the cloacal opening is circular with a central terminal position. Radiating around the cloacal opening are fine grooves (Fig.2A).

The cuticle includes all three types of areoles as in the males (Fig.2B, C), but along the ventral and dorsal midline, two further types of areoles are present. Both additional types are clustered together. Two kinds of filaments, one very long and solid, the other much thinner and shorter, arise from a more or less flat region which probably represents two areoles (Fig.2C). These central areoles are surrounded by 5-6 slightly elevated areoles which are curved towards the center (Fig.2C).

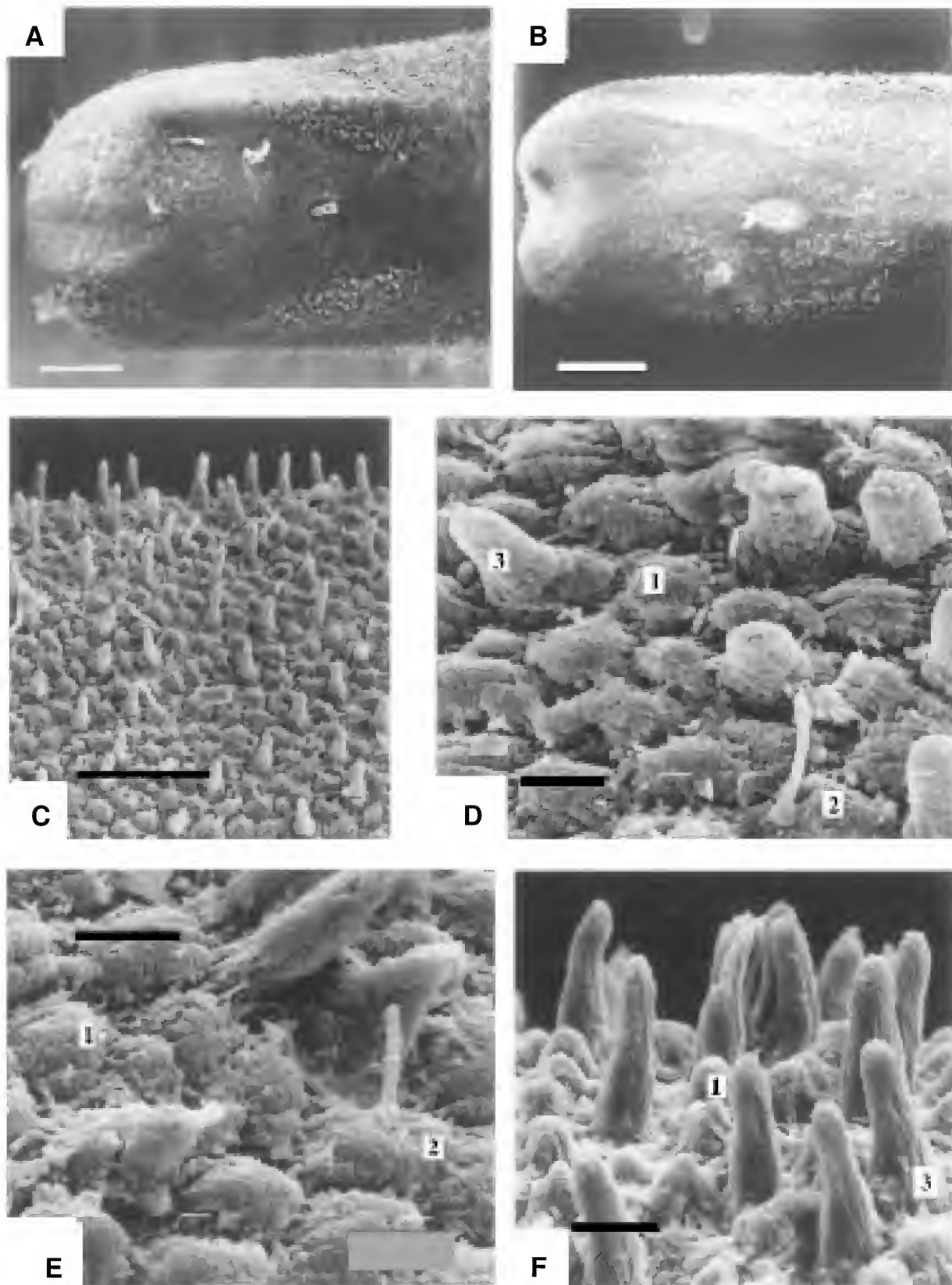
Dimensions – According to the literature (CAMERANO, 1897b; CARVALHO, 1946a; CARVALHO & FEIO, 1950; MIRALLES & CAMINO, 1983) females vary between 140 and 271mm in length and are maximally 2mm in diameter; males range from 85 to 355mm in length and from 0.7 to 2mm in diameter. Measurements of the newly reported specimens range in length from 63 to 206mm in males and from 112 to 240mm in females. The diameter varies between 0.5 to 1.0mm in males and between 0.6 and 1.8mm in females

Comments – CAMERANO (1897b) designates “numerous” specimens as *Chordodes brasiliensis*, in our SEM and LM reinvestigation we have analyzed all of these specimens (54♂ and 1♀) and we can confirm that only 35 males belong to *C. brasiliensis*, and the rest of the specimens (19♂ and 1♀) to *Neochordodes talensis*.

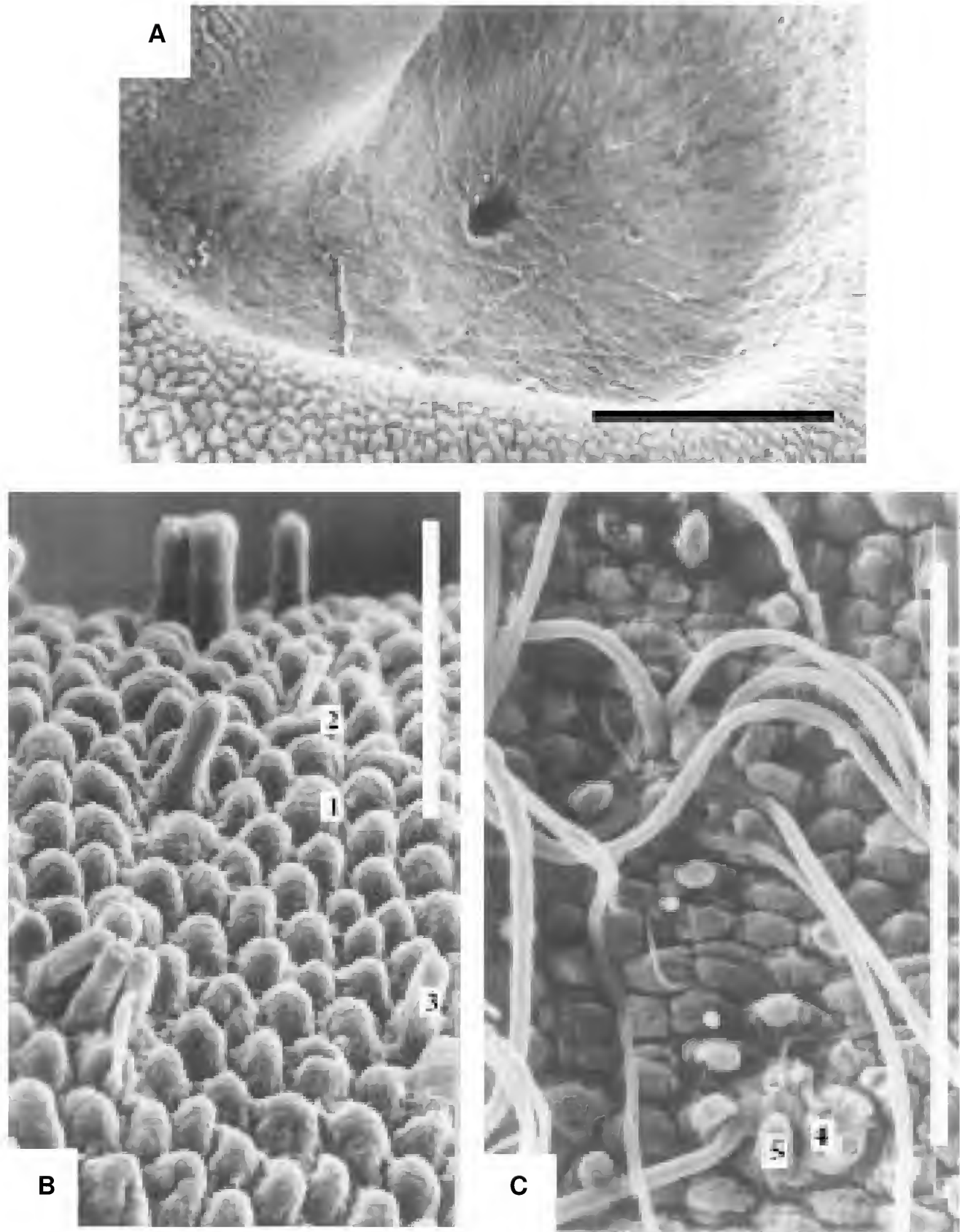
Our study confirmed the areolar types from previous investigations, *i.e.*, the abundant flat areoles, highly elevated areoles and tubercle areoles (see JANDA, 1894; CAMERANO, 1987a, 1987b; CARVALHO, 1946a, 1946b; CARVALHO & FEIO, 1950; MIRALLES

& CAMINO, 1983). Additionally, we could confirm the presence of further areoles in the female as noted by CAMERANO (1897a). Camerano reports paired areoles (“papille”) with long processes, but in his figures the paired character of areoles is not evident. Instead, filaments seem to originate from a broad region. This is in accordance with our findings, where filaments can not clearly be assigned to one areole. As paired crowned areoles with long filaments, surrounded by a circle of elevated areoles, are a common character in *Chordodes* (see, *e.g.*, SCHMIDT-RHAESA, 2002a, 2002b), it can be assumed that the structures in *C. brasiliensis* represent modified crowned areoles. The presence of two kinds of filaments, thick and thin, however, is new and unique for *C. brasiliensis*. CAMERANO (1897a) figured elevated areoles surrounding the areoles with the long filaments, including a curvation towards the center, but did not mention these as a particular type of areoles. What remains questionable is the nature of the abundant elevated areoles on the cuticular surface. As these may carry small processes, they might represent some form of crowned areoles. We think that future studies will allow a better idea about the real identity of these areoles.

Distribution – ARGENTINA - Buenos Aires: Sierra de la Ventana, Cerro Tres Picos (3♂, de Miralles & Camino, 1983), Arroyo El Loro, Río Sauce Grande (8♂, 4♀, MIRALLES, 1980). Córdoba: Alta Gracia, La Granja stream (2♀, MIRALLES, 1976), Alta Gracia 31°40'00"S, 64°24'00"W (1♂, new record). Corrientes: Corrientes Capital 27°28'S, 58°49'W (1♂, 1♀, new record). Entre Ríos: Gualeguaychú (1♂, CARVALHO, 1946a). Jujuy: San Lorenzo (2♀, CAMERANO, 1897a). Misiones: Puerto Bembey (3♂, 2♀, CARVALHO & FEIO, 1950), Cuña Pirú stream 27°08'00"S, 54°54'00"W (1♀, new record), Parque Nacional Iguazú, Base Yawi 25°36'00"S, 54°34'00"W (1♂, new record). Salta: Tala (35♂, 2♀, CAMERANO, 1897a), Salta capital 24°51'00"S, 65°29'00"W (1♀, new record). San Luis: El Reparito, Estancia Grande (1♂, MIRALLES, 1976). Tucumán: Las Tipas river (1♂, 2♀, MIRALLES, 1984, 1993). BRAZIL - Espírito Santo: Santa Teresa 20°06'02"S, 40°31'47"W (2♂, 3♀, CARVALHO, 1946b); Rio de Janeiro: 22°55'00"S, 43°30'00"W (1♂, new record), Niterói 22°56'00"S, 43°04'00"W (1♂, new record), Cachoeira de Macacu, Japuhiba 22°27'24"S, 42°39'24"W (1♀, new record), Minas Gerais: Viçosa 20°45'39"S, 42°52'10"W (1♀, new record). URUGUAY: Nueva Palmira (1♂, CARVALHO, 1946a), Tacuarembó (1♂, CARVALHO, 1946a), Mercedes (1♂, CARVALHO, 1946a), Paysandú (1♂, 1♀, CARVALHO, 1946a), unspecified location (CAMERANO, 1915).



Chordodes brasiliensis, ♂, SEM - fig.1- (A) posterior end (MZUT G2) unlobed; (B) posterior end (NHM 13) with a ventral groove and two lobe like structures; (C) midbody cuticle, general view (MZUT G2); (D) midbody cuticle, detail of areoles types 1, 2 and 3; (E) midbody cuticle, detail of areoles types 1 and 2 (MNRJ 5348); (F) midbody cuticle, lateral view showing areole type 3 (MLP 4903). Scale bars: (A-C) = 100µm, (D-F) = 10µm.



Chordodes brasiliensis, ♀, (MLP 5050), SEM – fig.2- (A) terminal end with radiating grooves (arrow) around the cloacal opening; (B) midbody cuticle, lateral side with type 1- 3 areoles; (C) midbody cuticle, ventral midline with areolar clusters with types 3 and 4 (crowned areoles). Scale bars: (A and C) = 100 μ m, (B) = 50 μ m.

Chordodes carmelitanus Carvalho & Feio, 1950
(Fig.3)

1950 *Chordodes carmelitanus*. Carvalho & Feio. Ann. Acad. Bras. Cienc., 22:197, pls.4-6.

Holotype – 1♀ from Fazenda da Alegria, Carmo do Rio Claro, Minas Gerais, Brasil. (Museu Nacional of Rio de Janeiro, Brasil, no accession number).

Material examined (holotype) – SEM of midbody. 1♀ (Cordoba: San Lorenzo Stream, Cura Brochero, Argentina, MLP 3579), 2♀ ♀ (Buenos Aires: Sierra de la Ventana, Argentina, MLP 3580).

Host – Unknown.

Redescription of holotype – Body length 220mm and diameter in the middle region 1.8mm. Body colour dark brown. Terminal end rounded and the cloacal opening situated terminally.

The cuticle contains three types of areoles. Areoles of type 1 and 2 are oval or rounded (Fig.3A, B), moderately elevated and with superficial or deep grooves in perpendicular direction to the body axis. The interareolar spaces between areoles type 1 and 2 are broad, structured into cord-like folds and contain scattered small protuberances. Type 1 areoles are the most abundant and among these there are scattered type 2 areoles with a short tubercle on the top that seems to originate from a depression. Crowned areoles (third type of areoles) always occur in pairs which are densely surrounded by a circle of areoles of type 1 (Fig.3B-D). They contain long slender apical filaments (up to 297µm).

Comments – Our reinvestigation in general confirms the description of CARVALHO & FEIO (1950), but differs in the interpretation. As first type of areoles, CARVALHO & FEIO (1950) described very small areoles. Observed with SEM, these areoles turn out to be irregular elevations of the cordlike structures in the interareolar space. Under lower magnifications (e.g., Fig.3D), these structures appear as areoles, but under higher magnifications, they do not possess a defined margin and are therefore not regarded as areoles by us. CARVALHO & FEIO (1950) summarized what we have called areoles type 1 and 2 as one type, but also noted the distribution of crowned areoles along the ventral midline.

Specimens from Buenos Aires and Córdoba (Argentina), reported by MIRALLES (1989) as *C. carmelitanus*, differ from the holotype and therefore we transferred them to the species *C. nobilii* (see next).

Distribution – BRAZIL - Minas Gerais: Carmo do Rio Claro (1♀, CARVALHO & FEIO, 1950).

Chordodes nobilii Camerano, 1901
(Figs.4-6)

1901 *Chordodes nobilii* Camerano. Boll. Mus. Zool. Anat. Comp. Torino, 16(410):1

Holotype – 1♀ from Cosquin, Cordoba, Argentina could not be located and seems to be lost.

Neotype – 1♂ (San Luis: Carpinteria, Piedra Blanca stream MLP 5290/1). Paraneotypes: 2♂ (San Luis: Carpinteria, Piedra Blanca stream MLP 5290/2).

Material examined – SEM of midbody (all reports from Argentina): Neotype 1♂ (San Luis: Carpinteria, Piedra Blanca stream MLP 5290/1), Paraneotypes 2♂ (San Luis: Carpinteria, Piedra Blanca stream MLP 5290/2), 1♂ (Buenos Aires: Sierra de la Ventana, El Loro stream, MLP 5063), 1♂ (MLP 5063), 3♀ (Buenos Aires: Sierra de la Ventana [as *C. carmelitanus*, MIRALLES, 1989], MLP 3580), 4♂ (Buenos Aires: Sierra de la Ventana, Sauce Grande stream, MLP 3582), 1♀ (Buenos Aires, Balcarce, MLP 5055); 1♂ (Cordoba, El Durazno, MLP 5291) 2♀ (Cordoba, MNB 4437), 1♀ (Cordoba: Cura Brochero, San Lorenzo stream [as *C. carmelitanus*, MIRALLES, 1989], MLP 3579), 2♂ and 1♀ (San Luis: Villa Larca, Aguas Blancas, San Ignacio stream, MLP 5289). SEM terminal end: Neotype 1♂ (San Luis: Carpinteria, Piedra Blanca stream MLP 5290/1). 1♂ (Buenos Aires: Sierra de la Ventana, Sauce Grande stream, MLP 3582), 1♂ (Cordoba, El Durazno, MLP 5291), 1♀ (Buenos Aires, Balcarce, MLP 5055).

Host – Unknown.

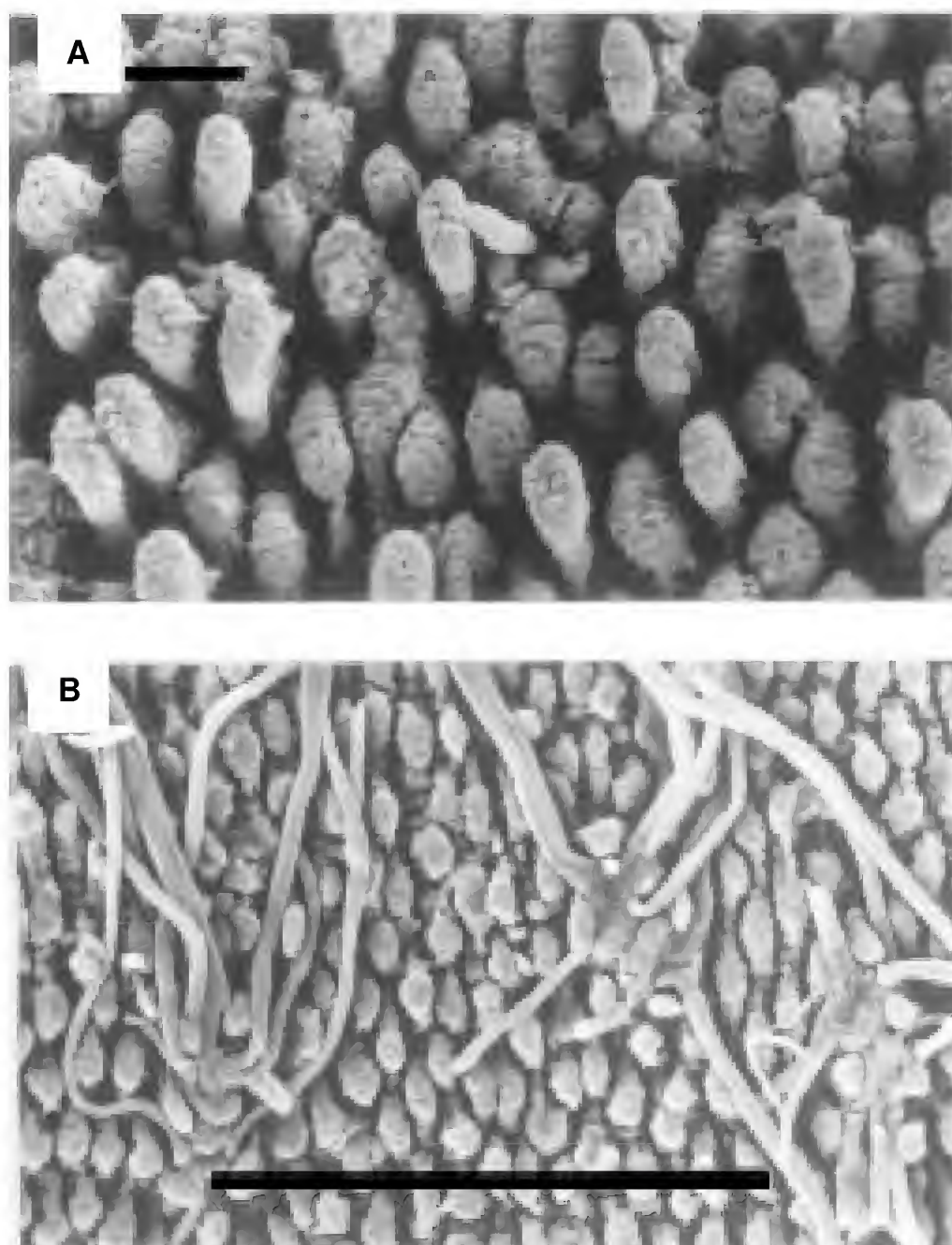
♂ – The body color ranges from light to dark brown. The anterior end is tapered and a dark collar is always lacking. The posterior end in most of the males is not divided into lobes (Fig.4A), but in two specimens we found a clear indication of two lobes at the ventral side of the posterior end (Fig.4C). The cloacal opening is round or oval and is surrounded by slender spines undivided at the top (circumcloacal spines) (Fig.4A-C). Anterolateral of the cloacal opening are paired regions in which numerous bristles are located (bristlefields). In the anterior and posterior region of the cloacal opening are short spines.

The body cuticle is densely structured by areoles. There are two types of areoles. The most abundant type (type 1) are slightly oval or circular in shape and have a warty surface (“blackberry-like”). Irregular minute projections are distributed on the whole apical surface (Fig.5B). Type 2 areoles are slightly larger than the first type and carry on their apical surface projections which are not scattered, but clustered. These projections can be extremely

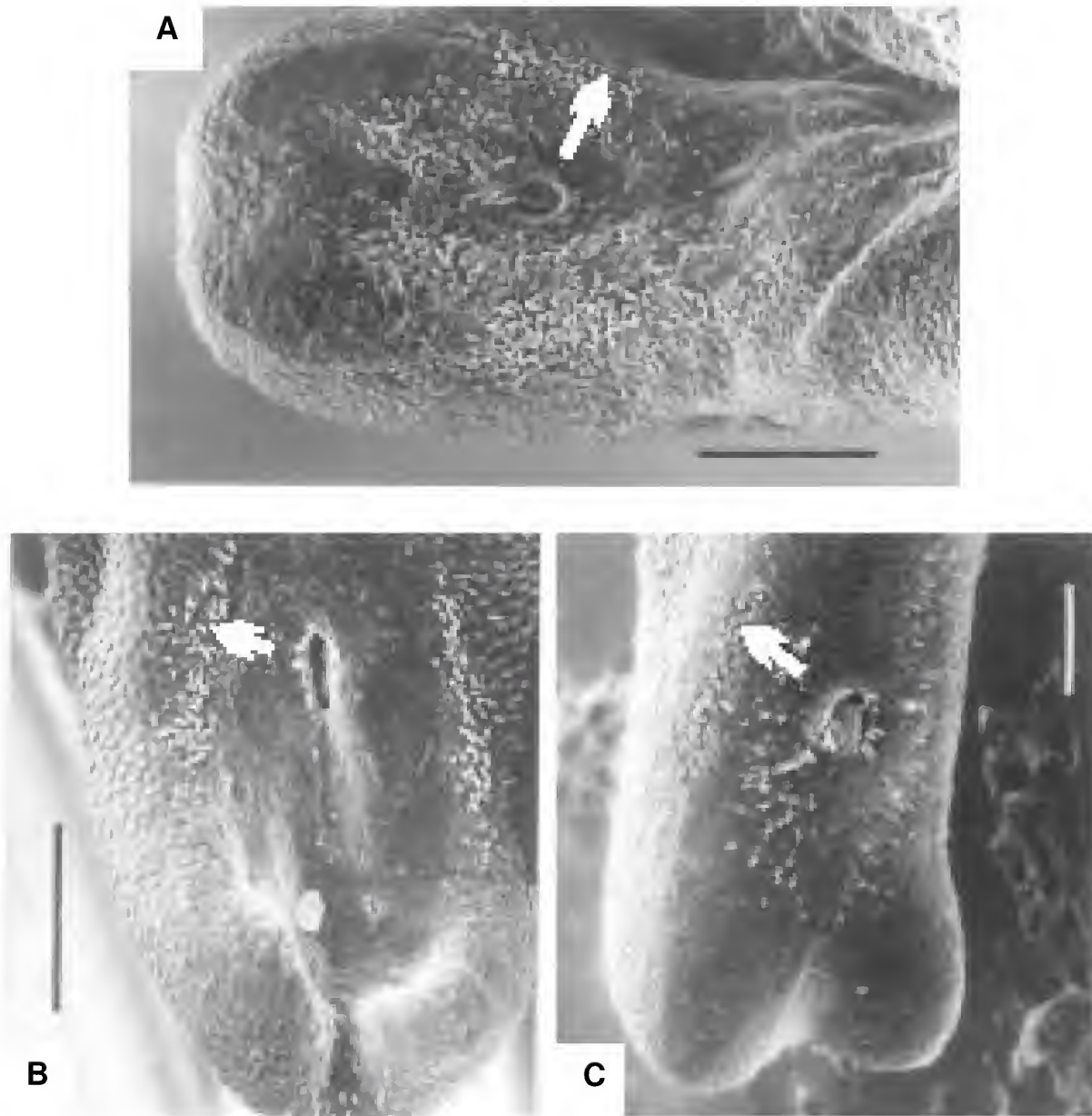
short or slightly longer and bristlelike (Fig.5A-D). Type 2 areoles occur individually or in clusters of 3 to 10 areoles. The cuticle between the areoles is structured into cord-like folds and there are scarcely distributed tubercles emerging among type 1 areoles (Fig.5A, D).

♀ – Posterior end round with a terminal cloacal opening. Radiating around the cloacal opening are fine

grooves (Fig.6A). In the cuticle, the same types of areoles are present as in the male, with additional crowned areoles. Areoles of types 1 and 2 are very similar to each other (Fig.6B, C). Crowned areoles (type 3) occur only along the ventral and the dorsal midline (Fig.6D, E). They have quite long apical filaments and appear in a cluster of two areoles (Fig.6E). The surrounding areoles are from type 1 (Fig.6E).



Chordodes carmelitanus, ♀ holotype, SEM – fig.3- (A) cuticle of midbody with type 1 areole and tubercle areoles (type 2), scale bar = 100µm; (B-D) ventral midline. Areolar clusters with types 3 and 1 (crowned areoles), scale bar = 10µm.

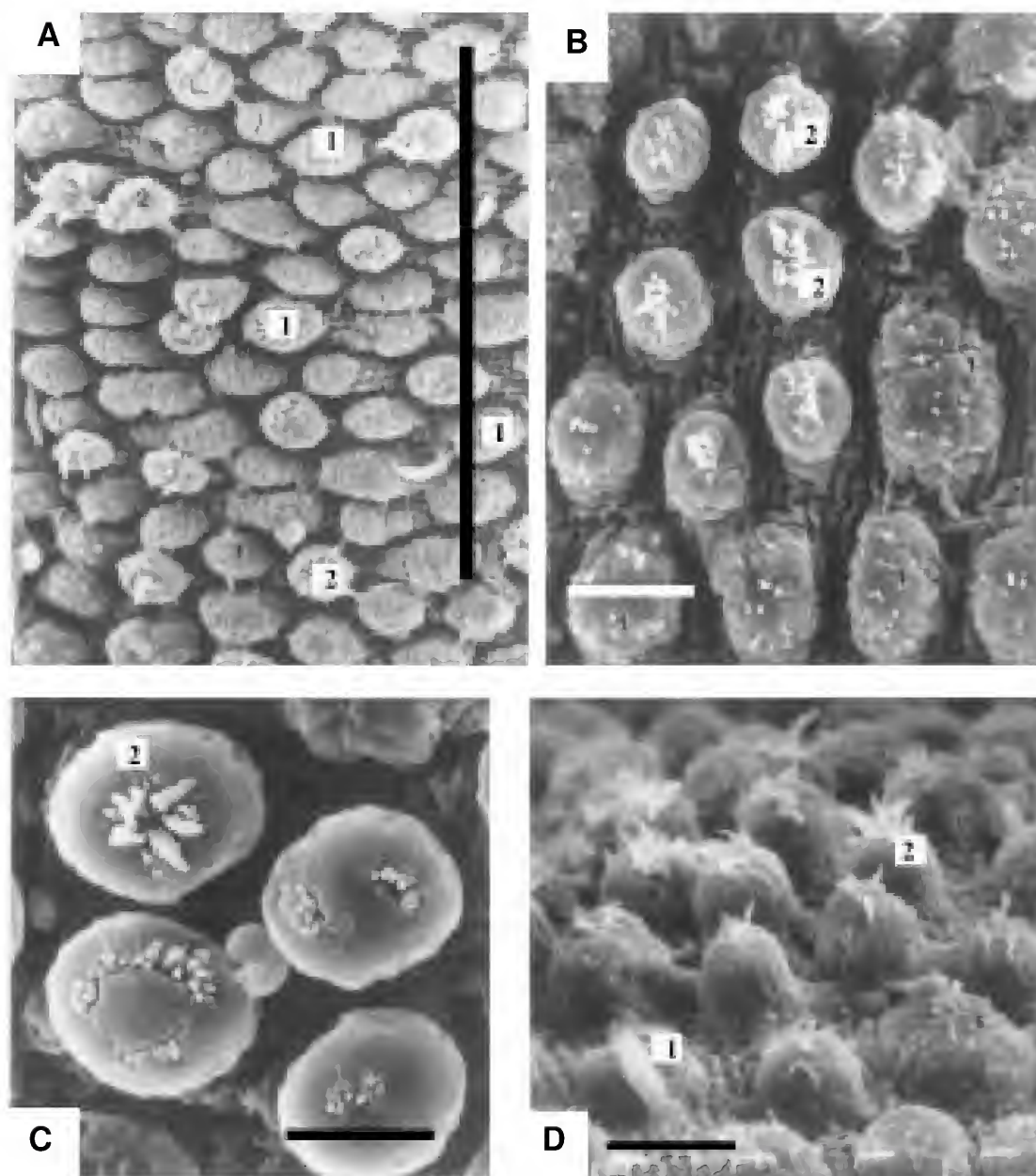


Chordodes nobilii, ventral view on male terminal end. SEM – fig.4- (A) Neotype (MLP 5290/1) undivided. (B) MLP 5291 and (C) MLP3582, with a ventral groove and two lobe like structures; (A-C) ventral cloacal opening with circumcloacal spines, anterolateral bristles (bristlesfield) (arrows) and posterior spines scale bar = 100 μ m.

One female from the Museum fur Naturkunde Berlin (MNB 4437) differed from the remaining females in that areoles of type 2 areoles are larger than the first type and crowned areoles are surrounded by slightly elevated areoles (Fig.7A, B). Dimensions – According to the literature, females vary between 149 and 386mm in length and are maximally 1.5mm in diameter (CAMERANO, 1901,

1915; MIRALLES, 1989). Measurements of the newly reported specimens range in length from 82 to 255mm in males and from 219 to 290mm in females. The diameter varies between 0.6 to 1.1mm in males and between 0.9 to 1.3mm in females.

Remarks – The holotype of *Chordodes nobilii* seems to be lost. It was originally described in the journal of the Museum for Zoology and Comparative



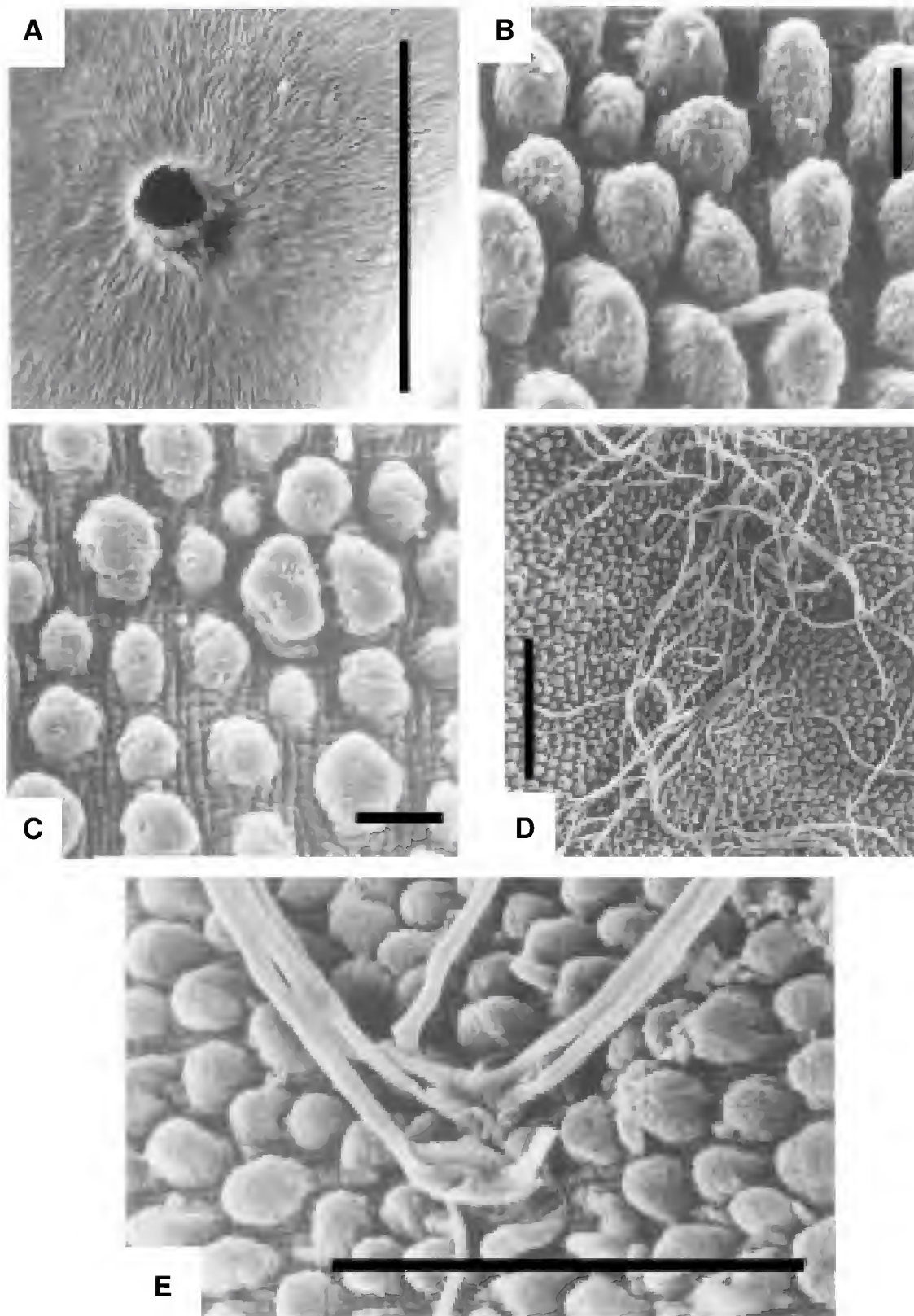
Chordodes nobilii midbody cuticle of males. SEM – fig.5- (A-D) areolar type 1 and crowned areoles (type 2): (A) neotype, MLP 5290/1, general view of the cuticle showing tubercles between type 1 areoles and single and clusters of crowned areoles (type 2), scale bar = 100µm; (B) MLP 5063: type 1 areoles, group of crowned areoles (type 2) and structure of the interareolar cuticle with cord-like folds; (C) MLP 5063, lateral view of the cuticle; (D) MLP 3930/2, cluster of crowned areoles with smooth surface, some of them with retracted filaments. (B-C) scale bar = 10µm.

Anatomy in Turin, Italy, but is not present there, nor could be located in any other collection. The original description (Camerano 1901) as well as later references to this species (CAMERANO, 1915; MIRALLES, 1969, 1976) did not include figures. Nevertheless, the description corresponds well with the specimen designed here as neotype.

The reexamination of two female specimens housed

in the Museum fur Naturkunde Berlin (MNB 4437) from Cordoba as *Chordodes nobilii* demonstrates that one of them differed slightly, but may still belongs to *C. nobilii* but the other belongs to *Pseudochordodes bedriagae* (see MIRALLES, 1973; DE-VILLALOBOS & RESTELLI, 2001).

Distribution – ARGENTINA - Buenos Aires: Sierra de La Ventana, El Loro stream 38°08'00"S, 38°08'00"W

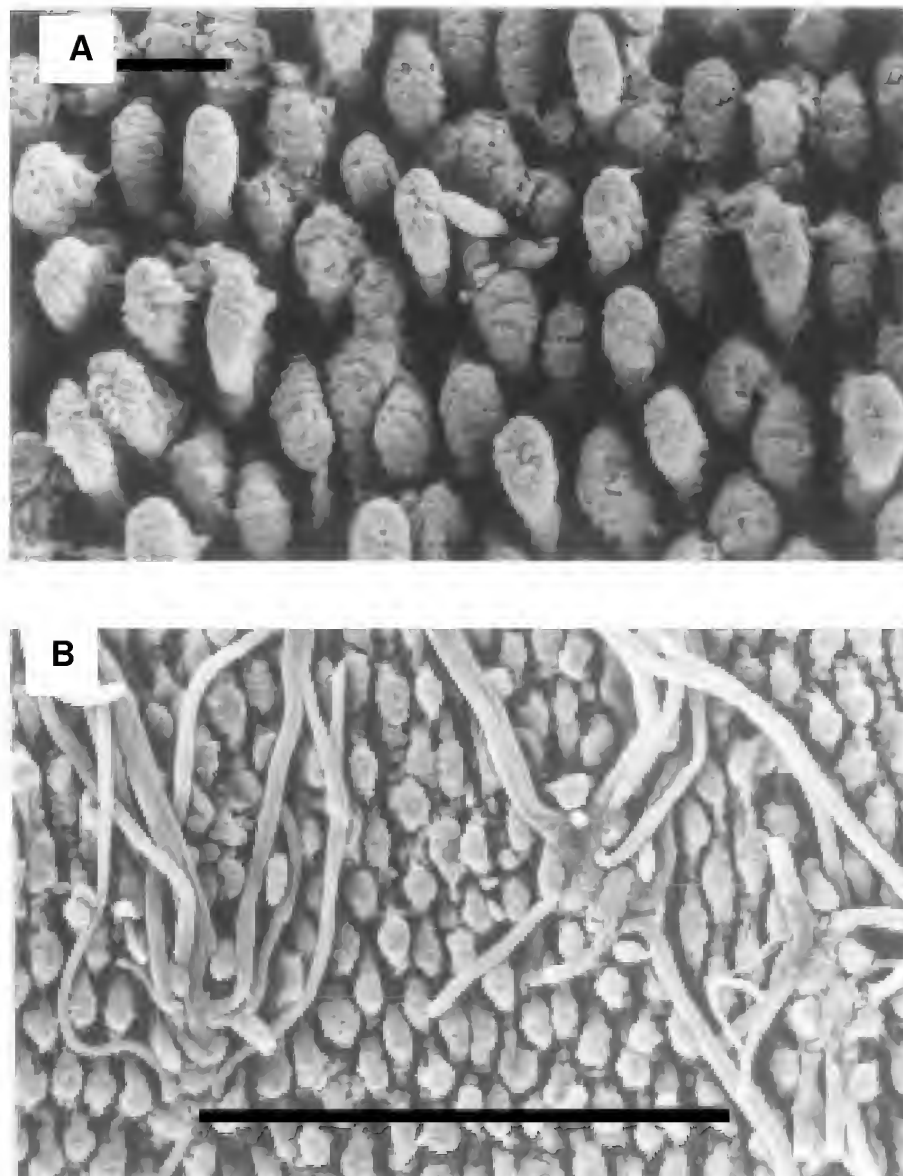


Chordodes nobilii, ♀, SEM – fig.6- (A) MLP 3580, terminal end with radiating fine grooves around the cloacal opening; (C) midbody cuticle with type 1 areoles. (B) MLP 3579, midbody cuticle with type 1 areoles, type 1 areoles and interareolar tubercles; (C) MLP 3580, midbody cuticle with type 1 areoles, type 1 areoles with various shapes and sizes; (D) 3579, cuticle of the ventral midline, overview of the cuticle with crowned areoles with long filaments (type 2); (E) MLP 3579, cuticle of the ventral midline, crowned areoles (type 2) in detail. Scale bars: (A, D-E) = 100µm, (B-C) = 10µm.

(1♂, new record), Sierra de la Ventana 3♀, MIRALLES, 1989), Sierra de La Ventana, Sauce Grande stream 38°05'00"S, 62°13'00"W (4♂, new record), Balcarce 37°45'00"S, 58°18'00" (1♀, new record). Cordoba: Cordoba 31°24'00"S, 64°11'00"W (1♀, new record), Cosquin (1♀, CAMERANO, 1901), Cura Brochero (3♀, MIRALLES, 1989), El Durazno 31°20'15"S, 64°40'09"W (1♂, new record). San Luis: Villa Larca, Aguas Blancas, San Ignacio stream (32° 38'09"S, 64°57'06"W) (2♂, 1♀, new record), Carpinteria, Piedra Blanca stream (1024m) (32°24' 43"S, 64°58'47"W) (3♂, new record).

CONCLUSIONS

This study by SEM allows us to confirm the observations previously made by CARVALHO & FEIO (1950) for *C. carmelitanus* that in females the crown areoles with long filaments are limited to the ventral and/or dorsal and ventral groove. This particular feature in females has been mentioned for other South American species such species such as *C. brasiliensis* (see JANDA, 1894, CAMERANO, 1897; CARVALHO, 1946b), *C. peraccae* (see DE-VILLALOBOS & ZANCA, in press), *C. balzani* (see CARVALHO & FEIO, 1950;



Chordodes nobilii, ♀ (MNB 4437) – fig.7- (A) midbody cuticle, scale bar = 10µm; (B) Nematomorpha, Gordiida, *Chordodes*, South America, scanning electron microscopy. Ventral groove with cluster of crowned areoles surrounded by slightly elevated areoles.

DE-VILLALOBOS *et al.*, 2004). *C. moraisi* (see CARVALHO, 1944; DE-VILLALOBOS & ZANCA, in press), *C. staviarskii* (see CARVALHO & FEIO, 1950; DE-VILLALOBOS & ZANCA, in press) and in the present study for *C. nobilii*. Although more studies are necessary on both sexes of genus *Chordodes* in South America, there seems to be a feature of sexual dimorphism as was considered by CARVALHO (1946b) for the species *C. brasiliensis*, by CAMERANO (1987) and CARVALHO AND FEIO (1950), DE-VILLALOBOS *et al.* (2004) for *C. balzani* and DE-VILLALOBOS & ZANCA (in press) for *C. moraisi* and *C. staviarskii*.

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COMPARATIVE MORPHOLOGY AND PHYLOGENY OF REPRESENTATIVES
OF THE SUPERFAMILIES OF ARCHITAENIOGLOSSANS AND THE ANNULARIIDAE
(MOLLUSCA, CAENOGASTROPODA) ¹

(With 354 figures)

LUIZ RICARDO L. SIMONE ²

ABSTRACT: As part of a larger project on the phylogeny of the Caenogastropoda superfamilies, a detailed morphological study of 19 non-marine species is provided, of the following taxa: a) Family Ampullariidae: 1) *Pomacea crosseana* (Hidalgo) (from Pantanal, Brazil); 2) *P. curumim* new species (from Xingu River, Amazon Basin, Brazil); 3) *P. scalaris* (Orbigny) (from Pantanal, Brazil); 4) *P. canaliculata* (Lamarck) (same); 5) *P. lineata* (Spix) (several coastal places of Brazil); 6) *P. sordida* Swainson (Rio de Janeiro, Brazil); 7) *P. bridgesi* (Reeve) (Pará, Brazil) (most published elsewhere); 8) *Asolene megastoma* (Sowerby) (Rio Grande do Sul, Brazil); 9) *Felipponea neritiniiformis* (Dall) (Paraná, Brazil); 10) *Marisa planogyra* Pilsbry (Pantanal, Brazil); b) Family Cyclophoridae: 11) *Neocyclotus prominulus* (Orbigny) (São Paulo, Brazil); 12) *Incidostoma tupy* new species (Rondônia, Brazil); 13) *Aperostoma branchetiana* (Moricand) (Minas Gerais, Brazil); c) Family Viviparidae: 14) *Viviparus acerosus* (Bourguignat) (Hungary); 15) *V. contectus* (Millet) (same); 16) *Notopala ampullaroides* (Reeve) (Australia); 17) *N. essingtonensis* (Frauenfeld) (same); 18) *Larina* cf. *stangei* (Adams) (same); d) Family Annulariidae: 19) *Annularia* sp. (Yucatan, Mexico). Based on this study, 143 characters (192 states) were searched, polarized, and a phylogenetic analysis is performed. The single obtained cladogram is the following: ((*Neocyclotus prominulus* (*Aperostoma blanchetiana* – *Incidostoma tupy*)) (((*Annularia* sp. – Cerithioidea) ((*Viviparus acerosus* – *V. contectus*) ((*Notopala ampullaroides* – *N. essingtonensis*) *Larina* cf. *stangei*))) (*Marisa planogyra* (*Pomacea crosseana* (*Felipponea neritiniiformis* (*P. scalaris* (*P. curumim* (*P. lineata* ((*P. canaliculata* – *Asolene megastoma*) (*P. bridgesi* – *P. sordida*))))))))), length 251; ci 77; ri 91. A pool of archaeogastropod characters, the rissooideans-littorinoidean *Annularia*, and the Cerithioidea ground plan were used as main outgroups, however the two latter taxa are operationally included as part of the ingroup. The analysis of obtained cladogram revealed that the taxon Architaenioglossa is paraphyletic, grouping 3 branches of basal caenogastropods successively distributed on the tree as follows: Cyclophoroidea (Cyclophoridae), Ampullarioidea (Ampullariidae), and Viviparioidea (Viviparidae), since the representatives of the remainder the caenogastropods (*Annularia* and Cerithioidea) were terminal in the ingroup. The current concept of Ampullarioidea (Ampullariidae plus Viviparidae) was also paraphyletic.

Key words: Ampullarioidea, Viviparioidea, Cyclophoroidea, Phylogeny, Morphology

RESUMO: Morfologia Comparativa e Filogenia de representantes das superfamílias de arquitenioglossos e Annulariidae (Mollusca, Caenogastropoda).

Como parte de um projeto sobre filogenia das superfamílias de Caenogastropoda um estudo morfológico detalhado de 19 espécies não marinhas é desenvolvido dos seguintes táxons: a) Família Ampullariidae: 1) *Pomacea crosseana* (Hidalgo) (Pantanal, Brasil); 2) *P. curumim* nova espécie (Xingu River, Amazônia, Brasil); 3) *P. scalaris* (Orbigny) (Pantanal, Brasil); 4) *P. canaliculata* (Lamarck) (mesmo); 5) *P. lineata* (Spix) (vários locais costeiros do Brasil); 6) *P. sordida* Swainson (Rio de Janeiro, Brasil); 7) *P. bridgesi* (Reeve) (Pará, Brasil) (maioria dos dados publicados em outro trabalho); 8) *Asolene megastoma* (Sowerby) (Rio Grande do Sul, Brasil); 9) *Felipponea neritiniiformis* (Dall) (Paraná, Brasil); 10) *Marisa planogyra* Pilsbry (Pantanal, Brasil); b) Família Cyclophoridae: 11) *Neocyclotus prominulus* (Orbigny) (São Paulo, Brasil); 12) *Incidostoma tupy* espécie nova (Rondônia, Brasil); 13) *Aperostoma branchetiana* (Moricand) (Minas Gerais, Brasil); c) Família Viviparidae: 14) *Viviparus acerosus* (Bourguignat) (Hungria); 15) *V. contectus* (Millet) (mesmo); 16) *Notopala ampullaroides* (Reeve) (Austrália); 17) *N. essingtonensis* (Frauenfeld) (mesmo); 18) *Larina* cf. *stangei* (Adams) (mesmo); d) Família Annulariidae: 19) *Annularia* sp. (Yucatan, México). Baseando-se neste estudo, 143 caracteres (192 estados) foram levantados, polarizados, e uma análise filogenética é realizada. O cladograma único é o seguinte: ((*Neocyclotus prominulus* (*Aperostoma blanchetiana* – *Incidostoma tupy*)) (((*Annularia* sp. – Cerithioidea) ((*Viviparus acerosus* – *V. contectus*) ((*Notopala ampullaroides* – *N. essingtonensis*) *Larina* cf. *stangei*))) (*Marisa planogyra* (*Pomacea crosseana* (*Felipponea neritiniiformis* (*P. scalaris* (*P. curumim* (*P. lineata* ((*P. canaliculata* – *Asolene megastoma*) (*P. bridgesi* – *P. sordida*))))))))), passos: 251; IC 77; IR 91. Um conjunto de caracteres de archaeogastropodes, o Rissooidea *Annularia*, e o plano básico de Cerithioidea foram usados como principais grupos externos, entretanto, os 2 últimos táxons foram incluídos operacionalmente como parte do grupo interno. A análise do cladograma obtido revelou que o táxon Architaenioglossa é parafilético, agrupando 3 ramos de cenogastropodes basais sucessivamente distribuídos na árvore como segue: Cyclophoroidea (Cyclophoridae), Ampullarioidea (Ampullariidae), e Viviparioidea (Viviparidae), uma vez que os representantes dos demais cenogastropodes (*Annularia* e Cerithioidea) resultaram como parte terminal do grupo interno. O senso prévio de Ampullarioidea (Ampullariidae mais Viviparidae) também resultou parafilético.

Palavras-chave: Ampullarioidea, Viviparioidea, Cyclophoroidea, Filogenia, Morfologia.

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INTRODUCTION

Architaenioglossa is an enigmatic taxon that encompasses non-marine mesogastropod prosobranchs, corresponding to three families: Ampullariidae (=Pilidae), Viviparidae and Cyclophoridae (s.l.). HASZPRUNAR (1988) presented the more accurate sense of this taxon, regarded as the sister taxon of the branch Caenogastropoda plus Heterobranchia, in the archaeogastropod grade. PONDER AND LINDBERG (1996, 1997), in their phylogenetic analysis of the Gastropoda, advocated that the architaenioglossans were basal members of the caenogastropod branch. Despite those studies, the validity of the formal taxon Architaenioglossa is still unclear, because it is not defined by any synapomorphy, other than the non-marine habitat. It is possible that this taxon actually represents a paraphyletic or even a polyphyletic group. Besides, their relationship with other gastropods is still controversial.

The literature on some architaenioglossans is relatively rich, mainly on the ampullariids, which have species with medical, sanitary, and gastronomic importance. However, despite of this, the taxonomy remains unclear.

The Ampullariidae are medium to large freshwater snails, with representatives in all tropical areas of the Americas, Africa and Asia. There are some papers describing their morphology, such as, *e.g.*, SCOTT (1957) with particular attention to South American representatives. BERTHOLD (1991) made an extensive study with representatives of all genera, and included aspects on morphology, phylogeny and evolution. BERTHOLD (1991), however, did not make a formal phylogenetic analysis of the group, but this, in part, was provided by BIELER (1993). PAIN (1972) referred on the family history. DEMIAN & YOUSIF (1973) provided embryological data. CASTELLANOS & FERNÁNDEZ (1976) provide biologic and biogeographic information. COWIE (1997) addressed the nomenclatural problems with the name Ampullariidae and the genera *Pomacea* and *Ampullaria*. Revisions of South American ampullariids include studies at the Instituto Oswaldo Cruz (*e.g.*, THIENGO, 1987, 1989, 1995). Viviparidae are freshwater, filter-feeders found in most part of Europe, southern Asia, north and east Australia, and the central-east region of North America. Analysis of the history and distribution of the viviparids can be found in PRASHAD (1928). As its name suggests, they are viviparous or

ovoviviparous, with females brooding the young in the pallial oviduct.

The Ampullariidae and the Viviparidae have been normally referred to the same superfamily in recent literature, sometimes as Ampullarioidea (*e.g.*, BOSS, 1982; PONDER & WARÉN, 1988), other times as Viviparioidea (*e.g.*, VAUGHT, 1989). This hypothesis is also investigated herein.

The Cyclophoridae are terrestrial, distributed worldwide, lacking gill. They are, sometimes, divided into several families (*e.g.*, six families in VAUGHT, 1989). They are, also, the subject of several monographic papers, which include taxonomical and some anatomical data. TIELECKE (1940), for example, introduced a classification based mainly on the characters of the shell and pallial oviduct. MORRISON (1955) established a taxonomy based mainly on the male reproductive organ of the American species. Some papers also provide further modifications and further critical analysis of unstable cyclophorid classification is profuse in the literature (*e.g.*, SOLEM, 1956; THOMPSON, 1963, 1967).

The Annulariidae are terrestrial snails from Central and North America, with known relationships with putative basal caenogastropods such as Littorinidae. THOMPSON (1978), pointed out the unusual radula and genital system and explored the concept of the family.

As part of a larger project on the phylogeny of the Caenogastropoda, representatives of each family of all superfamilies of this taxon have been studied in a detailed morphological and comparative scenario. For each caenogastropod superfamily, the following attributes have been tested: 1) the monophyly; 2) taxonomic status; and 3) the ground plan, *i.e.*, the attributes of their hypothetical ancestral. These three parameters can only be tested by means of a phylogenetic analysis. The Architaenioglossa is the focus of the present paper. As the group in general, and the South American members in particular, have a very confused taxonomy, this paper also provides a basis for future more detailed studies on each sub-group. Some previously published phylogenies are part of the project (SIMONE, 1999, 2000, on Terebridae; SIMONE 2001, on Cerithioidea and SIMONE in press, on Stromboidea, Cypraeoidea and Calyptraeidea) as well as other smaller papers, serving as outgroups. The terrestrial Annulariidae, which has a representative studied herein, are undoubtedly a non-architaenioglossan

caenogastropod (see THOMPSON, 1978; PONDER & WARRÉN, 1988). Its inclusion has as main objective to test how adaptation to a non-marine environment can influence this kind of analysis.

MATERIAL AND METHODS

Although some living species of *Pomacea* were examined in the laboratories of the Museu de Zoologia da USP (MZSP), most of the specimens studied were fixed in 70% ethanol. The extraction of the specimens from their shells were mostly easy, in some specimens the shell was broken. The dissections were performed under a stereomicroscope following traditional techniques, with the specimens immersed in fixative. All drawings were made with aid of a camera lucida. The hard parts, such as shells (of small specimens), jaws and radulae, were also examined in SEM, in the Laboratório de Microscopia Eletrônica of MZSP.

In the descriptions, a more detailed one is presented for the first species, *P. crosseana*, (it was the first species studied in the project). In the remaining species, and when possible, the description is basically comparative to *P. crosseana*, without any description of similar characters. A similar approach is given in the figures.

A part of the cladistic analysis was performed with the aid of the computer programs and "Tree Gardner 2.2" (RAMOS, 1997). The last basically works as an interface of the program "Hennig86" (FARRIS, 1988), the algorithm used was mh*, bb* and ie. For the polarization of the character states the outgroup method was used.

The section of comparative morphology is organized as a phylogenetic analysis, the presentation of each character begins with abbreviated descriptive sentence followed by plesiomorphic and derived conditions(s); also included are CI and RI (consistency and retention indices, respectively), values for the character under the most parsimonious hypotheses. Following the apomorphic state(s), a list of terminal taxa with the apomorphic condition is presented. In the next section, all character states are presented in the table 1.

The remaining Caenogastropoda studied in this project were selected as outgroups, despite sometimes they are not directly included in the data matrix. They are mainly the following: Cerithioidea (SIMONE, 2001); Littorinoidea (SIMONE, 1998); Rissooidea-Littorinoidea (SIMONE & MORACCHIOLI, 1994; SIMONE 1995a, *Annularia*

sp. – this study); Stromboidea (SIMONE in press c); Calyptraeidea (SIMONE, submitted); Tonnoidea (SIMONE, 1995b); Muricoidea (SIMONE, 1995c on *Thala crassa*; SIMONE, 1996b on *Buccinanops* spp); Conoidea (SIMONE, 1999, 2000, on Terebridae). As more distant outgroups, some archaeogastropods were also analyzed (e.g., SIMONE, 1996A; 1997; LEAL & SIMONE, 1998; 2000). However, in the analysis of the matrix in the computer programs, only three outgroups are included: 1) A pool of archaeogastropods, mainly based on SASAKI (1998). 2) The *Annularia* sp., studied herein, representing the Rissooidea-Littorinoidea branch, with a species adapted to the non-aquatic environment. 3) The Cerithioidea ground plan, i.e., the node # 1 of the cerithioidean cladogram, obtained in a previous study (SIMONE, 2001). Operationally, only the archaeogastropod set of characters was utilized as the outgroup, with *Annularia* sp. and Cerithioidea ground plan analyzed as part of the ingroup. So that, the monophyly of the "Architaenioglossa" could be tested.

Characters were polarized separately, and the polarization is justified, if necessary, in the discussion that follows each character. In that discussion, the final cladogram obtained is considered (i.e., the allocation and optimization of some character states are discussed) although, the cladogram is only formally presented in the following section.

Three parameters considered here are known as polemic, and sometimes there are authors who do not accept them. The FIRST is the use of the ingroup synapomorphies (those that support node 1, or the ingroup "autapomorphies" in this case). They are used herein because they are the main goal of this study, since the Architaenioglossa is still lacking a phylogenetic definition. This definition, as referred in the Introduction, is essential for the larger project on caenogastropod phylogeny. Besides, there are authors who advocate this approach (e.g., YEATES, 1992). The SECOND is to consider some multistate characters as additive (ordered). In those character states, the ordering has support from ontogeny or by comparison (i.e., each state is clearly a modification of the preceding one). For additive characters, an extra explanation is presented in the discussion of each character. Furthermore, a parallel analysis in which the character is considered unordered was performed and any change of the result is reported. The THIRD is the arbitrary choice of an optimization in the presented cladogram (Fig.353) in those few cases where more than one

optimization is equally parsimonious. It is possible to apply the heuristic options ACCTAN (assuming convergence is more likely than reversion) or DELTRAN (vice-versa), which would produce two trees with same the topology, a duality that is avoided here. In those cases where more than one optimization is possible, they are all reported, though only one is presented in figure 353.

Abbreviations in the figures: (aa) anterior aorta, (ad) adrectal sinus, (af) afferent gill vessel, (ag) albumen gland, (am) ampulla of anterior aorta, (an) anus, (ap) apical gland of penis shield, (ar) male pore, (as) aperture of seminal receptacle into pallial cavity, (au) auricle, (bb) bulged region of br, (bg) buccal ganglion, (bm) buccal mass, (bp) brood pouch, (br) subradular membrane, (bv) blood vessel, (ce) cerebral ganglion, (cg) capsule gland, (cm) columellar muscle, (co) collar vessel, (cp) capsules, (cv) ctenidial vein, (dc) dorsal chamber of buccal mass, (dd) duct to digestive gland, (df) dorsal fold of buccal mass, (dg) digestive gland, (di) diaphragm-like septum of haemocoel, (dp) dorsal-basal gland of penis shield, (dq) dorsal-basal gland of penis shield aperture, (ec) esophageal crop, (ed) ejaculatory duct immerse in integument, (ef) esophageal folds, (en) endostyle, (ep) esophageal pouch, (es) esophagus, (ey) eye, (fg) food groove, (fp) female pore, (fs) foot sole, (ft) foot, (ga) gastric ventral chamber, (gb) gastric dorsal chamber, (gf) gastric fold, (gi) gill, (gm) gastric muscle, (go) gonad, (gp) pleural ganglion, (gs) gastric shield, (gt) gastric transversal septum, (ha) haemocoel, (ic) intestinal chamber, (il) intestinal loop(s) into kidney chamber, (in) intestine, (ip) intestinal loop close to pericardium, (ir) insertion of m4 in tissue on radula (to), (is) insertion of m5 in radular sac, (jw) jaw, (ka) kidney anterior chamber, (kc) kidney connection between anterior and posterior chambers, (kd) kidney dorsal lobe (ki) kidney (kp) kidney posterior chamber (ll) left head-foot lobe (lp) lung pneumostome, (lr) right head-foot lobe, (lu) lung, (m1 to m14) extrinsic and intrinsic odontophore muscles, (ma) mouth abductor muscle, (mb) mantle border, (mc) buccal sphincter and circular muscles of oral tube, (me) mesentery, (mj) jaws, buccal, and oral tube muscles, (mo) mouth, (ne) nephrostome, (nr) nerve ring, (nv) nerve, (oa) odontophore secondary cartilage, (oc) odontophore cartilage, (od) odontophore, (om) ommatophore, (op) operculum, (os) osphradium, (ot) oral tube, (ov) pallial oviduct, (oy) ovary, (pa) posterior aorta, (pc) pericardium, (pd) penis duct, (pe) penis, (pf) penis furrow, (pg) pedal glands anterior furrow, (ph) penis shield notch, (pi) penis sac, (pl) penis shield longitudinal furrow, (pm) penis shield middle gland, (po) solid portion of penis sac

(penis base), (pp) penis papilla, (pr) penis sac connection with penis shield, (ps) penis shield, (pt) prostate, (pu) pedal ganglion, (py) pallial cavity, (ra) radula, (rm) retractor muscle of snout, (rn) radular nucleus, (rp) reno-pericardial aperture, (rs), radular sac, (rt) rectum, (sa) salivary gland aperture, (sc) subradular cartilage, (sd) salivary duct, (se) septum between esophagus and odontophore in buccal mass, (sg) salivary gland, (sl) snout tentacle, (sn) snout, (sr) seminal receptacle, (st) stomach, (su) supra-esophageal ganglion, (sv) seminal vesicle, (sy) statocyst, (te) cephalic tentacle, (tg) integument, (to) tissue on middle region of radula preceding its exposure, (tp) distal chamber of copulatory right cephalic tentacle, (ts) testis, (ug) urinary gutter, (up) ureter pore, (ur) ureter, (vd) vas deferens, (ve) ventricle, (vf) vas deferens pallial furrow, (vg) vaginal duct, (vo) visceral oviduct.

Abbreviations of institutions: (AMS) Australian Museum, Sydney; (BMNH) The Natural History Museum, London; (MNHN) Muséum National d'Histoire Naturelle, Paris; (MZSP) Museu de Zoologia da Universidade de São Paulo; (ZSM) Zoologische Staatssammlung München, Germany.

Some terms used in discussion merit some explanation. The word "archaeogastropod" is used in traditional sense, but it is recognized as a paraphyletic taxon. The term "basal" caenogastropods refers to those taxa which generally are in the beginning of the mesogastropods in most catalogues (*e.g.*, Abbott, 1974; Rios, 1994), in particular the Cerithioidea, Littorinoidea and Hydrobioidea. The term "higher" caenogastropods in general refers to Tonnoidea and Neogastropoda. Where mentioned "examined species" only the ingroup species are included.

SYSTEMATICS

Family Ampullariidae

Genus *Pomacea* Perry, 1810

Type-species *Pomacea maculata* Perry, 1810)

Ampullaria Lamarck, 1799:76 (Case 2996, ICZN, see Cowie, 1997).

Pomacea Perry, 1810:28.

Ampullarius Montfort, 1810:242.

Pomacea crosseana (Hidalgo, 1871)

(Figs.1- 2, 97- 98, 115-116, 150-173)

Ampullaria crosseana Hidalgo, 1871:206-207; 1872:142-143 (pl.7, fig.1); Sowerby, 1909:348.

Ampullarius crosseanus – MORRETES, 1949:66.

Type-locality: Brazil, Amazon River.

Description

Shell (Figs.1-2). Medium to large (up to 45mm), globose. Color homogeneous pale brown, sometimes successive spiral bands pale and dark brown. Periostracum thin, velvet-like. Spire small. Suture somewhat deep. Aperture elongated antero-posteriorly.

Head-foot (Figs.151-152, 158). Color beige, with irregular brown spots. Head broad, protruded. Cephalic tentacles stubby, slender and long, tip pointed. Ommatophore long, about ¼ of tentacle length, tip rounded, base at outer surface of tentacles, their base slightly overlapping. Eyes dark, at tip of ommatophores. Snout somewhat cylindrical, broad, anterior surface flattened; mouth longitudinal, in middle region of anterior surface. Two slender snout tentacles, originating laterally at anterior end of snout, about as long as cephalic tentacles, base broad gradually narrowing distally, tip somewhat pointed. Two nuchal lobes, or siphons, flap-like, projecting forward, located on both sides of head, origin at posterior region of head, between head and adjacent region of connection between head-foot and mantle. Left siphon long and broad, with secondary low fold connecting its right edge with right attachment between mantle and head-foot. Right siphon shorter and narrower than left siphon. Foot large, ample, dorso-ventrally flattened. Opercular pad large on dorsal posterior surface of foot. Anterior furrow of pedal glands narrow, borders thin, occupying almost entire anterior half of pedal margin. Columellar muscle broad, with lateral muscular expansions supporting connection of mantle border; very short (about 1/6 whorl), slightly longer at right.

Operculum (Figs.97-98, 151). Occupying entire aperture. Corneous, semi-circular, thick, flexible. Margins thin, sharp, almost circular, short expansion on inner-superior region. Nucleus almost central, slightly dislocated towards inner margin. From nucleus concentric growth lines. Inner surface smooth. Scar circular, large, close to inner margin.

Mantle organs (Figs.153-156). Mantle border thick, generally smooth, sometimes with series of small undulations at right; color homogeneous beige. Pallial cavity occupying about half whorl. Osphradium broad, elliptical, high, located in left region just posterior and parallel to mantle border.

Osphradium base a high, thick fold (stalk), elliptical in section. Osphradium filaments on tip of this basal fold; two series of thin, slightly triangular, septum-like filaments situated alternately in each side of tall, thin, fold-like, longitudinal, central axis (Figs.155-156). Lung large (about 1/3 of pallial cavity volume and area), outline approximately elliptical, dorso-ventrally flattened, walls thick, richly vascular, scarcely muscular. Lung vessels mostly transverse (from left to right), high, close to each other. Lung vessels connect anterior marginal vessel (from afferent gill vessel) with ctenidial vein (Fig.155). Pneumostome slit-like, margins muscular, located in anterior-left-ventral lung region, just posterior to left siphon. Gill long and narrow, slightly broader anteriorly, surrounding right and posterior lung margins from mantle border to left posterior end of pallial cavity, close to pericardium. Gill filaments triangular, slightly low, tips slightly right-central, somewhat displaced to right; right and left margins straight (Fig.156). Gill anterior end broadly pointed. Ctenidial vein narrow in anterior region, becomes broader short distance from its anterior end, where lung vessels connect (see below for more details). Pericardium, kidney and rectum (respectively) running along right margin of gill (Figs.153-154), with only anterior gill region free of these structures in females; in males this region occupied by penis shield. Gonoducts lying between rectum and right margin of pallial cavity; oviduct, when mature, dislocated ventrally. Pallial gonoducts described below.

Visceral mass (Fig.153). Globose, of about 4 whorls. Pericardium and kidney as anterior structures, bulge into pallial cavity. Stomach about 1/3 whorl posterior to pallial cavity. Digestive gland dark brown, almost black, surrounds stomach except for some ventral and dorsal areas. Gonad beige, located on digestive gland in superior and pericolumellar regions.

Circulatory and excretory systems (Figs.154, 157). Pericardium relatively large, located just posterior to left-posterior limit of pallial cavity, partly connected to pallial floor. Afferent gill vessel with branch crossing from right to left in anterior region of gill, running dorsal to gill and short distance beyond gill in pallial roof (Fig.155), and then as anterior border of lung. All lung drainage runs towards ctenidial vein, edging along left gill margin and right lung margin. Ctenidial vein connects with auricle just posterior to gill posterior end. Auricle somewhat short. Ventricle massive, almost spherical, posterior to auricle. Aortas located

posterior to ventricle; posterior aorta narrow; anterior aorta runs anteriorly on opposite side from posterior aorta. Just after separation of posterior aorta, lies anterior aorta bulb (ampulla), massive, walls muscular and thick, narrows after distance equivalent to ventricle length. Anterior aorta runs along haemocoel, with special branches in buccal mass region (see below). Kidney broad and ample (about half whorl), divided into 2 chambers. Posterior chamber most hollow, filled by intestinal loops (described below) connected to right surface by mesentery (Fig.157). Dorsal glandular lobe of kidney dorso-ventrally flattened, cream colored, surface almost uniform, covering dorsal wall of posterior chamber (disconnected from intestine). Anterior renal chamber ("ureter") slender and long, connected to posterior chamber by orifice at left; runs towards right attached to anterior edge of posterior kidney lobe and adjacent pallial roof, gradually narrows to pointed blind-sac. Inner surface of anterior renal chamber filled by two series of transverse septa, cream colored. Anterior series of septa larger and broader than posterior series and start between anterior and posterior renal chambers; posterior series of septa edging nephrostome. Both series of septa connected to central, longitudinal, dorsal fold. Nephrostome slit-like located in middle region between anterior and posterior renal chambers, separated from anterior renal chamber by posterior series of septa. Urinary gutter beginning ventral and at some distance from nephrostome as a tall fold, runs towards right; anteriorly attached to structures of right margin of pallial cavity, as oviduct-prostate and rectum, finishing close to right siphon.

Digestive system (Figs.158-169) – Buccal mass (Figs.159-161) large, occupies entire inner space of snout and about 1/3 remainder of haemocoel (Fig.158). Buccal sphincter (mc) ventrally thick and dorsally thin. Jaw muscles (mj) thick, origin in odontophore dorsal surface, insertion around mouth inside mc. Pair of jaw plates large and thick (Figs.150-160), outline elliptical, cutting-edge broad, composing anterior and median margins; small, broad projection in anterior region of median margin towards anterior. Pair of dorsal inner folds of buccal mass (Fig.160) broad and tall, surface with several superficial transverse furrows. Dorsal folds cover posterior margin of jaws, running towards posterior turning medially, covering a somewhat deep dorsal chamber. Dorsal chamber with several, longitudinal, low folds. Peri-buccal and odontophoral muscles (Figs.159, 161-167): m1)

jugal muscles, several small muscular fibers connecting buccal mass with adjacent region of haemocoel inner surface, more concentrated around mouth; m1a) dorsal protractor muscle of buccal mass, somewhat thin, origin in dorsal region of mouth runs posteriorly close to median line attached to surface of buccal mass, insertion in middle level of dorsal surface of buccal mass; m1b) two pairs of lateral protractor muscles of buccal mass, origin in lateral-dorsal region of mouth, run posteriorly edging latero-dorsal surface of buccal mass, insertion in posterior region of buccal mass, close to buccal ganglia; ma) pair of jaw abductor muscles, origin in several points of outer surface of jaw, runs immersed in mc and mj dorsally in 3 or 4 branches, after mc and mj, they unite as single pair, with insertion in adjacent region of dorsal-lateral surface of haemocoel; m2) pair of retractor muscles of buccal mass, origin in ventral-lateral surface of haemocoel adjacent to middle level of odontophore, run dorsally, by short distance to penetrate mj fibers, insertion in inner layer of longitudinal fibers of mj in three different and somewhat equidistant, small points, located in ventral and lateral region of jaw plates; m3) superficial, thin muscle immersed in membrane covering posterior region of odontophore, with transverse fibers just anterior to radular sac; m4) large pair of ventral tensor muscles of subradular membrane, origin in inner-posterior surface of odontophore cartilages (oc), most fibers of this muscle surrounding ventral and lateral surface of cartilages, connecting with cartilage on opposite side than their origin, some fibers surrounding posterior margin of cartilages, running from posterior to anterior region edging dorsal surface of cartilages, insertion along subradular membrane (br) and in posterior-inner surface of accessory cartilages; m5) pair of dorsal tensor muscles of radula, origin wide in m4 posterior-median outer surface, surrounding m4, running towards median and anterior, gradually narrowing, insertion in middle-dorsal region of radular sac preceding its exposed (in use) area in buccal cavity; m6) horizontal muscle, with transverse fibers, connecting dorsal surface of both cartilages, insertion at some distance from dorsal edge of cartilages (Figs.164, 166); m7) pair of very slender muscles, origin in posterior region of dorsal edge of cartilages, running posteriorly and ventrally, penetrating radular sac in region preceding its entrance in odontophore, insertion in ventral surface of radular sac like fan; m9) two pairs of

medial dorsal tensor muscles, anterior pair broad, flattened and thin, posterior pair narrower, origin in tissue (to) on middle region of radula (preceding buccal cavity), close to median line, running antero-laterally short distance to insert in posterior-dorsal edge of subradular membrane, also partly connected to adjacent outer surface of m4; m10) pair of ventral protractor muscles of buccal mass, narrow and thin, origin in ventral inner surface of mouth, run towards posterior lying ventral surface of buccal mass, insertion in postero-ventral region of odontophore close to median line, in both sides of radular sac; m11) pair of thin and long dorsal tensor muscles of subradular membrane, origin in ventral inner surface of haemocoel in region adjacent to middle level of odontophore, runs dorsally short distance, penetrate odontophore just anterior to radular sac, crossing dorsal to m7, insertion along ventral surface of subradular membrane close to median line (Figs.162, 166); m12) pair of narrow, short muscles annexed to m6 (Fig.167), origin in medial-anterior region of odontophore cartilages, just anterior to m6, running antero-laterally short distance, insertion in transition between subradular membrane and accessory cartilage just anterior to insertion of m4. Pair of odontophore cartilages large, flattened, outline elliptical. Pair of accessory cartilages thin, small, outline elliptical, in anterior-dorsal region of subradular membrane, just inside more protruded region of exposed part of radula. Subradular membrane (br) thin, strong and semi-transparent, covering inner surface of subradular cartilage, radular ribbon and adjacent areas. Subradular membrane margin mostly connected to dorsal surface of m4 pair, this pair working as tensor. Subradular cartilage forming expanded transparent projections of radula in buccal cavity, covering part of odontophore inside buccal mass. Radular sac short, little longer than odontophore. Radular nucleus broad, with pair of conspicuous blood vessels inserted in it, one terminal posterior and other ventro-anterior, this latter vessel running anteriorly along ventral surface of odontophore on median line. Radular teeth (Figs.115, 116): rachidian tooth short and broad, 7 stubby cusps, central cusps 2-3 times larger than neighboring cusps; pair of low and broad basal cusps; lateral tooth about 1.5 times broader than rachidian, curved inwards, with about 5 broad cusps, third cusp terminal and about 3 times larger than neighbor; inner marginal tooth tall, broad and flat, about same length as lateral tooth; tip bluntly

pointed, inner edge with conspicuous sub-terminal cusp, outer edge smooth or with up to 3 small, sub-terminal cusps; basal region with longitudinal concavity in outer edge where outer marginal tooth encased; outer marginal tooth tall, somewhat triangular, shorter and slender than inner marginal tooth, somewhat thick-longitudinal reinforcement along outer edge; tip sharp pointed and abruptly curved inwards, cusp small, sub-terminal on inner edge. Pair of esophageal pouches long, cylindrical, tip rounded, walls thin, located just posterior to buccal mass (Figs.159-161). Pair of inner dorsal folds of buccal mass abruptly narrowing in level of pouches and curving externally, penetrating into dorsal wall of pouches, at about half of pouches length, tapering gradually. Remainder of pouches inner surface smooth (Fig.160), apparently without glands. Anterior esophagus (posterior to pouches) narrow, short, inner surface with pair of broad longitudinal folds (originating from pouches folds) and some lower, narrower secondary folds. Middle esophagus very broad, bulging, walls thin, inner surface without folds. Pair of salivary glands massive, separated from each other, located just posterior to pouches. Salivary ducts in anterior region of glands, attached to dorsal surface of buccal mass, close to median line, passing through nerve ring, penetrating buccal mass wall in about middle level; to open lateral surface of anterior region of dorsal folds. Posterior esophagus long (about half of esophagus length), narrow, inner surface smooth. Stomach (Figs.168-169) large, spherical, with two chambers. Ventral chamber small, ventral wall thin, about five narrow ducts to digestive gland irregularly disposed in ventral surface. Dorsal chamber larger, walls thick, muscular, inner surface folded by muscle bundles. Ventral and dorsal gastric chambers separated from each other by tall, transverse, muscular septum (part of dorsal chamber walls); esophagus and intestine connected to both chambers. Columellar-gastric muscle well-developed, thick, origin in columellar surface of mantle in level adjacent to stomach (separated and posterior from columellar muscle), running antero-dorsally, penetrating between esophagus insertion and intestine origin, insertion spread in gastric dorsal muscular wall, more concentrated towards posterior. Esophagus insertion and intestine origin side by side in anterior-left stomach region. Intestine wide, inner surface smooth, running anteriorly and left to renal chamber, becoming exposed inside left-posterior region of renal chamber. Intestine abruptly turning

towards posterior-right, running parallel to preceding portion, surrounding posterior and right inner surface of renal chamber. Intestine bearing chamber occupying most of outer-left inner surface of this twisted portion, where it touches pericardium; intestine having constriction, in form of transverse fold (taller right), preceding this chamber; chamber forming blind sac positioned contrary to flow, bearing 5-6 secondary smaller, blind-sacs on outer surface. Intestine with three loops, connected to renal wall by mesentery, in middle level of right surface of renal chamber (Fig.157). Schematic representation (in ventral view) shown in figure 154. Anterior to loops, intestine running towards anterior, exiting to pallial cavity. Anus siphoned (*i.e.*, preceded by short unattached stalk of rectum), broad, with two inner successive edges covered by narrow longitudinal folds, located close to right siphon (Figs.153, 168, 170).

Genital system – ♂ (Figs.170-171): Testis lies on columellar surface of visceral mass, on digestive gland, at about three whorls since visceral apex. Visceral vas deferens narrow, runs in left (inferior) edge of testis last whorl. Vas deferens becomes thicker walled in pallial cavity, running at right of and close to rectum. Posterior to anus, vas deferens crossing over rectum, staying to left side of base of anus; where its abruptly expands as ejaculatory tube. Ejaculatory tube with loop along right wall of penis sac. Penis sac relatively large, located at left of anus; walls thin, aperture located anteriorly, turned to base of penis shield, this aperture preceded by long tubular region. From ejaculatory tube, vas deferens exits to penis sac T-shaped; anterior branch of this structure solid fold attached to dorsal wall of penis sac, preceding its aperture; Penis is posterior branch of that structure. Penis long, slender, intensely coiled, narrowing gradually; distal third very slender, about 10 times narrower than its base. Penis duct entirely closed (tubular), very coiled in penis base, gradually less coiled towards distal region. Penis duct aperture very small, in penis tip. Penis shield large (about 1/3 of pallial cavity volume), slightly triangular, located in superior (right) half of inner edge of mantle border, generally inside pallial cavity. Penis shield base very broad, thick, bulging due to basal gland. Basal gland aperture small, located in left-outer region of penis shield base. Penis shield gradually narrows, distal tip flat, with slightly rounded borders and central concavity. Penis shield furrow runs along central region of inner surface of shield, somewhat deep, small notch in right-basal region;

distal end of furrow Y-shaped, close to shield tip. No other penis shield gland detectable. ♀ (Figs.172-173): Visceral structures in similar location to corresponding structures of male (Fig.153). Ovary beige in color. Pallial structures not seen in details due to poor fixation. Relatively broad oviduct running at right of rectum for short distance and opening to large pallial oviduct. Pallial oviduct about ¼ of pallial cavity volume when mature; located at right and ventral to rectum, partly connected to pallial floor. Visceral oviduct inserts in right region of pallial oviduct. From this insertion broad, flat and coiled inner lumen starts, running towards anterior. Lumen immersed in capsule gland tissue. Albumen gland widely connected anteriorly to left side of posterior capsule gland, its lumen flat and broad, closed as blind-sac posteriorly. Pallial oviduct abruptly narrows in approximate anterior third level of pallial cavity as vaginal tube. Vaginal tube long, thick walled, circular in section, at right edge of rectum. Female pore small, papilla-like, at right of, and close to anus.

Nervous system – Nerve ring very similar to those described by SCOTT (1957) and BERTHOLD (1991) for other ampullariids. Hypoathroid, located in middle level of buccal mass. Both cerebral ganglia separated by long, thick commissure. Buccal ganglia large, located relatively close to median line in dorsal-posterior region of buccal mass, near bases of esophageal pouches. Statocysts with several small, iridescent, statoconia, located deeply in foot musculature, just ventral and slightly outside pedal ganglia.

Measurements of shells (in mm). MZSP 29522: ♀ #1, 42.0 by 35.8; ♀ #2, 38.6 by 31.1; ♂ #3, 37.9 by 33.1.

Distribution – Brazil, upper Amazon and upper Parana basins.

Habitat – On *Eichornia* and other aquatic plants of lakes and low flow rivers.

Material examined – BRAZIL - MATO GROSSO DO SUL: Passo do Lontra, MZSP 29522, 2♂, 3♀, 8 young specimens, MZSP 30758, ♀ (Figs.1-2) (Simone and Lipparelli cols., V/1993).

Discussion – The shell of *P. crosseana* is very similar to the sympatric and more abundant *P. canaliculata*. The two species are difficult to separate on shell characters alone. *P. crosseana*, however, is distinguishable by its elongated shell and generally uniform and paler color; although some exceptions occur. On the other hand, there are considerable

anatomical differences, as discussed in the comparison below. The simplest way for differentiate *P. crosseana* from *P. canaliculata* is by the penis shield features, which *P. crosseana* having flattened concave tip (Fig.170), while *P. canaliculata* has longer broad tip with an apical gland (Fig.205).

Pomacea curumim new species

(Figs.3-4, 57-60, 107-108, 117-118, 174-188)

Types – Holotype MZSP 30760. Paratypes – BRAZIL - PARÁ: Xingu River, Between Senador José Porfiro and Porto de Moz; 2°00'22.9-42.6"S 52°12'59-8"-13'04.6"W, MZSP 29844, 12 specimens (sta. AMZ94-52, Zanata and others, 08/XI/1994); 2°03'40.7"-04'15.4"S 52°14'43.5-47.4"W, MZSP 29845, 29 specimens (sta. LRP94-44, Rapp Py-Daniel and other cols., 08/XI/1994); 2°02'45.1"-03'24.8"S 52°14'56.2"-15'03.8"W, MZSP 29846 12 specimens (sta. LRP94-45, Rapp Py-Daniel and others cols., 08/XI/1994).

Type-locality – BRAZIL - PARÁ: Xingu River, Between Senador José Porfiro and Porto de Moz; 2°04'15"S 52°14'43.5"W (Rapp Py-Daniel and other cols., 08/XI/1994).

Diagnosis – Very small, globose shell, with large aperture. Lung reduced. Penis shield with single basal gland on right, an apical folded region, and notch in middle level.

Description

Shell (Figs.3-4, 57-60). Size small (up to 12mm), globose, outline almost circular but broader near to upper suture, color pale greenish beige. Periostracum thick, smooth or sometimes with axial or spiral striae in some areas. Spire small and low, eroded, about four low, convex whorls. Last whorl large, slightly long anteriorly and somewhat conical. Aperture elliptical, slightly long antero-posteriorly. Outer lip rounded, with cut edge. Inner lip concave in superior half, without callus; convex in inferior half, with cut edge. Siphonal region bluntly angular, shortly projected anteriorly. Umbilicus deep, narrow, simple.

Head-foot (Fig.174). Similar characters to those of preceding species but shorter antero-ventrally and broader laterally. Head very broad, tentacles lateral located. Columellar muscle very short and thick.

Operculum (Figs.107-108, 174). Similar attributes as those of preceding species, but slightly longer antero-posteriorly. Outer surface with uniform concentric striae. Nucleus at short distance from middle level of inner edge. Inner scar occupying

about 2/3 of inner surface, lie at short distance inner edge, and at some distance from remainder edges. Mantle organs (Figs.175-178, 187). Characters also similar to those of *P. crosseana*, distinctive or notable features following. Pallial cavity very short, less than half whorl. Penis shield occupies most of inner pallial space in males. Osphradium almost sessile, its base (stalk) in same level of mantle (Figs.175-177). Lung reduced, pneumostome very small pore. Gill proportionally large and straight; anterior end on mantle border or penis shield base (of males), just posterior to anterior end becomes broad, narrowing gradually. Gill filaments slightly low, curved to right, tip rounded. Ctenidial vein narrow. Between gill and right pallial structures narrow space.

Circulatory and excretory systems (Figs.178-179). Similar attributes as those of preceding species, with following distinctive features. Heart ampulla (of anterior aorta) almost spherical and short. Kidney dorsal lobe low, separated from intestinal loops, presenting 2 regions; posterior region narrow, transverse, with several transverse furrows, edges first intestinal loop; anterior region larger (about 4/5), covered by net of vessels intensely anastomosed, large vessel covers left side of connection with anterior lobe. Kidney anterior lobe short, broad, turned forwards, inner glandular folds similar to those of *P. crosseana*, but with an outstanding bulged portion preceding nephrostome. Intestinal loops inside kidney chamber described below.

Digestive system – Buccal mass and odontophore characters (Figs.180-183) similar to those of preceding species, with following differences and notes: outline shorter and circular; buccal mass in general dislocated slightly anterior to mouth; jaws with circular outline (Fig.182); (mj) thick, short, conic, (ma) pair thinner and simple, (m4) pair with wider portion free from odontophore cartilages in their median surface, (m6) with outer surface attached to adjacent inner surface of br, (m7) pair also connected to posterior-median extremity of odontophore cartilages, (m12) pair present. Radular teeth features similar to those of *P. crosseana* with following notable attributes (Figs.117-118): rachidian tooth proportionally larger, 5-7 cusps, central cusps about 1.5 times larger than neighbor cusps, pair of basal cusps oblique; lateral tooth as broad as rachidian, 3-4 cusps, second cusps terminal and about double than neighbor cusps; inner and outer marginal

teeth with larger sub-terminal cusp in inner edge and no cusps in outer edge. Esophageal characters, pouches and inner folds (Fig.182) similar to those of *P. crosseana*, except for continuous fashion of esophageal main folds in region of pouches aperture (without notch). Esophageal pouches with narrow dorsal inner fold each, connected to adjacent dorsal surface of esophageal main folds. Salivary glands fashion also similar to those of preceding species, except for aperture located in middle region of dorsal folds of buccal mass and with form of deep slit projected towards anterior. Stomach characters (Figs.186, 188) also similar to those of *P. crosseana*, including thick muscular walls, columellar-gastric muscle and inner transverse muscular septum. Stomach differs by smaller ventral chamber (with thin walls), and fewer ducts to digestive gland. Intestine initially very broad. Region adjacent to pericardium narrow, preceded by tall fold in its dorsal surface, fold posterior portion arched, transverse, lies ventral surface, finishes towards posterior protected by posterior portion (Fig.188). Remainder intestine runs somewhat similar to that of preceding species. In region of kidney broad and complex loop as shown in figure 179. Rectum broad and slightly short. Anus simpler, without double layer of papillate folds.

Genital system – ♂ (Figs.175, 187): Testis color cream, situated in upper region of digestive gland coils. Visceral and pallial vas deferens attributes similar to those of preceding species, except for broad expansion in region just at right from anus. Penis sac spherical, thin walled at left and thick muscular at right (penis base or ejaculatory tube). Penis sac amply opened in left edge towards penis shield base. Penis very shorter than that of *P. crosseana*, with relative uniform width along its length. Penis tip abruptly pointed. Penis shield very large (occupies most of pallial cavity inner space) and conic. Pair of penis shield glands, basal, dorsal gland massive, with location and aperture similar to those of *P. crosseana*. Other gland smaller, semi-spherical, located in right side just over base. Penis shield ventral groove deep, runs about along its center; notch in right side in middle region, where penis projects. Penis shield apical region slightly broad, most folded by transverse, successive, irregular furrows (mainly in ventral and right surfaces). Penis shield ventral groove runs very narrow and shallow at left side of apical folded region. ♀ (Figs.184-185): Visceral structures fashion similar to those of *P. crosseana*. Pallial oviduct massive, also of somewhat similar features

of preceding species. Visceral oviduct ends sub-terminally in sac-like bursa copulatrix, partially separated from remainder pallial oviduct by furrow. Bursa copulatrix flattened, broad, located along left side of pallial oviduct, connected to it in middle level. Capsule gland massive, its lumen irregularly coiled as shown in figure 185. Capsule gland lumen with 2 short coils anterior to bursa connection. Vaginal tube with about same length than capsule gland. Vaginal tube broad, walls relatively thin, inner surface with some longitudinal folds. Female pore small, at right and close to anus.

Measurements of shells (in mm) – MZSP 29845: ♂ 1, 8.9 by 9.1; ♂ 2, 8.8 by 7.8; ♀ 3, 9.2 by 8.2.

Distribution – For moment known in Xingu River (Above Amazon tributary), in region between Senador José Porfirio and Porto de Moz cities, Pará, Brazil.

Habitat – In clear, planar river, from 12.5 to 20m depth, 300 to 4000m distant from shore. Substrate sandy, rocky and forest.

Material examined – Types.

Etymology – The specific epithet refers to Tupy language, meaning small children (*curumim*). A reference to the small size in relation to normal large fashion of the other species.

Discussion – The species was initially interpreted as young samples of other species, after serial sections and exam of several specimens, the adult nature of the specimens was cleared. Complex pallial genital structures and full-developed gonad are present in most specimens, exceptionally larger than 10mm. The size and the less developed lung suggest a process of paedomorphosis. *P. curumim* is certainly the smaller known species of ampulariid. On the other hand, reduction of lung has been found in ampullariids from Lake Malawi (Africa) (BERTHOLD, 1990) with the explanation that the animals habitat is deep (1.5 to 90m) for they reach the surface.

Pomacea scalaris (Orbigny, 1835)
(Figs.5-9, 85-87, 119, 189-198)

Synonymy see CASTELLANOS & FERNANDEZ (1976: 14). Complement:

Ampullaria scalaris – ORBIGNY, 1835:31; 1843:369-371 (pl.50, figs.1-3) (see present figs.85-87); SCOTT, 1957:305-307 (pls.1, 3; pl.4, fig.5; pl.5; pl.6, fig.10; pl.7, figs.15-16; pls.10, 12; pl.13, fig.32; pl.22, fig.1); FIGUEIRAS, 1964:171; CASTELLANOS & FERNANDEZ,

1976:14-15 (pl.1, figs.1, 4, pl.2, fig.1; pl.3, fig.3);
MARTÍN, 1980:47-50 (fig.4).

Ampullarius scalaris – OLIVEIRA *et al.*, 1981:76.

Pomacea scalaris: – QUINTANA, 1982:111

Description

Shell (Figs.5-9, 85-87). Characteristic by a conspicuous shoulder in spire and last whorl. Color purple-brown, pale (almost white) between carina and suture. Other details in SCOTT (1957:305, pl.22, fig.1), CASTELLANOS & FERNÁNDEZ (1976:14).

Head-foot and operculum – Characters similar to those of *P. crosseana*. Other details in SCOTT (1957, pl.1).

Mantle organs (Figs.189-190, 193). Organization and features similar to those of *P. crosseana*, with remarks following. Osphradium on a stalk tall in right side and low in left side. Gill filaments narrow, pointed.

Circulatory and excretory systems (Fig.192) – Heart attributes like those of *P. crosseana*. Kidney features also similar to those of *P. crosseana*, except for following characters. Dorsal renal lobe tall, pale brown, covered by several vessels, strongly arched (edging intestinal loops mesentery). Anterior renal chamber relatively short (less than half of posterior renal chamber length). Inner organization of septa and folds similar to those of *P. crosseana*, except for longitudinal fold not connected to nephrostome edge.

Digestive system (Figs.191, 194-196) – Buccal mass characters similar to those of *P. crosseana*, remarkable features following. Jaw plates smaller, with circular outline (Fig.195). Dorsal folds with smooth surface; aperture of salivary glands located between their middle and posterior thirds. Dorsal chamber (between both dorsal folds) relatively deep. Odontophore muscles: ma, 2 narrow pairs; m4 pair with smaller area attached to inner surface of cartilages; m6 narrower; m10 pair narrow; m10a, a pair of broad muscles, origin in ventral surface of mouth, runs dorsal to m10, insertion in middle-ventral region of odontophore. Other details of odontophore in Scott (1957, pls.3-5, 7). Radular teeth characters similar to those of *P. crosseana*, with following distinctions (Fig.119): rachidian shorter, base somewhat triangular, 3-5 broad cusps, central cusps about 1.5 times larger than neighbor cusps, basal cusp narrow and oblique; lateral tooth little broader than rachidian, weakly curved inwards, 3-4 cusps, second cusps terminal and about 1.5 times larger than neighbor cusps; inner and outer marginal teeth slender and tall, longer than lateral tooth, inner marginal somewhat

broader than outer marginal tooth, tip narrowly rounded, sub-terminal cusp conspicuous, in inner edge [other details in Scott (1957, fig.10)]. Esophageal pouches and inner folds with characters similar to those of *P. crosseana*, except for broader pouches, with larger inner fold each (Fig.195). Stomach features also similar to those of *P. crosseana*, other details in Scott (1957, pl.10). Digestive gland brown in color. Intestinal loops inside renal chamber as shown in Fig.192. Anus with single layer of papillae.

Genital system – ♂ (Fig.198): Visceral and pallial structures with characters similar to those of *P. crosseana*, distinctive or notable features following. Testis beige in color. No bulged portion of vas deferens preceding anus. Penis sac with only 1/3 of its (posterior) walls thick. Penis sac aperture long tube, only opened in anterior end, close to penis shield groove base. Penis relatively short, uniform width along its length, apex pointed. Penis shield slightly conic, tip long, narrow, curved towards right. Other details in MARTÍN (1980, fig.4). ♀ (Fig.197): Visceral and pallial organs characters similar to those of *P. crosseana*, with following remarkable features. Visceral oviduct connects with pallial oviduct about in middle region of its ventral side. Bursa copulatrix immerse in capsule gland, insertion of visceral oviduct in its posterior-ventral region, connection with capsule gland lumen in its anterior-ventral region. Capsule gland lumen flat, irregular, connection with bursa narrow, abruptly expands and contours bursa dorsally, after certain distance from bursa connects in middle region of broad dorsal branch of capsule gland lumen. Ventral branch of capsule gland lumen connects with vaginal tube. Vaginal tube long, narrow, walls thick. Female pore small, at right from anus.

Central nervous system – Described in SCOTT (1957, pl.12).

Measurements of shells (in mm) – MZSP 29590 (Figs 5-6):33.0 by 29.0; (Figs.7-9): 48.6 by 47.7.

Distribution – Amazon and Paraná Macrobassins.

Habitat – In freshwater courses of low flow, under aquatic plants.

Material examined – Types - BOLIVIA: MNHN, 3 shells, syntypes. Ordinary material: BRAZIL - MATO GROSSO DO SUL: Passo do Lontra, MZSP 29590, 55 specimens (Simone and Lipparelli cols., V/1993).

Pomacea canaliculata (Lamarck, 1801)
(Figs.11-12, 88-89, 120-121, 199-205)

Synonymy see SCOTT (1957:299); CASTELLANOS & FERNÁNDEZ (1976:13). Complement:

Ampullaria insularum Orbigny, 1835:32; 1843:374-375 (pl.51, figs.1-2) (see present figs.88-89); MARTÍN, 1980:47-51 (figs.2, 6).

Ampullaria canaliculata – SCOTT, 1957:299-303 (pl.22, fig.3; pl.14, figs.34-35; pl.16, fig.42; pls.17-21); FIGUEIRAS, 1964:170; CASTELLANOS & FERNÁNDEZ, 1976:13 (pl.1, figs.3, 6; pl.3, fig.2); MARTÍN, 1980:47-52 (figs.1, 5).

Ampullarius canaliculata – OLIVEIRA *et al.*, 1981:78.

Pomacea canaliculata – ANDREWS, 1965b:71-91 (figs.1-5, 6b, 7b); QUINTANA, 1982:109; CAZZANIGA & ESTEBENET, 1984:213-222 (fig.1-6); BERTHOLD, 1989:143, 151, 153 (figs.2, 6e); CAZZANIGA, 1990:384-387 (figs.1-4); THIENGO *et al.*, 1993:68-70 (figs.1-6); THIENGO, 1995:66-68 (figs.2, 8-9, 14).

Types – See MERMOD (1952:88-89, fig.149).

Description

Shell (Figs.11-12, 88-89). Large, some specimens with about 100mm. Color pale to dark brown, with some spiral dark bands. Spire slightly short, suture deep. Other details in SCOTT (1957: 299) THIENGO *et al.* (1993, fig.1).

Head-foot and operculum. Characters similar to those of *P. crosseana*.

Mantle organs (Figs.199, 205). Features like those of *P. crosseana*, with succeeding distinctive or notable attributions. Osphradium similar to that of *P. scalaris*, but with taller filaments. Gill filaments narrower and pointed. Ctenidial-pulmonary vein separated into 2 parallel vessels in anterior $\frac{2}{3}$ of its length, close with each other, pulmonary branch dorsal and broader. These 2 vessels unite with each other and run as those of preceding species. Narrow ad-rectal sinus distinguishable. Other details in ANDREWS (1965b:figs.1-3).

Circulatory and excretory systems (Figs.202, 204) – Heart characters similar to those of *P. crosseana*, ampulla of anterior aorta broad. Kidney organization also similar to that of *P. crosseana*, distinguishing or remarkable features following. Dorsal renal lobe relatively small, surface most smooth, with deep notch adjacent to intestine loops; few and broad vessels present close to aperture to anterior renal chamber. Intestinal loops attributes inside renal chamber described below. Anterior renal chamber longer, with more septa, longitudinal

fold not directly attached to nephrostome wall. Urinary gutter of ordinary fashion. Other details in ANDREWS (1965b:figs.1b, 4-6)

Digestive system (Figs.200-204) – Buccal mass characters (Figs.200) comparable to those of *P. crosseana*, remarkable features succeeding. Size proportionally larger. Annex cartilages thinner and smaller. Jaw plates very large and thick, with small median-anterior projection. Dorsal folds broad, smooth, with long portion covering jaws. Odontophore muscles (Fig.200): m1a thinner; m1b as several thin pairs; ma as multiple, relatively narrower pairs; m3a pair of thin muscles with dorso-ventral fibers covering posterior surface of odontophore; m4 pair not so attached to inner surface of odontophore cartilages; m6 very thick; m7, m11 and m12 with insertions more anterior; m10 pair thick; m10c absent. Esophageal characters also similar to those of preceding species, including inner folds and pouches. Differs in taller esophageal folds posterior to pouches. Radular teeth attributes similar to those of *P. crosseana*, distinctions following (Figs.120-121): rachidian tooth broad and shorter, 5-7 cusps, central cusps about double than neighbor cusps, basal cusps weak; lateral tooth about as broad as rachidian, 3-4 cusps, second cusp terminal, broad, and several times larger than neighbor cusps; inner marginal tooth with about half weight and same length of lateral tooth, tip bluntly pointed, sub-terminal cusp in inner edge very small; outer marginal tooth about 3-4 times slender than inner marginal and encased in special concavity of outer edge of this tooth, tip sharp pointed, sub-terminal cusp small, in inner edge. Stomach features (Figs.201, 203) similar to those of *P. crosseana*, including gastric-columellar muscle, remarks following. Ventral chamber (with thin walls) very smaller, about 6 ducts to digestive gland. Gastric walls most thick muscular. Inner transverse muscular septum thick, with edges turned inwards. Intestine proximal portion relatively narrow. Digestive gland dark, almost black. Intestinal region adjacent to pericardium preceded by mosaic of several folds and chambers (Fig.201). Intestinal loops inside renal chamber complex, as shown in situ in figure 204. Anus with layer of papillae.

Genital system – ♂ (Fig.205): Testis beige, occupies last visceral whorls up to stomach. Pallial structures similar to those of *P. crosseana*, with following remarks. No bulged portion of vas deferens preceding anus. Penis sac with about $\frac{2}{3}$ thick; its posterior $\frac{1}{3}$ with thin walls. Penis sac aperture long tube edging thick penis sac portion,

ending in penis shield groove base; this tube with aperture all along its dorsal surface. Penis very long, narrows abruptly in its middle level, distal half very slender. Penis shield large (about half of mantle border width), almost cylindrical. Penis shield groove deep, notch in before distal third, evolved by apical gland. Apical gland only in ventral surface, with mosaic of irregular furrows and folds (Fig.205). Other details in LOPES (1956b, figs.30-46), SCOTT (1957, fig.42), THIENGO *et al.* (1993, figs.3-5), MARTÍN (1980, figs.1, 2, 5, 6), BERTHOLD (1989, fig.6e). ♀ : Adequate description in SCOTT (1957, figs.34-35); THIENGO *et al.* (1993, fig.6).

Measurements of shell – MZSP 29633: 54.7 by 50.5 (Figs.11-12).

Distribution – Amazon and Paraná Basins.

Habitat – In freshwater courses of low energy, under aquatic plants.

Material examined – Types - ARGENTINA: Rio de La Plata, MNHN, 2 shells, syntypes of *Ampullaria insularum* Orbigny. Ordinary material: BRAZIL - MATO GROSSO DO SUL: Passo do Lontra, MZSP 29633, 45 specimens (Simone and Lippareli cols., V/1993).

Pomacea lineata (Spix, 1827)
(Figs.13-15, 64-65, 74-84,
95-96, 122, 125-126, 206-214)

Synonymy see CASTELLANOS & FERNÁNDEZ (1976). Complement:

Ampullaria fasciata – SWAINSON, 1822:21 (pl.103) (*non* ROISSY, 1805 *nec* LAMARCK, 1819); SPIX (1827:3, pl.5, fig.2) (see present figs.81-82).

Helix lineata Spix, 1827:3-4 (pl.4, fig.4; pl.5, fig.2) (see present figs.79-80).

Ampullaria fingulina Spix, 1827:2 (pl.4, fig.4) (see present fig.83-84).

Ampullaria physis Hupé, 1857:67 (pl.12, fig.2) (see present fig.78).

Ampullarius lineatus – OLIVEIRA *et al.*, 1981:77.

Ampullaria testudinea Reeve, 1856 (pl.24, fig.114) (see present figs.74-75); SOWERBY, 1909:358; BAKER, 1913:660.

Ampullarius (Ampullarius) testudineus – MORRETES, 1949:68.

Pomacea lineata – THIENGO, 1987:564-568 (figs.1-21); 1995:66-68 (figs.1, 4-7, 11-13, 16-17).

Description

Shell (Figs.13-15, 64-65, 74-84). Medium size (up to 45mm). Outline globose. Color of spire dark brown, almost black; last whorl greenish brown

with about 8 spiral, dark brown bands. Spire moderately tall (about half of body whorl length), slightly pointed; about 5 convex whorls. Last whorl almost spherical or weakly broader in superior region. Protoconch of 2.5 smooth whorls. Border between protoconch and teleoconch gradual and inconspicuous. Sculpture almost absent, only series of spiral lines uniformly distributed, after 5-6 lines slightly taller line with hair. Aperture elliptical. Outer lip and siphonal region rounded. Umbilicus deep and narrow. Other details in THIENGO (1987, fig.1).

Head-foot and operculum (Figs.95-96). Features similar to those of *P. crosseana*. Head-foot color beige, with dark brown spots thorough exposed areas (except sole). Pedal gland furrow restrict to anterior sole edge.

Mantle organs (Figs.206, 210, 212). Similar features to those of *P. crosseana*, with following notable or differentiable characters. Osphradium on low stalk, relatively small, stalk slightly taller at right; osphradium base without edges covering filaments. Ctenidial and pulmonary veins separated from each other in anterior half (similar to those of *P. canaliculata*). Gill broader, shorter, and not so curved; its posterior end almost in middle region of pallial cavity posterior border. Gill filaments narrow, tall, tip slender and rounded, strongly curved towards right, tip blunt. Other details in THIENGO (1987, fig.17).

Circulatory and excretory systems (Figs.208, 211) – Heart and kidney characters similar to those of *P. crosseana*, remarks following. Heart proportionally smaller, ampulla about as large as ventricle. Anterior renal chamber broad and slightly short; internally 2 series of transverse septa separated by narrow longitudinal fold, all them restrict to dorsal surface. Nephrostome located in middle-posterior edge of this chamber. Posterior renal chamber broad and flat; dorsal renal lobe with circular outline, not attached to intestine, ventral surface covered by several anastomosed vessels. Connection between anterior and posterior renal chambers simple, protected at right by relatively broad vessel. Intestinal loops inside kidney chamber described below. Other details in THIENGO (1987, figs 6-8).

Digestive system (Figs.207-209, 211) – Buccal mass feature (Fig.207) similar to those described for *P. crosseana*, with following distinctive or remarkable attributes. Jaw plates very large. Aperture of salivary glands located about in middle region of

dorsal folds, edged by several small folds. Dorsal folds with strong transverse furrows. Dorsal chamber between these both folds relatively deep, 2 to 4 longitudinal, somewhat tall folds running up to anterior esophagus, where faint. Odontophore muscles (Fig.207): m3 as transverse cover edging radular sac entrance in odontophore, covers also m10 insertion; m10 pair very narrow; m11 pair inserted anterior, m12 pair broad. Radular teeth attributes similar to those of *P. crosseana*, notable as follows (Figs.122, 125-126): rachidian broad and shorter, 5-7 cusps, central cusps 3-4 times broader than neighbor cusps; lateral tooth about as broad as rachidian, 3-4 cusps, second cusps terminal and several times larger than remainder cusps, tip bluntly pointed; inner marginal tooth with about half of rachidian width and about same lateral tooth length, basal concavity (where outer marginal encases) conspicuous and lying about $\frac{2}{3}$ of tooth's length, tip sharp pointed, sub-terminal cusp small and at some distance from tip; outer marginal tooth with about half of inner marginal width and about its same length, slender, weakly sigmoid, tip sharp pointed, secondary cusp at short distance from tip. Accessory pair of cartilages very thin. Branch of anterior aorta irrigating odontophore (running with m11) presents muscular fibers in its walls. Esophageal inner folds and pouches characters similar to those of *P. crosseana*, except for presence of 3-4 tall folds between both longitudinal folds of each pouch. Stomach features (Figs.208-209, 211) also similar to those of *P. crosseana*, including strong gastric-columellar muscle, remarks following. Ventral gastric chamber (with thin walls) small, about 4 ducts to digestive gland. Transverse muscular septum tall, with edge turned inwards. Intestinal origin preceded by small dorsal diverticulum. Digestive gland almost black. Intestine initially broad, its region adjacent to pericardium preceded by pair of sac-like, thick walled chambers. Ventral chamber simple, small; dorsal chamber larger, with other 3 inner sub-chambers (Figs.209, 211). Intestinal loops inside renal chamber shown in Fig.208. Anus with simple layer of papillae.

Genital system – ♂ (Figs.210, 213): Visceral structures similar to those of *P. crosseana*, and described by Lopes (1956a) Thiengo (1987, figs.5, 9-10, 12-13). Testis pale beige. Seminal vesicle single, sac-like, small, located in posterior region of pallial vas deferens. Pallial vas deferens broad, wall thick glandular; anterior region narrower, connected to penis sac crossing ventral to rectum.

Bulged short portion of vas deferens preceding anus present. Penis sac antero-posteriorly long; anterior half solid, posterior half thin walled, its left edge bears tubular projection united to penis shield right base; this tubular projections presents longitudinal dorsal aperture. Penis very long and coiled, base broad, gradually narrows up to very slender end long distal region. Penis duct broad and highly coiled at penis base, becomes less coiled and narrower between basal and middle penis thirds. Penis shield very large, occupying more than half of mantle edge (free portion) length, and about half of pallial cavity volume. Gill finishes on penis shield left base. Penis shield form almost conical, basal half broad, basal gland large, with normal fashion of aperture at dorsal surface. Distal half marked by abrupt reduction between it and basal half, curved towards right. Middle gland small, elliptical, located in right edge close to central furrow, in middle shield level. Apical gland long, narrow, ventral surface transversally furrowed (more details in THIENGO, 1987). Notch between apical and middle glands, restrict to right edge. ♀ (Fig.214): General organizations similar to that described for *P. crosseana*, and well described by Thiengo (1987: figs.11, 15-16, 18-20). Remarks following. Ovary beige, relatively small, restricts to columellar surface of visceral whorls; ovary acina narrow, successively ramified, somewhat separated from each other. Pallial oviduct very large (more than half of pallial cavity volume when mature). Visceral oviduct very narrow, inserting in anterior end of seminal receptacle in middle level of pallial oviduct ventral surface. Seminal receptacle large and flat, with about half of pallial oviduct width and length, located in its ventral region immerse in glandular tissue. Seminal receptacle walls iridescent muscular, outline elliptical. Narrow projection of seminal receptacle runs from its posterior end, curving abruptly towards anterior, running at left from it at about its same length; this projection wall also iridescent muscular, finishes as blind-sac. Remainder lumen of pallial oviduct bearing several loops and flattened and arched chambers obeying a shape as represented in figure 214; origin narrow, sub-terminal, in anterior end of seminal receptacle projection. Albumen gland as first loop, located along left surface of pallial oviduct. Capsule gland occupying remainder regions of pallial oviduct, without clear separation of albumen gland. Vaginal tube originating in middle region of pallial oviduct right surface, running towards anterior separated from it. Vaginal tube broad, inner lumen

also broad, its posterior region with transverse, tall, thick folds situated alternately. Its anterior region (about 2/3 of its length) with longitudinal, tall and thick folds; lateral-right fold larger, its walls curves positioned with its free edge touching its base, forming secondary inner tube. Genital pore broad and low papilla, located at short distance and slightly anterior to anus.

Measurements of shells (in mm) – MZSP 27996: #1, 35.8 by 31.2; #2, 36.6 by 30.7. MZSP 31147: ♂ 1) 33.3 by 28.2; ♂ 2) 34.7 by 29.6; ♀ 3) 32.1 by 28.5; ♀ 4) 32.0 by 27.1; ♀ 5) 32.5 by 27.5 (photo); MZSP 32197, ♀ 2) 44.8 by 37.5 (larger specimen).

Distribution – Central America, Amazon and Paraná Macrobassins. Coastal basins of Paraíba to Alagoas; Fernando de Noronha oceanic island.

Habitat – Similar to those of preceding species. On streams of low flow, close to margins and under aquatic plants.

Measurement of shells (in mm) – MZSP 26684: #1: 41.8 by 37.2; #2: 35.5 by 31.2.

Material examined – Types: without locality, BMNH, 1 shell, holotype of *Ampullaria testudinea* Reeve. BRASIL; MNHN, 2 shells, syntypes (?) of *A. lineata* Spix of collection Ferussac (1837). PARAGUAY; NMHN, 2 shells, syntypes of *Ampullaria physis* Hupé. Remainder photos of Spix's types are courtesy of Dr. Silvana Thiengo, Fundação Oswaldo Cruz (Figs.79-84). Ordinary material: BRAZIL - PERNAMBUCO: Fernando de Noronha Archipelago; Atalaia Beach, MZSP 31147, 23 specimens (Simone, Souza Jr. and Martins cols., 18/VII/1999). PARAÍBA: Cabedelo, MZSP 27108, 1♂, 2♀ (A.C.C. Almeida col., IV/1989). ALAGOAS: Ponta Verde, Sonho Verde Beach, MZSP 32197, 23 specimens (Simone col., 16/VII/1989). BAHIA: Ilheus, Almada river, MZSP 26684, 2♂, 2♀, 6 shells (S.Thiengo col., 4/II/1984). SÃO PAULO: Guarapiranga Dam, near to OSEC, MZSP 27996, 11 specimens (P.Auricchio col., 21/V/1990).

Pomacea sordida (Swainson, 1823)
(Figs.16-17, 72-73, 99-100, 123-124, 215-222)

Ampullaria sordida Swainson, 1823 (pl.143) (no locality); PHILIPPI, 1851:38 (pl.10, fig.3); REEVE, 1856 (pl.3, fig.14); COUSIN, 1887:278; SOWERBY, 1909:357; TILLIER, 1980:24 (pl.2, fig.1).

Ampullaria intermedia Férussac, 1824 (pl.68, figs.1-2); 1827:135; ORBIGNY, 1835:31; 1837:371; HUPÉ, 1857:66.

Ampullaria autumnalis Reeve, 1856 (pl.4, fig.16).
Ampullaria melanicheila Reeve, 1856 (pl.5, fig.24)
(see present figs.72-73).

Ampullarius (Ampullarius) sordidus – MORRETES, 1949:67; OLIVEIRA *et al.*, 1981:76.

Pomacea sordida – LOPES, 1955:208-210 (figs.17-23); QUINTANA, 1982:111; THIENGO (1989:351-355, figs.1-9).

Description

Shell (Figs.16-17, 72-73). Adequate description in Thiengo (1989, 352, fig.1), characteristic by flatter fashion and an ampler umbilicus.

Head-foot and operculum (Figs.99-100). Similar features as those of *P. crosseana*.

Mantle organs (Figs.215-216, 218). Organization similar to that described for *P. crosseana*, with following remarks. Osphradium proportionally smaller, its basal, stalk-like portion low, lacking marginal fold covering base of filaments. Lung ampler, occupying about half of pallial roof area. Ctenidial vein separated into 2 in its posterior $\frac{1}{3}$, bearing pulmonary vein (although this vein apparently also receives gill blood flow). Gill weakly curved. Gill filaments tall; rod narrow, extending beyond filament; tip rounded.

Circulatory and excretory systems (Fig.217) – Both with similar fashion than that described for *P. crosseana*, with following remarkable features. Heart large, about half of kidney volume. Auricle with secondary connection to anterior-inner surface of pericardium, at right from ctenidial vein insertion. Aortas and ampulla connected to adjacent dorsal surface of pericardium. Anterior renal chamber broad and slightly short; internally 2 series of transverse septa separated by narrow longitudinal fold, all them main connected to dorsal surface and also reaching ventral surface. Nephrostome located in middle-posterior edge of this chamber. Connection between anterior and posterior renal chambers simple, protected at right by relatively broad vessel. Posterior renal chamber with tall renal dorsal lobe, this lobe covered by conspicuous, branched, anastomozed vessels. Intestine free from renal lobe.

Digestive system – Foregut characters similar to those of *P. crosseana*, remarks following. Dorsal chamber (between both longitudinal dorsal folds of buccal mass) with 4 longitudinal secondary folds that faint along anterior esophagus. Odontophore muscles (Figs.219, 221): m1b, generally composed by 3 narrow pairs; m1d, pair parallel to m1b, but insertion more

posteriorly, in lateral-posterior region of buccal mass dorsal surface; m3 transverse, slightly thick, covering radular sac; m6 short and broad. Pair of pouches with dorsal inner fold having highly irregular surface, and lacking any longitudinal fold. Radular sac short, extending little beyond odontophore. Radular teeth of similar attributes as those of *P. crosseana*, notable features following (Figs.123-124): rachidian tooth with rectangular outline, 7 cusps, central cusp with about twice neighbor cusps size; lateral tooth with about 1.5 times rachidian width, 3 cusps, middle cusps terminal and several times larger than remainder cusps. Mid and hindgut features (Figs.215, 220) also similar to those of *P. crosseana*, distinctions following. Posterior region of esophagus smooth internally. Stomach ventral chamber very small (about $\frac{1}{10}$ of dorsal chamber). Transversal septum low and restrict to ventral surface. Gastric walls slightly thinner muscular. Gastric muscle narrower. Digestive gland very dark, almost black. Intestine origin with smooth inner surface. Intestinal chambers in its region crossing pericardium double (Fig.220), proximal chamber transverse and ventral, its blind-sac, narrow distal end located inside aperture of distal chamber; distal chamber longitudinal and dorsal. Remainder intestine inner surface with several transverse, low folds. Intestinal loops inside renal chamber particularly complex, obeying pattern showed in situ in figure 215.

Genital system – ♂ (Figs.215, 222): Visceral and pallial structures organized similarly to those of *P. crosseana*, differing by following features. Testis pale beige lying along superior and columellar surfaces of visceral whorls, finishing half whorl posterior to pallial cavity. Pallial vas deferens thick walled (prostate) and somewhat conical; in its anterior end abruptly narrows and connects with penis sac crossing dorsal to rectum. Penis sac almost circular, its projection connected to penis shield almost as broad as penis sac. Penis sac anterior $\frac{1}{3}$ solid, posterior $\frac{2}{3}$ thin walled. Penis sac projection opened longitudinally along its dorsal surface; this aperture protected posteriorly by low fold originated from penis base. Penis of moderate length and coil degree, base broader, narrows gradually up to very slender apical region. Penis duct also with moderate degree of coiling. Penis shield broad; tip blunt, thick, curved towards right. Basal penis shield gland with aperture located in its dorsal-left side and presents normally 3 closely located slits. Secondary small gland located ventrally in right edge of penis shield base. Notch of penis shield furrow located in its middle level. Apical gland very large, composed by 5-7 successive broad

folds lying along left edge of shield. Groove, coming from penis shield longitudinal furrow, surrounds basal edge of this apical gland, runs along dorsal surface of this gland and finishes broadly opened in middle region penis shield apex. More details in LOPES (1955, figs.19-23) and THIENGO (1989, figs.4-7). ♀ : See description of Thiengo (1989, figs.8-9). Ovary, like digestive gland, almost black. Vaginal tube somewhat narrow, inner surface with some longitudinal, irregular, tall folds. Female pore a sub-terminal, ventral, transverse slit, located at right from anus.

Central nervous system – Features similar to those described for preceding ampullariids, except for lateral position of buccal ganglia.

Measurements of shells (in mm) – MZSP 32195: ♀ 1) 44.8 by 38.6; ♂ 2) 32.8 by 31.9.

Distribution – Bolivia, Brazil (RJ, SP, PR, SC), Paraguay, La Plata River (Argentina).

Habitat – Among aquatic plants of low-flow streams.

Material examined – Type: without locality, BMNH, 1 shell, holotype of *Ampullaria melanocheila* Reeve. Ordinary material: BRAZIL - RIO DE JANEIRO: Silva Jardim, MZSP 32195, 1♂, 2♀ (S.Thiengo col. and leg, X/1999).

Pomacea bridgesi (Reeve, 1856)
(Figs.18-21, 67-71, 127-128)

The study on this species has been published in a separated paper: THIENGO & SIMONE, in press. However, the data on *P. bridgesi* have been included in the present analysis. Some shells are shown in the present paper (Figs.18-21, 67-71) including some type specimens, and radular SEM pictures (Figs.127-128).

Genus *Asolene* Orbigny, 1837
Type-species – *Helix platae* Maton, 1809
Asolene megastoma (Sowerby, 1825)
(Figs.23-24, 90, 129, 223-229)

Synonymy see CASTELLANOS & FERNÁNDEZ (1976:18). Complement:

Ampullaria neritoides Orbigny, 1835:31; 1843:368-369 (pl.49, figs.1-2) (see present fig.90).

Asolene (Pomella) megastoma – SCOTT, 1957 (pl.2; pl.4, fig.6; pl.7, figs.17-18; pls.8-9; pl.11, fig.29; pl.13, fig.33; pl.14, fig.36-37; pl.15; pl.23, fig.9); CASTELLANOS & FERNÁNDEZ, 1976:18 (pl.1, fig.2; pl.4, fig.5); OLIVEIRA *et al.*, 1981:76.

Pomella megastoma – FIGUEIRAS, 1964:173.

Description

Shell (Figs.23-24, 90): very large (about 100mm). Spire short, almost plane. Aperture very ample. Umbilicus lacking. Other details in Scott (1957:314-315, pl.23, fig.9), CASTELLANOS & FERNÁNDEZ (1976:18).

Head-foot and operculum (Fig.223). Characters similar to those described for *P. crosseana*. Distinctive features following. Form very broad, head relatively small. Snout somewhat an inverted cone, base narrow. Lobes (siphons) relatively short. Tentacles broader in base.

Pallial organs (Figs.224-225). Similar features to those of *P. crosseana*. Except for osphradium peduncled; osphradium base short and smaller (about half of osphradium area). Gill filaments narrower. Other details in SCOTT (1957, fig.20).

Circulatory and excretory systems – Heart attributes similar to those of *P. crosseana*, but with auricle connected to anterior wall of pericardium. Kidney closely similar to that described for *P. canaliculata*. Dorsal renal lobe thick, brown, surface with irregular folds, most converging to aperture of anterior lobe; no connection with intestine. Anterior lobe long, broad, with 2 series of thick septa, pale beige, separated by longitudinal, tall fold. This longitudinal fold ventral edge free, connects only with nephrostome anterior edge. Intestinal loops inside kidney described below.

Digestive system – Buccal mass and odontophore muscles characters (Fig.226) similar to those of *P. crosseana*, but with most structures thicker and proportionally larger, including jaw plates. Some distinctive and notable features follow. Odontophore muscles: m1a thick; ma pair multiple; m3a pair, transverse portion anterior to radular sac covers m9; m7 pair origin located in postero-median margin of odontophore cartilages; m10 pair insertion part in m4 and part in m5, on their anterior surface (other details of odontophore in Scott, 1957, pls.7-9). Dorsal folds with very irregular-folded surface. Radular tooth similar to those of *P. crosseana*, with following remarks (Fig.129): rachidian broad and shorter, smooth cut-edge lacking cusps except broad, blunt central projection, basal cusps long and oblique; marginal tooth about as broad as rachidian, slightly sigmoid, broadly pointed tip lacking secondary cusps; inner marginal tooth 2-3 times broader than inner marginal tooth, both with very small, sub-terminal cusps in inner edge. Pair of pouches longer, inner surface with pair of opposite located longitudinal

folds, being dorsal folds broader. Esophagus characters (Fig.226) also similar to those of *P. crosseana*, except for thicker muscular walls. Stomach features (Figs.227-228) also similar to those of that species, including columellar-gastric muscle and transverse muscular septum. Differs by smaller ventral chamber (with thin walls), bearing 4-5 ducts to digestive gland close with each other; and by transverse muscular septum presenting taller edge turned inwards. Intestine initially broad, inner surface smooth. Intestinal portion adjacent to pericardium preceded by 2 chambers with aperture turned towards stomach; dorsal chamber as small, simple blind sac; ventral chamber larger and more complex, located just proximal to dorsal chamber, bears 3 distal flat ramifications (Fig.227). Digestive gland dark brown, with about 3 whorls posterior to stomach. Intestinal loops inside of kidney chamber as shown in situ in figure 227, complex, wholly connected by mesentery. Rectum narrow. Anus small, with simple borders.

Genital system – ♂ (Fig.224): Visceral and pallial structures with characters similar to those of *P. crosseana*. Distinctive or notable features following. Gonad pale cream, in columellar side of first visceral whorl. No broad region of pallial vas deferens by side of anus. Penis very slender and convolute, basal half folded by successive transverse furrows. Penis distal half narrowing gradually. Penis tip very slender. Penis sac anterior half very thick walled, posterior half very thin walled. In this posterior half dorsal fold runs from penis base to aperture of this chamber. This aperture broad, edged ventrally by thick fold with coiled distal border. Penis shield conic, very large (occupies most of pallial cavity and about half of mantle border length). Basal penis shield gland and aperture similar to those of *P. crosseana*, no other detectable basal glands. Penis shield ventral groove narrow, deep, running approximately along central region; secondary, smaller, oblique groove present at left. Penis distal region with irregular folded, massive, elliptical gland restrict to ventral side; main and secondary penis shield grooves converge in proximal margin of this distal gland and edge it in its left-proximal border. Other details in SCOTT (1957, pl.15). ♀ (Fig.229): Visceral and pallial organs similar in characters to those of *P. crosseana*. Pallial oviduct very massive, greatly bulging inside pallial cavity. Visceral oviduct connects with bursa copulatrix in middle level of left pallial oviduct side. Bursa copulatrix, just after visceral oviduct insertion, elliptical and circular in

section; bears flat, posterior, somewhat same lengthened expansion towards posterior, at some distance from visceral oviduct insertion. Capsule gland lumen flat, sinuous, complex; coils as shown in figure 229. Insertion of bursa narrow, located approximately between middle and posterior thirds of capsule gland region. Capsule gland connection with vaginal tube located approximately between middle and anterior thirds of capsule gland, towards ventral. Vaginal tube broad, walls thick, inner surface smooth, length about half of that capsule gland. Female pore small, papilla-like, located close to and at right from anus. Other details in SCOTT (1957, pl.14, figs.36-37).

Measurements of shell (Figs.23-24) – 83.0 by 87.0.

Distribution – Uruguay River (RS, Brazil; Argentina, Uruguay).

Habitat – In rivers with some degree of flow energy.

Material examined – Types - URUGUAY: Uruguay River, MNHN, 1 shell, probable holotype of *Ampullaria neritoides* Orbigny. Ordinary material: BRAZIL: Uruguay River; RIO GRANDE DO SUL: Itaqui, MZSP 250, 2♂, 8♀ (E.Garbe col., 1915).

Genus *Felipponea* Dall, 1919

Type-species:

Ampullaria (Felipponea) neritiniiformis Dall

Felipponea neritiniiformis (Dall, 1919)

(Figs.130, 230-231)

Synonymy see CASTELLANOS & FERNÁNDEZ (1976:19). Complement:

Felipponea neritiniiformis – SCOTT, 1957:317-318 (pl.6, fig.14; pl.23, fig.10); FIGUEIRAS, 1964:173; CASTELLANOS & FERNÁNDEZ, 1976:19 (pl.2, fig.5; pl.5, fig.15).

Asolene neritiniiformis – OLIVEIRA *et al.*, 1981:76.

N.B.: VAZ & MARTINS (in press) have provided a whole description of this species in a submitted paper. The present description is greatly reduced, restrict to some aspects only. Complementary data must be reported to that paper.

Shell. Relatively small (about 30mm). Color pale greenish beige to brown, frequently with spiral dark bands. Spire tall, eroded. Umbilicus very narrow. Other details in DALL (1919:10-11), SCOTT (1957:317-318), CASTELLANOS & FERNÁNDEZ (1976:19).

Head-foot. Similar to *A. megastoma*, but not so broad. Head narrower. Siphons (nuchal lobes) formed by low folds (not so tall as those of *Pomacea* spp).

Pallial cavity (Fig.231). Osphradium elliptical, almost sessile (stalk very short and broad).

Circulatory and excretory systems – Heart with anterior aorta ampulla similar to those of preceding species.

Digestive system – Buccal mass and odontophore muscles characters very similar to those of *A. megastoma*, including m3a as fold covering radular sac, m10 pair long and narrow; differs by ma as single pair and by narrower m1 pairs. Jaw plates, dorsal folds, esophageal pouches and folds similar in features as those of *A. megastoma*. Radular teeth features similar to those of *P. crosseana*, with following remarks (Fig.130): rachidian longer, outline almost square, 5-7 small cusps, central cusp about 1.5 times larger than neighbor cusps, basal cusp weak, somewhat longitudinal; lateral tooth about as broad as rachidian, 3-4 small cusps, first cusp terminal, second cusp about 3-times larger than neighbor cusps; inner marginal tooth with about double of outer marginal tooth width, both with tip sharp pointed and sub-terminal cusps in inner edge somewhat long (other details in SCOTT, 1957, pl.23, fig.10). Stomach characters similar to those of *A. megastoma*, except for thinner muscular gastric walls and by transverse muscular septum lacking long edge turned inwards. Intestinal region adjacent to pericardium preceded by pair of small, dorsal, sac-like chambers with aperture towards posterior. Intestinal loops inside renal chamber shown in figure 230.

Genital system – ♂ : Penis shield somewhat similar to that of *P. lineata*, but with shorter tip lacking glands. Pair of glands in base of penis shield, being right gland smaller and more superficial. Penis shield furrow relatively deep, running almost all along its length. ♀ : Pallial oviduct proportionally large, with features similar to those of *A. megastoma*. Vaginal tube broad, walls glandular, origin about in half level on capsule gland.

Material examined – BRAZIL - PARANÁ: Ivaí River, Floresta, MZSP 29713, 5 specimens, MZSP 30759, 5 specimens (A.L.Falavigna col.).

Genus *Marisa* Gray, 1824

Type-species: *Helix cornuarietis* Linné, 1758

Marisa planogyra Pilsbry, 1933

(Figs.22, 25-28, 101-102, 131-132, 232-241)

Synonymy see SCOTT (1957:321). Complement: *Marisa planogyra* – SCOTT, 1957:321-322 (pl.23, fig.8); CASTELLANOS & FERNÁNDEZ, 1976:21

(pl.2, fig.6; pl.5, fig.16-17); MARTÍN, 1980:47-50 (fig.3). OLIVEIRA *et al.*, 1981:78; MELLO, 1988:7-13 (figs.1, 3a-e); MELLO & MARINI, 1995:70-71 (fig.1).

Description

Shell (Figs.22, 25-28). Practically planispiral, with apex slightly dislocated to left. Aperture relatively small, elliptical. Other details in SCOTT (1957:321-322), CASTELLANOS & FERNÁNDEZ (1976:21). Color usually pale beige, with dark brown spiral bands, however, some uniform colored specimens occur (Figs.22, 25-27).

Head-foot (Figs.234, 237). Characters somewhat similar to those of *P. crosseana*, distinctive features following. Form relatively narrower laterally and longer antero-posteriorly. Anterior furrow of pedal gland restricted to anterior foot edge. Lobes (siphons) also long; right siphon with longer longitudinal fold running along floor of pallial cavity. Columellar muscle very longer, thinner and flattened, about 1 whorl length.

Operculum (Figs.101-102, 234). Also of similar characters than that of *P. crosseana*, except for more rounded outline.

Pallial cavity (Figs.232-233, 235). Narrow and deep (about $\frac{3}{4}$ whorl). Organs arrangement somewhat similar to that of *P. crosseana*, with following distinctive or notable features. Osphradium small, elliptical, on short stalk. Lung narrow and very long, almost as long as pallial cavity. Inner lung surface with transverse vessels like those of *P. crosseana*. Pneumostome an oblique, muscular edged slit located close to anterior-left region of lung ventral surface. Gill narrow and long, edges entire lung right margin. Gill filaments short, relatively broad, right margin slightly straight, left margin convex, apex rounded. Between gill and rectum a relatively narrow space, but broader as those of preceding species.

Circulatory and excretory systems (Fig.236) – Heart relatively small and narrow. Auricle just posterior to pallial cavity posterior end. Ventricle posterior to auricle. Anterior aorta ampulla broad and long. Kidney features somewhat similar to those of *P. crosseana*, with following distinctive or interesting attributes. Renal dorsal lobe slightly thin, dark brown, surface with some irregular-sized vessels; one of this vessels broader, connected to right edge of aperture to anterior renal chamber. Renal dorsal lobe free from intestine. Anterior renal chamber conic, narrow and short (about half of remainder kidney length). Anterior renal chamber with 2

same-sized dorsal series of transverse septa, separated by a tall, dorsal, longitudinal fold; this longitudinal fold not connected to nephrostome edges. Urinary gutter also similar of those of preceding species but longer; at some distance from mantle border abruptly twist and run in floor of pallial cavity (Figs.232-233).

Visceral mass (Figs.233, 236) – Length about same than that of pallial cavity, about 2.5 planispiral whorls. Stomach and adjacent digestive tubes occupy last half whorl. Gonad located in first half whorl, extending little beyond this by outer surface. Remainder visceral space occupied by dark brown digestive gland.

Digestive system – Buccal mass, odontophore muscles and esophageal characters similar to those of *P. crosseana*, distinctive or remarkable features following (Figs.237-238). Jaw plates thinner. Odontophore muscles (Fig.238): ma in 2 narrow pairs; m4 pair not attached to inner surface of odontophore cartilages (only covering them) and constituted by 2 thick layers (fused with each other laterally), also connects with tissue preceding exposed part of radula (to) via m9; m5 pair thicker and shorter; m10 pair narrower; m12 pair broader. Accessory pair of cartilages softer and thinner. Radular teeth attributes similar to those of *P. crosseana*, with following remarkable notes (Figs.131-132): rachidian shorter, 7-9 tall and broad cusps, central cusp larger (about double than neighbor), remainder cusps decreasing towards lateral, pair of basal cusps narrow, low and oblique; marginal tooth strongly curved inwards and distally, 3-4 large and tall cusps, second cusp terminal and about double sized than neighbor cusps, conspicuous longitudinal, middle reinforcement in basal half; inner and outer marginal teeth tall slender, terminally curved, similar with each other (inner slightly broader than outer marginal tooth), both several times narrower than marginal tooth, tip pointed, sub-terminal cusp with about half of tip size. Esophagus uniformly narrow (without bulged posterior portion). Esophagus inner surface with about 6 longitudinal, slightly tall folds all along its length. Stomach with similar attributes as those of *P. crosseana*, including gastric-columellar muscle, distinctive features following (Figs.239-240): gastric muscular wall very thinner; transverse muscular septum absent; low longitudinal fold separates gastric chamber into esophageal and intestinal portions, inserts in posterior region of gastric-columellar muscle. Single duct to digestive gland bifurcating

at short distance from its origin, running towards opposite side. Intestine initially broad, inner surface smooth except for pair of shallow, dorsal diverticles in its limit with stomach. Intestinal portion adjacent to pericardium preceded by pair of small, sac-like chambers with apertures towards posterior; each chamber aperture edged by thick border, left chamber encased inside aperture of right chamber (Fig.239). Remainder intestine slightly narrow, running somewhat similar to that of *P. crosseana*. Intestinal loops inside renal chamber showed in situ in Fig.240. Rectum narrow and very long. Anus simple, small.

Genital system – ♂ (Figs.232-233): Testis cream in color, located in posterior end of visceral mass first whorl. Visceral vas deferens very narrow, lying in columellar surface of visceral whorls. Pallial vas deferens also narrow and very long, lies at right from rectum. Genital organs close to mantle border, with organization somewhat similar to those preceding species. Pallial vas deferens crosses dorsal to pre-anal region of rectum without bulged portion. Penis sac most with thin walls, very short portion with thicker walls in penis base. Penis relatively short, width uniform along its length, narrows at short distance from pointed apex. Penis sac amply opened in left region, in penis shield base. Penis shield conic, large (about half of mantle border width). Basal gland situation and aperture similar to those of preceding species. Pair of small glands in each side of basal half of penis shield, being right gland smaller and more superficial. Penis shield groove relatively shallow, runs about in central region of shield ventral surface. Penis shield groove with secondary fold in its basal-right region coming from penis sac aperture. Penis shield groove runs almost entire shield length, finishes at some distance from shield tip. Penis shield distal half narrowing gradually, conspicuous notch at right located approximately in middle shield level. Penis shield slightly pointed, lacking glands. Other details in Mello (1988: 8-12, fig.1), Martín (1980, fig.3). ♀ (Fig.241): Pallial oviduct somewhat similar to those of preceding species, but smaller and narrower. Visceral oviduct inserts sub-terminally in bursa copulatrix, inside pallial oviduct mass. Bursa copulatrix conic, long, inserts in capsule gland lumen between its middle and posterior third parts. Bursa immersed in capsule gland. Capsule gland lumen flat and as blind-sac in posterior third, remainder intensely coiled (Fig.241). Vaginal tube narrow and very long (about twice capsule gland length), runs at right from urinary gutter and rectum. Female genital pore

small, at right and close to anus. Other details in MELLO (1988:12, figs.1a-e).

Measurements of shells (in mm) – MZSP 29673: ♂ 1, 11.7 by 32.0; ♂, 12.0 by 30.0; ♀ 2, 11.0 by 28.8.

Distribution – Paraná Macrobasin, central South America.

Habitat – Between *Eichornia* and other aquatic plants.

Material examined – BRAZIL - MATO GROSSO: Poconé, MZSP 29674, 15 specimens (L.S.Rocha col., 28/III/1997). MATO GROSSO DO SUL: Passo do Lontra, MZSP 29673, 2♂, 2♀, 1 shell (Simone and Lipparelli cols., V/1993).

Discussion – *M. planogyra* is very close related to *M. cornuarietis* (Linné, 1758), from which is very difficult separated conchologically. The anatomical differences between both species are neither well explored, except for study on their genital system (MELLO, 1988). That paper convincingly provides data for specific separation in the penis shield glands (*M. planogyra* has 2 glands, while *M. cornuarietis* 4 glands) and length (*M. cornuarietis* longer). Based on that paper, the specimens studied herein are all *M. planogyra*. Sexual dimorphism has been found in shell and foot color in *M. cornuarietis* specimens (Demian & Ibrahim, 1972).

Superfamily Cyclophoroidea

Family Cyclophoridae (=Potieridae, Amphicyclotidae)

Genus *Neocyclotus* Fischer & Crosse, 1886

Type-species: *Cyclostoma dysoni* L.Pfeiffer

Neocyclotus prominulus (Orbigny, 1840)

(Figs.29-31, 91-94, 109-111, 133-134, 242-258)

Synonymy see KOBELT (1902:238). Complement: *Cyclostoma prominula* – ORBIGNY, 1846:362-363 (see present figs.91-94).

Neocyclotus prominulus – KOBELT, 1902:238; MORRETES, 1949:65.

Incerticyclus prominulus – TORRE *et al*, 1942:277 (p1.39, fig.7-9).

Aperostoma (?) *prominula* – MORRETES, 1953:47.

Description

Shell (Figs.29-31, 91-94). Size small (up to 15mm), discoid and flattened. Spire small, low. Suture deep, each whorl circular in section. Sculpture successive, uniform axial threads. Other details in KOBELT (1902:238), TORRE *et al*. (1942:277).

Head-foot (Figs.242, 245). Head little projected (almost inlaid). Snout stubby, most sessile, low. Mouth longitudinal, in anterior-dorsal snout surface. Pentacles shorter than snout, base at side

and posterior to snout base. Ommatophore short, located about in middle level of outer tentacle surface. Eyes small, dark. Foot thick, relatively small. Furrow of pedal gland edging entire foot sole, deeper anteriorly. Columellar muscle very thick and short (about $\frac{1}{3}$ whorl). Columellar muscle distal end somewhat bifid, with right branch flatter and taller. Males with exophalic penis located just posterior to right tentacle (described below).

Operculum (Figs.109-111, 242). Outline circular, calcareous, thick, edge double (Fig.111). Nucleus central, smooth; multispiral shallow furrow originated from nucleus. Outer surface opaque. Inner surface glossy, low projection central, from which scar turns around in growth (seen by previous scars). Inner scar rounded, with about $\frac{1}{4}$ of opercular area.

Mantle organs (Figs.243-244, 246-247). Pallial cavity of about half whorl, relatively narrow. Mantle border thick, simple. Osphradium and gill lacking. Broad vessel (probably homologous to ctenidial vein) edges left margin of pallial cavity, anterior region with 2 branches (being collar vessel one of them), becomes broader towards posterior, inserts in left extremity of pericardium. Pericardium and kidney as left-posterior limits of pallial cavity. Between left vessel-kidney and rectum a broad smooth area without large transverse vessels (between kidney and rectum a narrower area). Rectum very broad (about $\frac{1}{2}$ of pallial cavity width), edging pallial cavity right border, abruptly narrows, Anus small, shortly siphoned, close to right end of mantle border. Pallial oviduct and prostate located between rectum and right border of pallial cavity, displacing it towards left (both described below).

Visceral mass (Figs.246-247). About 2.5 whorls in length. Kidney and pericardium as left-anterior limit; pallial gonoducts and rectum as right-anterior limit. Gonad located in first whorl outer surface, covering small portion of digestive gland. Stomach large and long, with about half whorl in length, half whorl posterior to pallial cavity. Stomach separates almost completely digestive gland into posterior and anterior branches, being connected with each other by thin and narrow ventral portion. Last half whorl of visceral mass filled by digestive gland (posteriorly) and intestinal loops (anteriorly). Other details below.

Circulatory and excretory systems (Figs.244, 247-248) – Heart relatively small, located behind to left-posterior corner of pallial cavity. Narrow vessel edges anterior surface of kidney, entrance into

pericardium and inserts in auricle. Auricle and ventricle small, connected with each other by narrow and short tube, Auricle at right and slightly anterior to ventricle. Aortas bifurcate shortly after ventricle origin of common aorta, anterior aorta with about double width than posterior aorta. Broad vessel of left margin of pallial cavity runs dorsal-left to pericardium; just before this region smaller branch which edges pericardium inserts. After pericardium contoured, this vessel connects with other vessel coming from visceral mass and runs towards kidney. Kidney with 2 chambers. Anterior renal chamber totally filled by glandular tissue, somewhat triangular in section, connects with pericardium by small and narrow slit. This glandular tissue almost solid, formed by several branched, transverse, glandular septa. Posterior renal chamber simple hollow sac mostly filled by intestinal loops (described below). Nephrostome a small slit located in ventral surface of anterior renal chamber, close to posterior limit of pallial cavity. Urinary gutter starts just ventral to nephrostome, runs as shallow groove in pallial floor towards left and by left side of head-foot.

Digestive system – Buccal mass (Figs.249-251) relatively large (about $\frac{1}{3}$ of haemocoel volume) (Fig.245). Oral tube short, walls thick, circular muscle (mouth sphincter - mc) broad. Buccal mass dorsal wall (Fig.251) thin, anterior half covered by jaws. Jaw plates very large, slightly triangular, connected with each other in median line. Surface constituted by several oblique striae. Jaws anterior cut-edge thin, sharp, arched. Dorsal folds tall, narrow in region just posterior to jaws, gradually become broader and newly narrow after buccal mass end. Odontophore muscles (Figs.249-250, 252-253): m1, several small and narrow muscle fibers connecting buccal mass with adjacent inner surface of haemocoel; m1a, pair of narrow dorsal jugal muscles, origin in dorsal inner surface of haemocoel, in approximate middle level of odontophore, runs towards ventral and anterior, insertion in anterior region of buccal mass dorsal surface; m1b, pair of narrow and thin jugal muscles, origin close to m1a origin, runs towards ventral and posterior, insertion in each side of odontophore posterior region; mj, jaws and peribuccal muscles, relatively thick, origin in odontophore lateral-ventral surface, insertion in dorsal wall of buccal mass around jaws; ma, pair of thick and short muscles, origin in lateral-anterior inner surface of haemocoel, runs towards medial through mj fibers, insertion along outer surface of

jaws; m3d, pair of thin and narrow muscles, origin in posterior-dorsal-lateral region of buccal mass, run in surface towards ventral and anterior, insertion along ventral surface of odontophore close to median line; m4, broad pair of radular tensors, possessing some branches: m4 main body surrounding inner, ventral and lateral surfaces of cartilages, connected to cartilages only in ventral and lateral surfaces and in some sparse branches to inner surface; m4v, ventral branches, pair covering outer-lateral surface of cartilages, origin in m4 main branches posterior region, runs towards anterior, insertion along subradular membrane inner surface from median line to lateral; m4a, thinner pair covering ventrally m4 main branch, origin along their lateral surface, insertion with tissue on radular ribbon (to) in region preceding its exposure; m5, pair of dorsal tensor muscles of radula, relatively thin, origin broad on m4a, run towards medial and anterior covering m4, insertion relatively narrow in dorsal surface of radular sac preceding exposed region of radula; m6, horizontal muscle, connects dorsal surface of both cartilages along and at some distance from their medial edge; m7, pair very thin and narrow, origin in posterior end of cartilages, each runs towards medial connecting with its pair, penetrate and insert in inner surface of radular sac; m10, pair of protractor muscles of buccal mass, origin in ventral-inner surface of mouth, runs towards posterior, insertion in ventral-anterior surface of odontophore, close to median line; m10c, similar to m10 but running dorsal to it, insertion more anterior and dorsal to those of m10; m11 pair of narrow, thin and long muscles, origin in ventral surface of haemocoel close to median line at middle level of odontophore, run dorsal, penetrate in odontophore in medial line, after run attached to subradular membrane, insertion along median line. Other non-muscular buccal mass structures: oc odontophore cartilages, single, large, flat pair, outline oval; ih, inner ligaments between radular sac and inner surface of m6; br, subradular membrane similar to those of ampullariids. Pair of buccal ganglia located laterally in posterior-ventral region of buccal mass (Fig.249), their commissure relatively broad. Pair of nerves penetrates in odontophore just anterior to m11 penetration. Radular sac long (about 3 times longer than buccal mass length), not coiled, only twisted posteriorly. Radular nucleus thick. Radular teeth (Figs.133-134): rachidian long and narrow, 3 stubby cusps, central cusp about double than neighbor cusps;

lateral tooth with about double of rachidian width, situated obliquely (lateral end in level of rachidian distal roll), 3 cusps, middle cusp terminal, 3-4 times larger than neighbor cusps, base long and narrow; inner marginal tooth tall, slender, somewhat flat, 3 terminal and broad cusps, central cusp about 1.5 times larger than neighbor cusps; outer marginal tooth sigmoid, about same length than inner marginal tooth, base broad and flat, with broad projection, middle region slender and curved, distal region slightly broader, pointed, secondary cusps small, sub-terminal, on inner edge. Salivary glands somewhat triangular, separated from each other, located posterior to esophageal pouches. Salivary gland ducts long and convolute, runs on dorsal surface of anterior esophagus and buccal mass, penetrate in dorsal wall of buccal mass close to their apertures.

Anterior esophagus with pair of tall dorsal folds (continuation from those of buccal mass), which gradually faint in middle esophagus (Figs.249, 251). Pair of large, lateral pouches located just posterior to buccal mass, both connect with esophagus by narrow aperture, after aperture abruptly expand and become reniform sac. Pouches inner surface covered by several papillae. Dorsal esophageal folds cover each pouch aperture. Especial branches of anterior aorta irrigate each esophageal pouch, connected with them close to their connection with esophagus. Middle esophagus broad, inner surface with sparse, oblique, low folds. Posterior esophagus narrow, inner surface smooth. Stomach (Figs.247, 254) long and broad. Esophagus inserts in stomach in middle level of its ventral surface, but retains separation from gastric chamber by longitudinal, tall fold. Stomach mostly a simple sac, without inner especial structures, inner surface most smooth. Duct to digestive gland single, located in ventral-right region of anterior third part of stomach. Transverse groove present in anterior third of stomach, begins in aperture of duct to digestive gland, runs in ventral surface up to opposite side where faint, just in beginning of longitudinal, low fold of intestine. Digestive gland beige, with small brown spots (other details above). Intestine broad, with several loops inside posterior renal chamber as shown in Fig.247. Fecal pellets elliptical, large, fill intestine after its first loop in renal chamber. Rectum and anus described above.

Genital system – ♂: Testis (Fig.246) (described above) cream in color. Visceral vas deferens very

narrow, runs along ventral surface of stomach up to median-ventral-posterior edge of pallial cavity. Prostate large, located in right side of pallial cavity, part attached to pallial floor; visceral vas deferens inserts in middle region of prostate left side. Prostate elliptical in section, inner lumen flat (Fig.246). Prostate aperture a small, anterior papilla, opens towards pallial cavity floor where groove begins. Pallial sperm groove runs short distance up to penis base. Penis relatively small (little longer than tentacle), located just posterior to right tentacle (Fig.242). Penis base broad, gradually narrows, in its middle region newly expands and curves towards right (Figs.242, 255). Penis tip broad, asymmetrical. Penis sperm groove runs all along penis length, approximately in middle of its ventral surface. Penis sperm groove distal end on small papilla. ♀ (Figs.247, 256-258): Ovary small, occupies only columellar side of visceral first whorl (Fig.247). Visceral oviduct very slender, thin and long, runs along ventral surface of stomach up to middle region of pallial cavity posterior edge. In this region abruptly curves towards posterior and runs obliquely to right, augmenting very gradually. After distance equivalent to about ¼ whorl suddenly curves towards posterior, running parallel to its preceding portion. Close and anterior to its first curve inserts in seminal receptacle base. Seminal receptacle very long, increase gradually, rounded distal tip. Seminal receptacle aperture small slit in middle region of pallial oviduct vaginal groove. Capsule gland as remainder, massive region of pallial oviduct; possesses 2 flat, thick-glandular walled chambers. Right chamber a blind-sac connected to left chamber posteriorly. Left chamber with pair of tall, oblique folds preceding its connection with right chamber, and several other low, narrow folds along posterior half of its left wall. Left chamber opens anteriorly in female pore as simple, thick-walled slit.

Central nervous system (Figs.245, 249) – Nerve ring located anterior to buccal mass, just posterior to mouth. Hypoathroid type, with long commissure between both cerebral ganglia. Statocyst with several statoliths.

Measurements of shells (in mm) – MZSP 24542: ♀ 1, 8.6 by 13.6; ♀ 2, 7.7 by 12.8; ♂ 4, 7.4 by 12.7; MZSP 24538, ♀ : 10.4 by 15.7.

Distribution – South Rio de Janeiro and São Paulo Atlantic Rain Forest.

Habitat – Terrestrial, under plants.

Material examined – Types - BRAZIL; MNHN, 2 shells, probable syntypes of *Cyclostoma prominula* Fer. in Orbigny. Ordinary material: BRAZIL - SÃO PAULO: São Vicente (O.Schubart col.), MZSP 24547, 1♀ (27/I/1960), MZSP 24545, 1 specimen (27/I/1960), Prainha, MZSP 24542, 11 specimens, 8 shells, (27/I/1958), MZSP 24539, 3 specimens (15/II/1953), MZSP 24543, 3 specimens (27/I/1959), MZSP 24540, 1 specimen (15/II/1953), Paranapoã, MZSP 24548, 1 shell (1/II/1960), Porchat Island, MZSP 24544, 3 specimens (29/I/1959), Itararé, MZSP 24546, 8 specimens (29/I/1960); Itanhaém, Viuva Conde Farm, MZSP 24535, 1 shell (O.Schubart col., 9/IX/1941); Iporanga, MZSP 15615, 7 specimens (Leme and Papavero cols., 1/XI/1983), MZSP 24538, 1♀ (O.Schubart col., 30/XI/1952); Iguape, MZSP 24532, 2 shells (Leme and Biasi cols., 1-5/XI/1968); PARANÁ: Serra da Graciosa, MZSP 29575, 1 shell (AVC Dutra col., X/1979).

The anatomy of *Neocyclotus inca* (Orbigny, 1835) has been provided by SALGADO *et al.* (1989), reporting a similar organization to *N. prominulus*. These species are different mainly in the penis fashion.

Genus *Incidostoma* Morrison, 1942

Type-species:

Aperostoma (Incidostoma malleatum Morrison, 1942)

Incidostoma tupy new species

(Figs.32-36, 135-136, 259-270)

Types – Holotype: MZSP 29560, 1♀ from type-locality. Paratypes – BRAZIL - RONDÔNIA: Nova Esperança, MZSP 29578, 2♂ (MZ polonoroeste sta. 831888, 6-9/XII/1983), MZSP 29561, 2 specimens (sta.831874, 6-7/XII/1983); Nova Brasília, 11°09'S 61°34'W, MZSP 29561, 2 specimens (PNW 840566, 6-11/XI/1984); Jarú, MZSP 24553, 1♀ (K.Okushigue col., 10/IX/1976).

Type-locality – BRAZIL - RONDÔNIA: Santa Cruz da Serra [MZSP 29560, Vanzolini col., (MZ poloeste sta. 840169)].

Diagnosis – Malleated surface weakly developed. Aperture ample, separated from preceding whorl. Outer lip free.

Description

Shell (Figs.32-36). Size about 30mm, discoid, flat, about 4.5 whorls. Color uniform brown. Outer surface rich of undulated and delicate growth lines; malleated surface (*i.e.*, several low, small concavities sprayed by surface) almost absent, seen

in some area in outer surface preceding aperture. Walls thin. Protoconch dome-shaped, small, of 1 whorl, surface smooth and opaque, suture well-marked, transition with teleoconch unclear. Teleoconch with convex whorls, almost planispiral. Spire very low, approximate angle of 170°. Each whorl covers small area of preceding whorl. Umbilicus very ample end deep. Peristome white, somewhat thick, weakly prosocline, oval. Notch deep in superior corner, close to suture; its lips surround small orifice, anterior-left edge touches adjacent virtual suture; satellite growth lines contours notch in preceding area, gradually becoming perpendicular to suture at short distance from aperture.

Head-foot (Figs.259-260). Characters similar to those of *N. prominulus*, with following remarkable features. Snout slightly taller, with mouth turned ventrally. Pedal gland furrow restrict to anterior edge of foot sole. Urinary gutter at right of head deeper. Penis of males proportionally larger.

Operculum (Figs.259-260): Somewhat similar in characters to those of preceding species, except for simple (not double) outer edge, and broader last whorls of outer sculpture.

Mantle organs (Figs.261-262). Features somewhat similar to those of *N. prominulus*, with following distinctive or notable attributes. Lung with net of vessels more clear, with 6-7 branched vessels alternating drainage to left (ctenidial?) vessel and to ad-rectal sinus. Probable hypobranchial gland present as lobe bulging at right from kidney, part covered dorsally by rectum [normally connected to excretory features, commented below (excretory system and discussion)].

Circulatory and excretory systems (Figs.161-162) – Heart and pericardium characters similar to those of *N. prominulus*, differ only in having left (ctenidial) vessel plus vessel edging kidney inserted directly to auricle. Kidney also with similar attributes as those of *N. prominulus*, including anterior (solid-glandular) and posterior (hollow, filled by intestinal loops) renal chambers. Differs only by more protruded nephrostome and presence of solid excretory hypobranchial gland (as described in mantle organs). Urinary gutter deeper.

Digestive system (Figs.263-264) – Buccal mass attributes similar to those of *N. prominulus*, with following remarks. Dorsal folds with tall middle region as stalk for aperture of salivary glands. Odontophore muscles: m1b pair thinner, closer to median line; m3 pair similar but with an additional branch connecting with each other running on

posterior odontophore surface, dorsal to radular sac; m11 pair thicker. Radular teeth features similar to those of *N. prominulus*, with following remarkable notes (Figs.135-136): rachidian slender, almost triangular, 3 cusps, central cusp several times larger than neighbor cusps, distal edge concave; marginal tooth with about twice rachidian length, 3 cusps, central cusp terminal and several times larger than remainder cusps, basal region long, narrow and oblique; inner and outer marginal teeth slightly broader. Esophageal pouches, folds and regions similar in features to those of *N. prominulus*, except for taller folds edging pouches aperture and more developed irrigation of blood vessel in region of these tall folds. Large blood sinus located in ventral region between esophagus and buccal mass, this sinus evolves radular sac and possesses thick branches to salivary glands, to esophageal pouches and to odontophore. Middle esophagus with 4-5 narrow, longitudinal folds. Salivary gland cluster as single mass located posterior to pouches. Stomach attributes also similar to those of *N. prominulus*, except for: 1) more anterior insertion of esophagus; 2) posterior region of stomach (as blind sac) longer, its inner surface covered by transverse folds (sorting area?); 3) fold continuation from esophagus taller; 4) groove running from duct to digestive gland aperture deeper. Intestinal loops, characters and digestive gland features like those described for *N. prominulus*.

Genital system – ♂ (Figs.259, 265-266): Visceral and pallial organs with characters similar to those of *N. prominulus*, with remarkable features following. Prostate circular in section. Sperm groove between prostate and penis base longer. Penis very larger (about same length than that of entire head-foot). Penis base broad, gradually narrows, middle third part of uniform width. Penis distal third broad, flat, slightly triangular. Penis sperm groove runs along lateral edge of penis and also superior edge of penis tip. Penis groove ends in pointed, small papilla (Fig.266). Penis papilla stay turned inwards, bulged, semispherical structure precedes it. Immature penis simpler, with tip coiled (Figs.267-268). ♀ (Figs.261, 269-270): Visceral and pallial structures with characters similar to those of *N. prominulus*, with following remarks. Albumen gland more differentiated, as thicker region of visceral oviduct last loop. Seminal receptacle similar located, but possessing aperture direct to pallial cavity (and not inside pallial oviduct). Seminal receptacle aperture a small papilla located in posterior edge of pallial cavity close to pallial

oviduct. Capsule gland similar to that of *N. prominulus*, with same components. Genital pore a thick edged slit.

Central nervous system (Fig.263) – Similar characters to those of *N. prominulus*.

Measurements of shells (in mm) – Holotype: 17.4 by 31.3; MZSP 29561: 17.0 by 29.2; 19.3 by 30.9.

Distribution – Known in some points of Rondônia State, Brazil, Amazon Forest.

Habitat – No data.

Material examined – Types.

Etymology – The specific epithet refers to the ancient indigenous people living in region.

Discussion – The superior notch of outer lip clearly allows the generic attribution of the new species, also with the aid of generic key of TORRE *et al.* (1942:187). *I. tupy* differs from *I. malleatum* (Morrison, 1942) (without locality), *I. pergrandis* (Kobelt, 1912) from Colombia and *I. kobelti* (Morrison, 1942) (from Colombia) by less developed malleated surface, ampler aperture more separated from preceding whorl, and by more developed axial sculpture. MORRISON (in TORRE *et al.*, 1942) presented the distribution of the genus for Colombia, Ecuador and Peru, (Andes localities). The present description expands the geographic distribution towards east, for Brazilian territory (Rondônia) relatively away from Andes. However, *I. malleatum*, just the type species of the genus, remains lacking a more precise locality.

The presence of the hypobranchial gland in cyclophorids has been related to the excretion (ANDREWS & LITTLE, 1972), but a clear gland is found only in *I. tupy* (Fig.262 in middle-superior region).

Genus *Aperostoma* Troschel, 1847

Type-species: *A. blanchetianum* Moricand
Aperostoma blanchetiana (Moricand, 1826)
(Figs.37-39, 112, 137-138, 271-275)

Synonymy see TORRE *et al.* (1942:244-245).
Complement:

Neocyclotus (Neocyclotus) inca – (part) KOBELT, 1902:236 (in synonymy) (non ORBIGNY, 1835).
Aperostoma (Aperostoma) blanchetianum: TORRE *et al.*, 1942:244-245 (pl.35, figs.7-9).

Description

Shell (Figs.37-39). Discoid and flat. Color brown with paler spiral bands variable in localization and

number in specimens. Spire somewhat tall. Umbilicus slightly narrow. Aperture rounded, slightly prosocline, very weak notch in superior corner in form perpendicular. Other details in TORRE *et al.* (1942:245)

Head-foot and operculum (Figs.112). Characters similar to those of *I. tupy*.

Mantle organs (Fig.271). Features similar to those of *I. tupy*. Narrow fold of hypobranchial (?) gland present edging rectum.

Circulatory and excretory systems (Fig.271) – Characters similar to those of preceding cyclophorids, remarkable features following. Lung vessels preceding auricle somewhat similar to those of *I. tupy*, but left (ctenidial) vessel strongly curved preceding its connection, and secondary vessel running along border between kidney and pericardium (not running on pallial surface). Kidney also with 2 chambers, anterior (solid-glandular) chamber longer antero-posteriorly. Nephrostome a slit preceded by short stalk.

Digestive system (Fig.272) – Morphological attributes in general similar to those of *I. tupy*, distinctive or notable features following. Jaw plates separated from each other, outline somewhat circular, with small projection in median-anterior edge. Buccal mass dorsal chamber (between both dorsal folds) with taller longitudinal folds. Odontophore muscles: m1, several pairs in ventral region connecting odontophore outer surface with mouth; m1b absent. Radular teeth with similar attributes as those of preceding cyclophorids, remarkable features following (Figs.137, 138): Rachidian slender and long, 3 cusps, central cusp about 3 times larger than remainder cusps, distal edge concave, with an additional central concavity; marginal tooth with 3-4 cusps, penultimate cusp terminal and several times larger than remainder cusps; inner and outer marginal teeth broader, outer marginal strongly sigmoid. Large sinus around radular sac with branches to both pouches and salivary glands present. Stomach with groove adjacent to duct to digestive gland longer, surrounds transversally entire gastric circumference with short portion parallel to its initial region. Gastric inner surface with an additional longitudinal, low, flattened fold located between esophagus aperture and duct to digestive gland.

Genital system – ♂ (Figs.274, 275): Similar characters to those of *I. tupy*, with following remarkable features. Prostate longer, broader and curved, walls transversally folded. Sperm groove

between prostate and penis base longer. Penis large, curve, middle third part narrower than basal and distal regions. Penis apex broad, flat, asymmetrical, expanded, thick. Penis sperm groove runs along inner edge and superior edge of penis tip; finishes in penis right side. Final part of penis groove with pair of small papillae; left papilla broader, tip rounded, more basal located; right papilla slender, pointed and more distal. ♀ (Figs.273): Visceral and pallial structures with characters closely similar to those of *I. tupy*, including albumen gland developed and seminal receptacle opened directly into pallial cavity. Differs by narrower genital pore.

Measurements of shells – MZSP 16534♂: 14.4 by 20.8; MZSP 16534: 14.3 by 21.5.

Distribution – Bahia and Minas Gerais states.

Habitat – No data.

Material examined – BRAZIL - MINAS GERAIS: Buritis, Jaboticaba stream, MZSP 16534, 3♂, 2♀ (sta. 642152, Vanzolini col.).

Discussion – The shell attributes of the examined specimens are closely similar to those described by TORRE *et al.* (1942:245) for *A. blanchetiana*, allowing the specific identification. However, there is another very similar species, *A. merrilli* Morrison, 1942 (from Bragança Railway, Amazon valley, Brazil).

Superfamily Viviparioidea
Family Viviparidae
Genus *Viviparus* Montfort, 1810

Type-species:

Helix fluviatorum Montfort = *viviparus* Linné
Viviparus acerosus (Bourguignat, 1862)
(Figs.40-41, 103-104, 139-140, 276-295)

Viviparus acerosus – FECHTER & FALKNER, 1993:119 (fig.5); FALNIOWSKI *et al.*, 1996.

Description

Shell (Figs.40-41). Globose, color greenish-brown. Spire tall, apex slightly rounded. Suture deep, each whorl circular in section and scarcely attached to neighboring whorls. Body whorl harmoniously sized with spire. Umbilicus wide. Periostracum heavy, smooth. Sculpture lacking except growth lines and axial undulations. Aperture circular, lips somewhat projected. Young specimens (from brood pouch) with up to 4 whorls; protoconch smooth, of 1 whorl; remaining whorls sculptured with several narrow, spiral lines uniformly distributed, 2 or 3 of them markedly larger and equidistant from each other, bearing periostracal hair.

Head-foot (Figs.276, 279-280, 291, 293). Head slightly protruded, relatively small (about $\frac{1}{3}$ of head-foot width). Snout cylindrical, anterior margin flat. Tentacles long (about 1.5 times longer than snout), stubby, base at side of snout base. Ommatophore short, located between basal and middle third of outer surface of each tentacles. Pair of siphons (lobes) similar to those of ampullariids, but shorter. Food groove edged by thick, low borders; running slightly to right of middle region of pallial floor. Food groove with posterior end fainting; anterior end in right siphon (nuchal lobe), dividing it into two projections, anterior (dorsal) projection with medial limit close to base of snout (Fig.293: lr). Foot large (about $\frac{2}{3}$ of head-foot volume), sole simple. Opercular pad larger than its base in dorsal foot surface, with edges projecting beyond it. Anterior furrow of pedal glands restricted to anterior foot, edged by thick borders. Columellar muscle thick, length about $\frac{3}{4}$ whorl. Head-foot connection with mantle border very thick and richly vascular. Male genital structures described below.

Operculum (Figs.103-104, 276). Occupying entire shell aperture. Horny, somewhat similar in characters to those of ampullariids. Outline slightly circular, with low projection in inner-superior region. Nucleus sub-central, located closer to inner margin. Sculptured with concentric growth lines. Inner surface glossy; scar sub-circular, close to inner margin, occupying about $\frac{2}{3}$ of opercular area.

Mantle organs (Figs.277-278, 281). Pallial cavity of about 1 whorl. Mantle border simple, thick. Osphradium ridge-like, oblique, almost parallel to mantle border, length about $\frac{1}{2}$ of that mantle border, very close to gill. Ctenidial vein narrow, uniform in width throughout. Gill long and narrow, about same length as pallial cavity; anterior end at mantle border. Gill filaments very tall and narrow, arched towards right; apex slightly pointed, close to food groove. Gill filaments with short, low, glandular portion preceding afferent gill vessel, forming glandular ridge along left gill margin (endostyle) (Figs.277, 281). Glandular tissue (hypobranchial gland?) covering afferent gill vessel; but broad space apparently lacking hypobranchial gland between gill base and rectum. Right margin of pallial cavity filled by oviduct in females. Ad-rectal sinus modified in ureter, broad, running all along pallial cavity right margin in males or edging oviduct in females. Rectum on dorsal and left sides of ad-rectal sinus. At right end of mantle border, in females, presenting three openings, most posterior and smaller is ureter pore, anus most

anterior, and female pore larger, located between anus and ureter pore.

Visceral mass (Figs.277-278). Long, with about 4 whorls, approximately smaller than pallial cavity. Kidney anterior, with stomach and adjacent intestine just posterior to it. Gonad and digestive gland occupying about 2.5 whorls posterior to stomach. Gonad brown, located in columellar surface of each whorl. Digestive gland pale green. Details of each structure below.

Circulatory and excretory systems (Figs.278, 282) – Heart relatively small, located behind posterior-left region of pallial cavity, partly posterior to anterior lobe of kidney. Auricle connection with ctenidial vein just posterior to gill; possessing portion protruding anterior to this connection. Ventricle posterior to auricle, narrow connection between both. Kidney with two chambers and ureter. Anterior kidney chamber small, triangular in section, entirely filled by glandular tissue (having only small inner hollow portion close to nephrostome). Anterior kidney chamber with four almost plane surfaces: 1) posterior surface towards pericardium, with ventral, small, middle slit as reno-pericardial pore; 2) left with pallial cavity; 3) ventral right with ureter; 4) dorsal with mantle. Nephrostome an elliptical, small pore, without muscular edges, located in middle-posterior region of ventral-anterior surface of anterior renal chamber. Posterior renal chamber simple hollow sac filled by anterior region of stomach and intestinal loops. Ureter apparently specialization of broad adrectal sinus (Figs.278, 281), runs between rectum and oviduct (in females) or right pallial cavity edge (in males). Posterior end of ureter ventral to anterior renal chamber; anterior end in muscular, papilla-like ureter pore just posterior to anus (or just posterior to female pore). No special inner glands in ureter. No urinary gutter.

Digestive system – Buccal mass just posterior to mouth, extends slightly posterior to snout inside haemocoel (Fig.280). Mouth longitudinal, ventral. Jaw plates small, thin, outline elliptical (Fig.283). Dorsal folds broad, smooth and simple. Deep dorsal chamber between both dorsal folds, inner surface smooth. Odontophore and peribuccal muscles (Figs.284-288): mc, circulatory fibers of buccal sphincter, thick and broad; m1, several pairs of small muscular fibers connecting buccal mass outer surface with adjacent regions of haemocoel, no differentiated pair; mj, pair of jaw and peribuccal muscles, origin in odontophore cartilage lateral-

anterior surface, insertion along dorsal wall of buccal mass just dorsal to jaws; m2, pair of retractor muscles of buccal mass (retractor of pharynx), origin in lateral inner surface of haemocoel posterior to buccal mass, run towards anterior, insertion in posterior-lateral surface of odontophore (Figs.284, 286), most part on membrane which covers odontophore and small part in m4; m4, pair of large ventral tensor muscle of radula and subradular membrane, origin in odontophore cartilages around mj, cover cartilages almost completely (only dorsal edge free), insertion in small lateral region of tissue on radular ribbon preceding buccal cavity (to), subradular membrane also connecting along lateral and anterior edges of m4, part of dorsal branch m4 of with weak fibers along it; m5, pair of dorsal tensor muscles of radula, originating on m4 posterior-lateral region, running medially covering m4, insertion along radular sac in region opposed to m4 insertion (each m5 does not connect with its pair); m6, horizontal muscle, similar to those of ampullariids, little shorter in length than cartilages; m7, narrow, long pair, origin in m4 dorsal branch at medial-posterior edge, run posteriorly on subradular membrane (br) inner surface fusing with each other, penetrating in radular sac, insertion along radular sac and radular nucleus (Figs.287, 288); m7a, pair of thick muscles, originating in ventral surface of haemocoel close to median line and in level just posterior to odontophore, run dorsally and, after, anteriorly attached to radular sac ventral surface, insertion in m5 anterior edge (Figs.285, 288); m9 absent; m10, pair of ventral protractor muscles of buccal mass, origin in ventral inner surface of mouth, run posteriorly on mc, insertion in ventral-anterior region of odontophore; m10a, paired continuation of m10, running close to median line and attached to membrane covering odontophore, insertion along this membrane in its medial-ventral-posterior region; m11, pair of long and relatively broad muscles, originating on haemocoel inner ventral surface in region posterior to odontophore, close to origin of m7a, running dorsally, penetrating in odontophore just anterior to radular sac, insertion along subradular membrane close to median line reducing anteriorly; m12, small pair of muscles similar to those of ampullariids, origin in lateral-anterior inner surface of m4 and br, running towards medial and dorsal, insertion shortly on cartilages anterior-outer surface close to m6 (Fig.287). Other odontophore structures: br, subradular membrane, similar to those of

preceding species, cover inner surface of (and probably secretes) subradular cartilage, most inserted in lateral and anterior edges of m4, but also connects with radular sac (via m5 pair) and peribuccal epithelium (via mj); reinforcement of subradular membrane in its dorsal-middle region with posterior, "W"-shaped edge; oc, pair of odontophore cartilages, similar to those of preceding species, flat, outline elliptical; om, odontophore outer membrane, transparent, covering outer surfaces of odontophore, except narrow portion close to median line where is penetrated by radular sac, some muscles (m7, m7a, m11) and some nerves; to, tissue on radular ribbon preceding buccal cavity, length more or less equivalent to portion of radula passing through odontophore. Buccal ganglia located laterally, on each side of border of odontophore and dorsal wall of buccal mass, close and dorsal to m2 insertion. Salivary glands (Figs.280, 283, 284) clustering as single mass posterior to nerve ring (localized posterior to buccal mass) and as two narrow glandular masses through it. Salivary ducts as continuation from these two masses, run on dorsal wall of buccal mass outer surface, penetrating into wall just close to their apertures, in anterior extremities of dorsal folds, close to median line.

Radular sac about as long as buccal mass (Figs.284-286), radular sac surrounded by large blood sinus. Radular teeth (Figs.139, 140): all teeth with similar shape, tall, as flat rod, tip rounded, curved inwards, bearing several small, sharp cusps. Rachidian shorterst tooth, with 7-9 cusps, central cusp about three times broader than neighboring cusps (but same length); lateral tooth with 7-9 cusps, central cusp terminal, about three times width of remaining cusps (but same length); inner marginal tooth similar to lateral tooth, slightly longer; outer marginal tooth similar to inner marginal tooth, differing only in uniformity of cusps (lack central differentiated cusp).

Esophagus relatively narrow and long. Anterior esophagus with pair of dorsal, broad, longitudinal folds (as continuation from dorsal folds of buccal mass), without pouches (Figs.283, 284). Middle esophagus with several (about 10) inner, narrow, low, longitudinal folds. Posterior esophagus with smooth inner surface. No detectable esophageal glands.

Stomach (Figs.278, 289-290) large, about half whorl in length, located half whorl posterior to pallial cavity; posterior half immersed in digestive gland. Esophagus insertion in posterior-left gastric extremity, as gradual enlargement, curved towards

left. In this curve very small duct to digestive gland. Stomach, after this first curve, abruptly expands becoming almost as wide as whorl; posteriorly narrowing, without clear separation with intestine. Main duct to digestive gland located in posterior-left-ventral surface of stomach. Stomach inner surface most smooth; pair of low, narrow folds runs on its dorsal surface (as continuation from esophagus), and curve towards posterior and run along gastric dorsal wall. Another tall and complex fold, as small chamber, located in posterior extremity of stomach, at some distance from esophageal insertion and close to smaller duct to digestive gland (Fig.189). This tall fold with outer surface possessing 4-5 secondary folds, and smooth inner surface. Narrow fold, also initiated in esophageal insertion, running further posteriorly, lying anteriorly to posterior taller fold. No clear style sac. Intestine narrowing after leaving stomach, and abruptly curving towards right and runs parallel to gastric anterior wall. This curve located adjacent to pericardium, not possessing any special inner structure (like those of ampullariids). Intestine, then, curving towards anterior in middle gastric region, and lies parallel to its preceding loop on dorsal wall of posterior renal chamber (Figs.278, 290); then exiting to pallial cavity. Rectum narrow, running along ureter outer-dorsal wall. Anus described above.

Genital system – ♂ (Figs.291-293): Testis pale green, lies on superior and columellar surface of visceral whorls, from first whorl to pallial cavity. Visceral vas deferens very narrow, running on columella and inferior-ventral margin of testis, with successive, very narrow branches from different portions of testis. In pallial cavity, vas deferens opening to large prostate gland (Fig.292), running along pallial cavity floor for about 1/3 of its length. Pallial vas deferens, after this distance, narrowing abruptly, becoming duct, curving towards left, penetrating into haemocoel integument. Remaining $\frac{2}{3}$ of vas deferens lies immersed in integument, surrounded by very thick, muscular walls in several layers, forming an ejaculatory duct. Ejaculatory duct bulging into haemocoel, displacing inner structures (as esophagus) towards left; its lumen small, closer to left side. Ejaculatory tube anteriorly with broader lumen and thinner muscular walls, abruptly narrowing, penetrating through right cephalic tentacle. Vas deferens runs all along right tentacle, its inner surface relatively broad, with some inner, longitudinal, low folds. Vas deferens opens in tentacle tip as broad papilla with rounded tip. Right

tentacle possesses deep concavity located at right from genital papilla (Figs.291, 293). Papilla can retract into this concavity. ♀ (Figs.294-295). Ovary greenish brown, located in same position as testis (Fig.277). Visceral oviduct very narrow, runs along columella. Pallial oviduct very large, occupying about half of pallial cavity space and also bulges posteriorly to last whorl of visceral mass, displacing kidney and intestine to left. Visceral oviduct making large loop and penetrating pallial oviduct dorsally, between posterior and middle third; connecting sub-terminally, forming small papilla inside narrow dorsal chamber. This dorsal chamber running posteriorly, continuous with ventral chamber. This dorsal chamber running to posterior end of pallial oviduct, abruptly curving ventrally and greatly increasing in size. Ventral chamber of pallial oviduct functioning as large brood pouch (although possessing some small capsules in final portion of dorsal chamber), walls thin, semi-transparent, smooth. Low and very thin fold running along dorsal-left side of entire ventral chamber, curved to right, starting close to dorsal chamber aperture, tapering posterior to genital pore. Ventral chamber (brood pouch) filled by about 20 capsules, size varying. Each capsule covered by transparent, heavy, horny membrane, filled by hyaline, yellow, jelly mass and young specimens of about 4 whorls. Vaginal tube with thick, muscular walls and some inner transverse folds, located as continuation from brood pouch. Female genital pore small, close to mantle border, with several inner folds.

Central nervous system (Figs.284) – Unlike preceding species, but similar to remainder caenogastropods, of epiathroid type, and located posterior to buccal mass. Statocysts with several statoliths. More details in *Viviparus contectus*.

Distribution – Europe.

Habitat – No data beyond freshwater environment. Filter feeding.

Material examined – HUNGARY - ALFÖLD: Canal Tápió, (circa 60km SE of Budapest), MZSP 29403, 1♂, 2♀ (J.Hemmen leg).

Viviparus contectus (Millet, 1813)
(Figs.10, 42-43, 61-62, 141-142, 296-301, 348)

Viviparus contectus – FALNIOWSKI, 1989:59 (key); FECHTER & FALKNER, 1993:119-119 (fig.7); ELEUTHERIADIS & DIMITRIADOU, 1995:41-52; FALNIOWSKI *et al.*, 1996; KATOH & RIBI, 1996:67-82.

Description

Shell (Figs.10, 42-43, 61-62). Characters similar to those of *Viviparus acerosus*, differing in being broader, whorls shorter and more convex, and by paler color. Young specimens (from brood pouch) similar to those of preceding species (Figs.61-62). Head-foot and operculum. Similar to *V. acerosus*, differing only in darker pigment.

Mantle organs (Fig.296). As *V. acerosus*.

Visceral mass. Closely similar to those of *V. acerosus*, except gonad and digestive gland almost same color (pale beige) and testis shorter (restricted to last visceral whorl posterior to stomach).

Circulatory and excretory systems – Similar to *Viviparus acerosus*.

Digestive system (Fig.297) – Similar to *V. acerosus*, except for following features. Odontophore muscles: m2 pair with small portion of insertion also connected to lateral side of anterior esophagus; m7a, m10a pairs also present. Radular teeth similar to *V. acerosus* (Figs.141-142), but differing in: rachidian slightly longer, with 9-11 cusps; lateral tooth with 8-11 cusps. Stomach with same folds (including tall posterior complex fold) and ducts to digestive gland.

Genital system – ♂ : Visceral and pallial structures similar to those of *V. acerosus*, including ejaculatory tube running in integument and modified right tentacle as penis. Differing only by shape of papilla of right tentacle tip (where vas deferens opens), being pointed and more elongated (Figs.298-299), with concavity at side of papilla deeper. ♀ : Visceral and pallial organs similar to those of *V. acerosus*, but with final region of visceral oviduct and dorsal chamber of pallial oviduct (Fig.301) shorter, and connection between both simpler. Also presenting papilla separating visceral oviduct from dorsal chamber of brood pouch. Additionally, dorsal chamber running directly towards posterior, increasing gradually. More capsules, about 30, in ventral chamber of pallial oviduct (brood pouch), chaotically organized.

Central nervous system (Fig.300, 348) – As in *V. acerosus*. But commissure between both cerebral ganglia relatively long. Supra and subesophageal ganglia located far from nerve ring. Each pair of connectives uniting cerebral-pleural ganglia with pedal ganglia “V”-shaped, with dorsal portion of each connective far from each other. Cerebral ganglia separated from each other, connected by a relatively long and wide commissure, form

triangular, dorso-ventrally flat; lateral edge possessing ophthalmic nerve in anterior region and tentacular nerve in posterior region. Right pleural ganglion with about half of cerebral ganglion size, located at short distance ventral from it, right cerebro-pleural connective narrow, with length equivalent to half of pleural ganglion length; form elliptical. Left pleural ganglion somewhat diffuse, with borders not so clear; left cerebro-pleural connective length equivalent to that of right one, but wider. Pedal ganglia antero-posteriorly long, located deeply inside pedal musculature, close to each other and to median line; dorsal region long and narrow, middle region wider, with a projection directed to its pair, becoming unclear if this is ganglion or commissure (both pedal ganglia separated by a shallow transversal furrow), anterior possessing a median nerve and a lateral, broad anterior projection. Cerebro-pedal connective (cl) narrow and long, connecting anterior corner of cerebral ganglia (just ventral and anterior to ophthalmic nerve) with dorsal end of pedal ganglia. Pleuro-pedal connective (pn) about twice wider than cerebro-pleural connective, boundary with pleural ganglia unclear, looking like their continuation. Cerebro-pedal connectives ventrally close to pleuro-pedal connectives, gradually becoming far from them towards dorsal, inserting respectively in cerebral and pleural ganglia far from each other, with a distance equivalent to that of cerebral ganglia.

Measurements of shells (in mm) – MZSP 29402: ♀ 1, 32.7 by 26.2; ♂ 2, 34.5 by 25.7.

Distribution – Central Europe.

Material examined – HUNGARY - ALFÖLD: Canal Tápió (circa 60km SE of Budapest), MZSP 29402, 1♂, 4♀ (J.Hemmen col.)

Genus *Notopala* Cotton, 1935

Type: *Paludina hanleyi* Frauenfeld, 1864:339 OD

Notopala ampullaroides (Reeve, 1863)

(Figs.44-46, 63, 105-106, 143-144, 302-319, 349-352)

Synonymy see SMITH (1992).

Description

Shell (Figs.44-46, 63). Somewhat similar, but shorter than those of *Viviparus*, of about 5.5 whorls. Color pale brown. Adult with eroded apex. Sculpture series of spiral, somewhat uniform striae, disappearing on last whorl. Aperture rounded, prosocline, peristome white. Umbilicus narrow, located at middle of inner lip. Young

specimen (found in brood pouch) (Fig.63) with up to 3.5 whorls; first whorl smooth, concave, dome-shaped; remainder of whorls almost smooth, with 3 equidistant spiral cords formed by successive small nodes, third cord located on periphery forming low carina.

Head-foot (Figs.302, 306, 315). Features similar to those of *Viviparus*, remarks following. Color dark grey, with some pale grey spots, sometimes coalescent. Food groove forming tall fold (Figs.302-303), appearing abruptly in posterior end of pallial cavity; left edge taller and curved inwards; right edge low and broad. Pedal furrow wider, occupying anterior half of foot edge.

Operculum (Fig.302). Characters similar to those of *Viviparus*, except for nucleus being almost central, slightly towards inner edge; sculpture concentric.

Mantle organs (Figs.304, 307). Organization and components similar to *Viviparus*; distinctive features noted below. Mantle edge thick, smooth, color dark grey. Osphradium long and broad, located on ctenidial vein. Osphradium right edge with series of small and well-spaced projections. Ctenidial vein broad throughout. Gill filaments tall and slender, tip sharp pointed. Endostyle broad, also at right of gill.

Visceral mass (Figs.304-305). Similar to other viviparids, but slightly lower, about 2.5 whorls. Gonad occupying superior and columellar regions of each whorl. Color of both gonad and digestive gland greenish beige.

Circulatory and excretory systems (Figs.305) – Similar to *Viviparus*, remarks following. Heart large (about ¼ of posterior renal chamber volume); auricle broad, connected to ctenidial vein posteriorly. Anterior aorta about 3-times broader than posterior aorta. Heart and posterior kidney chambers connected with each other, pericardium membrane separating them lacking (Fig.305). Posterior kidney chamber without apparent glandular tissue, greatly compressed by intestinal loop and by posterior region of pallial oviduct in females. Anterior kidney chamber solid, somewhat long and flat; posterior surface (with posterior kidney chamber) concave, triangular, with small, tight pore located in anterior-right region; its surface with pallial cavity (left) concave and broad, anterior end rounded; its surface with ureter (right) convex, with similar form of surface with pallial cavity; nephrostome located in middle region of latter part, papilla-like, with muscular, slightly tall

edges. Ureter (Figs.304-305, 307) and renal aperture as in *Viviparus*.

Digestive system – Most features similar to of preceding viviparids; distinctive or remarkable characters following. Jaw plates thin, laterally located (Fig.310). Buccal mass dorsal folds tall and narrow, located close to median line. Aperture of salivary glands very small, close to median line, located in anterior end of dorsal folds. Odontophore muscles (Figs.308-309, 311-314): m1 pair single, slightly thick; m2 pair with double insertion surrounding buccal ganglion; m4 insertion in tissue on radular ribbon preceding buccal cavity (to) by means of short and thin muscles; m7 pair very narrow; m7a pair well-developed, insertion with 2 branches running in opposite direction; m10 broad and thin; m11 pair thick and broad. Salivary glands long, slender and intensely convolute (Figs.308-309); located posterior to nerve ring; both narrowing and crossing through nerve ring dorsally. Radular features similar to those of preceding viviparids (Figs.143-144). Salivary ducts immersed in dorsal wall of buccal mass in posterior-lateral region (just dorsal to buccal ganglia) and run immersed in dorsal folds. Anterior esophagus with pair of inner folds continuous with dorsal folds of buccal mass; gradually these folds unite with each other and run as single, broad fold, from distance equivalent to buccal mass length, abruptly disappearing. Posterior esophagus with irregular, narrow inner folds; posterior region slender. Middle and hindgut with characters similar to those of *Viviparus* (Figs.305), notable features following. Esophageal insertion in stomach sub-terminal, on its lateral-ventral surface. Stomach broad and long, somewhat conic. Stomach inner surface mostly smooth; narrow and low transverse fold running in dorsal surface, at level of esophageal aperture; pair of narrow, low folds (origin in dorsal surface) at level of digestive gland duct; folds running opposed to each other, surrounding at some distance duct to digestive gland; both folds approach one another in ventral surface, running parallel along intestinal surface, disappearing gradually. Duct to digestive gland single, small, located in middle region of anterior half of ventral surface of stomach. Stomach-intestinal border unclear, stomach narrowing gradually up to right region of pericardium. Digestive gland greenish beige, of 1.5 whorls posterior to stomach, and about half whorl surrounding it. Intestine, rectum and anus as in *Viviparus*.

Genital system – ♂: Similar to that of *Viviparus*, remarkable features following. Testis large (Fig.317: pt), located in pallial cavity instead of visceral mass; lying along right edge of pallial cavity, bordering ureter; color beige, thick glandular walls. Pallial vas deferens originating short distance from posterior end of testis, in its ventral-left surface. Ejaculatory duct similar to those of preceding viviparids, immersed in integument (Fig.315), walls thick, with concentric muscles, bulging into haemocoel. Ejaculatory duct abruptly narrowing in base of right cephalic tentacle, walls becoming thinly muscular; it running along tentacle to its apex. Right (copulatory) cephalic tentacle base broad (Figs.315, 316), inner duct also broad; in middle level, both tentacle and inner duct abruptly narrows. Distal half of right tentacle strongly and irregularly curved towards left (Fig.316). ♀ (Figs.318-319): Characters similar to those of *Viviparus*, with following distinctive or notable features. Ovary greenish beige, located in columellar and superior regions of visceral whorls, from apex to posterior end of stomach (Fig.304). Visceral oviduct very narrow, running in middle region of columellar surface of visceral mass. Pallial oviduct very large, its posterior third encroaching into renal chamber. Albumen gland solid, running in left-posterior region of posterior third of pallial oviduct, surrounding rectum. Albumen gland narrowing anteriorly, becoming duct; with visceral oviduct inserting in this region. Albumen gland narrow, with walls thick, inner surface longitudinally folded; zigzagging just within posterior edge of pallial cavity, then running towards posterior. Short distance from albumen gland posterior end, abruptly becoming broader, running anteriorly. Capsule gland posterior third of pallial oviduct, dorsal to kidney, walls thickly-glandular, inner surface longitudinally folded; special broader furrow running in ventral-left inner surface. Brood pouch anterior 2/3 of last portion of pallial oviduct, walls thin, semi-transparent inner surface smooth. About 20-30 capsules, containing specimens from 1 to 4 whorls, larger specimens located anteriorly. Anterior end of pallial oviduct with narrow duct and muscular walls; finishing in low papilla. Female pore small, sub-terminal, ventral.

Central nervous system (Figs.306, 309, 349-352) – Located posterior to buccal mass. Cerebral ganglia flat and triangular; commissure between both cerebral ganglia (cc) with about $\frac{1}{3}$ of ganglia length, located in anterior region of ganglia medial edge; a pair of small nerves located

in this commissure (Figs.350-351), running towards anterior; two pairs of broad nerves (lateral pair broader) running towards anterior, innervating dorsal-lateral surface of buccal mass (bn), these nerves as anterior vertex of ganglia; ophthalmic nerves (of) originating dorsally to these buccal mass nerves, running short distance, penetrating in ommatophores base orifice in haemocoelic surface; tentacular nerves (tn) about half-wide than ophthalmic nerves, originating in cerebral ganglia posteriorly and separated to them, running a short distance, penetrating into tentacles base. Pleural ganglia with about a third of cerebral ganglia size; both asymmetric, right ganglion (re) smaller than left (le) and possessing three nerves in anterior end, two running posteriorly (broader one as connective with visceral ganglion), and one running anteriorly; equivalent nerves inserted in left pleural ganglia in opposed side, close to connective with pedal ganglion. Connective between both cerebral and pleural ganglia (cn) very short, marked only by a single and abrupt curve in posterior vertex of cerebral ganglia. Connective between cerebral and pedal ganglia (cl) broad, separated from cerebro-pleural connectives, originated in anterior vertex, ventral to buccal mass nerves, length little shorter than cerebral ganglion length, inserting in posterior third of pedal ganglia. Pedal ganglia antero-posteriorly very long (about twice cerebral ganglia length), no clear border with pleural connective, running towards anterior penetrating in pedal musculature; pedal ganglia form similar to those of *Viviparus*, but shorter. Pedal commissure (uc) relatively long (about half of pedal ganglion width) and well discernible. Statocysts with about half size of pedal ganglia, located ventral and lateral to them, inside pedal musculature; internally several sand-like statoconia. Pair of visceral connectives (vc) very long (same length of haemocoel), relatively thick close to their insertion on pleural ganglia, narrowing gradually, becoming very narrow. Visceral ganglion (Fig.349: vi) relatively small, located in anterior edge of pericardium.

Measurements of shells (in mm) – AMS 202766 ♀ 1: 26.7 by 23.2 (Figs.44-46); ♀ 2: 20.7 by 17.2; ♂ 3: 18.6 by 17.5.

Material examined – AUSTRALIA: North Australia; Northern Territory, Douglas R. crossing, 13°40.0'S 130°39.54'E, 1.5m depth, AMS 202766, 19 specimens (sta. 21437B; W.F.Ponder, C.Miller, D.L.Beechey and V.Kessner cols., 25/VI/1996).

Notopala essingtonensis (Frauenfeld, 1862)
(Figs.47-48, 51, 66, 145, 320-321)

Synonymy see STODDART (1982:169); SMITH (1992).

Description

Shell (Figs.47-48, 51, 66). Characters very similar to those of *N. ampullaroides*, distinctions following. Outline more elongated. Color pale green. Sculpture of 3 low, spiral, equidistant, dark threads per whorl; series of low, narrow spiral striae between threads. Umbilicus very narrow. Aperture almost circular slightly prosocline. Young specimen similar to that of preceding species (Fig.66). Other details in STODDART (1982).

Head-foot and operculum. Features similar to those described by *N. ampullaroides*, except for darker grey color.

Mantle organs (Fig.321). Similar to those of *N. ampullaroides*, except for somewhat broader gill filaments. Osphradium slightly longer and narrower, bearing more small projections along right edge.

Circulatory and excretory systems – As those described for *N. ampullaroides*.

Digestive system (Figs.145) – Most features closely similar to those of *N. ampullaroides*. Although, m6 is slightly shorter (about 2/3 of cartilage length).

Genital system – ♂ (Fig.320): Posterior structures as described for *N. ampullaroides*, except for form of copulatory right cephalic tentacle, longer, narrowing gradually (slightly longer than left tentacle), with broad and low projection located in its middle-ventral surface. Copulatory tentacle inner duct broad in its base, abruptly narrowing, very slender along tentacle's length. ♀: No available female with well-preserved visceral region was available, precluding analysis of visceral and posterior pallial structures. All other structures apparently closely similar to those described for *N. ampullaroides*.

Central nervous system – Similar to that of *N. ampullaroides*.

Measurements of shells (in mm) – AMS 153577 ♀ 1: 27.1 by 20.8; ♂ 2: 22.9 by 18.6; ♂ 3: 23.6 by 18.5.

Distribution – Australia: Queensland, NT (SMITH, 1992).

Habitat – Lentic freshwater, lotic freshwater.

Material examined – AUSTRALIA - QUEENSLAND: Walkers Ck., 35 km south of Normanton, on Normanton-Karuba Rd., AMS 153577, 3♂, 3♀ (sta. 21169, D.F.McMichael col., 14/XII/1963).

Genus *Larina* A. Adams, 1854
 Type: *L. strangei* A. Adams, M)
Larina cf *strangei* A. Adams, 1854
 (Figs.50, 52-54, 146, 322-329)

Possible synonymy – *Larina strangei* A.Adams, 1854:41 (pl.27, fig.3); PRASHAD, 1928:179; WENZ, 1938:705 (fig.2032).

Description

Shell (Figs.50, 52-54). Similar to those of *Notopala*. Distinctions following. Outline shorter and broader, somewhat discoid. Spire shorter, of 3 whorls; suture slightly deep. Color dark brown. Sculpture of irregular, spiral, low, narrow striae. Periostracum thick, smooth, except for 8 lines of periostracal hairs, each along spiral threads, clearer in young shells (Fig.50). Aperture rounded, prosocline (about 30° of longitudinal axis).

Head-foot (Fig.322). Similar to those of *Notopala*, except: foot slightly larger; color pale grey; pedal gland furrow lying along anterior half of foot edge.

Operculum (Figs.323-324). Almost circular. Outer sculpture concentric, low. Nucleus almost central, slightly towards middle level of inner edge. Inner scar occupying about ¼ of inner surface area, closer to inner edge.

Mantle organs (Fig.325). Generally like those of *N. ampullaroides*, remarks including following. Osphradium slightly longer, also on ctenidial vein and possessing series of small projections along its right edge. Gill filaments with broader base, narrowing abruptly; their distal 2/3 long and filiform; apex narrow and rounded. Endostyle ridge-like, running along entire gill right margin. Ad-rectal sinus conspicuous.

Circulatory and excretory systems (Fig.326) – Morphological attributes similar to those of *Notopala* species, with similar absence of separation between pericardium and posterior renal chamber. Anterior renal lobe broader laterally, both pores, including muscular, papilla-like pore to ureter, similar to *Notopala*.

Visceral mass (Fig.236) – Organization similar to preceding viviparids, but shorter, having only 1 whorl posterior to stomach. Gonad and digestive gland pale greenish beige.

Digestive system (Figs.326-327) – Foregut characters generally similar to those of *Notopala*. Jaw plates somewhat thicker. Aperture of salivary gland larger, disposed longitudinally in anterior half of buccal mass dorsal folds. Odontophore muscles:

m2 pair also with double insertion surrounding buccal ganglia; m7 pair very narrow; m7a pair similar, with double branches (one running towards posterior and other anterior) in radular sac; m11 pair also broad. Radular teeth shown in Fig.146. Salivary gland smaller, also convolute. Anterior esophagus slender; anterior region with pair of longitudinal folds (continuation from buccal mass dorsal folds), which gradually weaken and disappear. Middle and posterior esophagus also slender, inner surface covered by oblique, irregular, low, narrow folds. Middle and hindgut with similar features as those of *Notopala*, except for stomach having strong constriction in middle level of right surface, internally corresponding to thin gastric shield. Pair of ducts to digestive gland, located close together in ventral-anterior surface. Digestive gland with 2 incompletely separated lobes, one posterior and other ventral to stomach, each connected to duct from stomach. Rectum with elliptical fecal pellets, lacking any apparent organization.

Genital system – ♂ (Fig.322): Organization of posterior structures similar to those of *Notopala*, remarks following. Testis also pallial, lying on right of rectum. Ejaculatory tube also muscular, immersed in integument. Right cephalic copulatory tentacle about double left tentacle length, base twisted, narrowing gradually along its length; tip somewhat rounded and slightly broader than preceding region. Vas deferens very narrow throughout right tentacle. ♀ (Figs.326, 328-329): Visceral and pallial structures with similar features to those of *Notopala*. Albumen gland surrounding rectum behind pallial cavity. Albumen gland duct anterior and somewhat broad and thick. Visceral oviduct anterior end very narrow (Fig.328:vo), joining albumen gland duct as it exiting pallial cavity. Subsequently, albumen gland duct having long loop dorsal to ureter (about ¼ of brood pouch length), lies towards posterior, running close and at right from albumen gland and ventral to rectum. Capsule gland thick glandular walled, running about ¼ whorl in dorsal region of posterior renal chamber, twisting and lying towards anterior. Capsule gland inner surface with about 10 longitudinal, tall folds, its connection with brood pouch slightly narrow, at level of posterior region of pallial cavity. Brood pouch as for *Notopala*.

Central nervous system – Nerve ring similar to *Notopala*. Buccal ganglia large, located laterally to posterior region of buccal mass

Measurements of shells (in mm) – AMS 338590:

♀ 1: 16.0 by 16.0 (photo); ♀ 2: 16.4 by 16.2; ♂ 4: 8.7 by 9.1.

Distribution – Mid coastal Queensland.

Habitat – Under rocks and wood, in small to medium rivers (Ponder, person. communic.).

Material examined – AUSTRALIA - QUEENSLAND: Dawson R. nr. Theodore, on Taroom-Theodore Rd., 24°56.49'S 150°4.18'E, 0.01-0.1m depth. AMS 338590, 2♂, 13♀ (sta. 28911A; W.F.Ponder and D.Lindberg cols., 05/VII/1997).

Discussion – The present studied sample of *Larina* is not attributed with certainty to the species of the genus, with which it is very similar, pending a review of the taxonomy of the group (PONDER, personal communication). PRASHAD (1928) suggested that *Larina* is the only viviparid living in an estuarine environment, the others being freshwater, and had doubts about the familial placement of the genus, since the anatomy was unknown. Despite the imprecision of the identification of the present sample must be considered, *Larina* appears to be clearly similar to *Notopala*, and may belong to the same viviparid subgroup as that genus. See additional discussion on differences in the central nervous system in the character discussion section.

Superfamily Littorinoidea

Family Annulariidae

Genus *Annularia* Schumacher, 1817

Type-species: *Turbo lincina* Linné

Annularia sp.

(Figs.49, 55-56, 113-114, 147-149; 330-347)

Description

Shell (Figs.49, 55-56). Of small size (up to 15mm), tall, long, apex lost. Spire of about 3 whorls convex of somewhat same size. Sculpture successive axial threads, orthocone. Aperture rounded, with projected lips. Umbilicus narrow.

Head-foot (Figs.330-332, 336). Head broad, outstanding, color beige. Snout long and broad, slightly dorso-ventrally flattened; anterior margin plane, flat, with short lateral pointed expansions. Tentacles stubby and long (about same snout length). Ommatophores small, in outer side of their bases. Tentacles tip broad, rounded, brown pigmented. Foot relatively short, borders thick. Anterior furrow of pedal glands short. Another furrow runs in pedal sole along median line, from middle-ventral region of anterior furrow to posterior third of foot sole. Opercular pad large, lateral

margins extending little beyond foot edges. Males with long penis located posterior removed and at right from head (described below). Columellar muscle thick, of $\frac{2}{3}$ whorl, with apparently 2 regions separated by low fold. Haemocoel narrow and long, anterior half with walls thick muscular, posterior half walls thin. Pair of narrow and thin ventral retractor muscles of snout, passing through nerve ring. Some secondary thin and narrow ventral pairs of retractor muscles present, attached to haemocoel inner surface. Diaphragm-like septum in limit between head-foot haemocoel and visceral mass, thin, scarcely muscular.

Operculum (Figs.113-114). Sub-circular, thick, calcareous, palcispiral. Pale brown basal plate connected to opercular pad. White hard fold on spiral suture, protruded outside, margins irregularly broken.

Mantle organs (Figs.333, 337). Mantle border simple, smooth slightly thick. Some specimens (about 50%) with tall septa posterior to mantle border restricting pallial cavity aperture. Pallial cavity of about 1.5 whorls. Osphradium a small, low and long fold located in anterior-left corner of cavity. Similar sized glandular fold present at left of osphradium. Gill absent. Vessel net of lung somewhat sparse, intercalated branches of adrectal and left collar main vessels (circulation described below). Rectum very broad, sometimes occupying about half of cavity volume, replete of elliptical fecal pellets. Anus siphoned, small, located close to right margin of cavity posterior removed from mantle border. Pallial gonoducts run at right and dorsal to rectum (described below). Posterior limit of pallial cavity with pericardium (left) and kidney (right).

Visceral mass (Figs.243, 333). Of about 3 whorls, 2 first whorls most filled by digestive gland. Last whorl most occupied by stomach. Gonad relatively narrow, running in columellar surface.

Circulatory and excretory systems (Figs.335, 337) – Heart relatively small, located longitudinally in left limit of pallial cavity, part connected to columellar muscle. Auricle anterior, directly connected to left collar vessel. Adrectal vessel draining to kidney. Ventricle elliptical, posterior. Kidney divided into 2 regions. Posterior region a hollow chamber mostly filled by intestinal loops, loops connected to dorsal wall by mesentery. Posterior renal region with about half whorl. Anterior kidney region with about half of posterior region size, triangular, flat; entirely filled by folded renal tissue and separated from neighbor structure

by membrane. Anterior renal region limited posteriorly by its posterior chamber, anteriorly by pallial cavity and at left by pericardium. Nephrostome a small slit in middle-dorsal region of membrane between kidney and pallial cavity. Renal lobe(s) and nephridial gland not distinguishable, probably mixed in that single folded mass. Renal tissue not connected to intestine, attached to dorsal wall of anterior kidney region and detached from ventral walls, this narrow space nephrostome connects with pallial cavity. Shallow and narrow urinary furrow starts ventral to nephrostome, in pallial cavity floor, runs edging left pallial structures, contours right insertion of mantle in head-foot and gradually fades towards ventral in short distance.

Digestive system – Mouth in center of anterior snout surface (Fig.336). Buccal mass large, half inside snout and half protruded in remainder haemocoel (Fig.336). Odontophore about $\frac{2}{3}$ of buccal mass volume. Jaw plates missing. Dorsal wall of buccal mass inner surface with pair of dorsal folds low and narrow. Aperture of salivary glands small longitudinal slits, located in median and anterior region of dorsal folds (Fig.342). Between both dorsal folds shallow and smooth surface. Buccal mass and odontophore muscles (Figs.334, 338-341): m1) several small muscular fibers of jugal muscles, particularly more concentrated around posterior region of buccal mass, no pair outstanding; mj) peribuccal muscles with some layers of circular, oblique and longitudinal fibers mostly originated from outer surface of cartilages; m2) absent; m3) single thin and flat muscle in posterior-dorsal region of odontophore, insertion in both lateral ends; m4) pair similar to those of preceding species but constituted by single muscular mass (and not several pairs), origin in dorsal, ventral and ventral surfaces of odontophore cartilages, surround most of these cartilages tensioning subradular membrane (br) contour mj, insertion in tissue on radula preceding its exposed area (to); m5) thick and short, origin on m4 median-posterior outer surface, runs towards dorsal, insertion in radular sac dorsal surface; m6) horizontal muscle, short, thin, restrict to anterior, subterminal region of cartilages; m7) pair narrow, thin and long, origin in m4 ventral branch, runs towards posterior attached to subradular membrane on median line, in posterior level of odontophore connect with each other, insertion in single bundle inside radular sac region just posterior to odontophore; m9) pairs of narrow, superficial and flat muscles in dorsal-

posterior region of odontophore just anterior to m3, origin lateral in superficial membrane of odontophore, run towards posterior and medial slightly perpendicular to m4 fibers, insertion on "to" just posterior to m4 insertion; m10) pair broad, slightly thin, origin in ventral region of mouth, run towards posterior, insertion in odontophore ventral and lateral surfaces; m11) absent; m14) pair of superficial ventral protractor muscles of odontophore, thin and flat, origin in ventral-anterior surface of snout inner wall, run towards posterior lying odontophore ventral surface, insertion in posterior-ventral end of odontophore. Odontophore cartilages (Fig.341) long, flat and slightly arched, anterior end somewhat bifid. Septum between esophagus and odontophore tall; in this region dorsal inner folds bifurcate, outer branch very short, inner branches run along esophagus. Radular teeth (Figs.147-149): rachidian tooth tall and slightly barrow, outline triangular, cut-edge curved, cusps lacking, bluntly pointed tip, base broad and flat; lateral tooth tall, slender, outline slightly triangular, about as broad as rachidian, curved inwards, tip bluntly pointed, cusps lacking; inner marginal tooth narrow, tall, width about half of that of rachidian, uniform width along its length, base with longitudinal concavity where outer marginal tooth encases, tip broad, 4 stubby cusps in cut-edge of almost same size; outer marginal tooth broad, about twice rachidian width, base narrower than distal region, thicker reinforcement along inner edge, remainder middle and basal regions thin and flat, distal (cut) edge ample, about 50 long, slender, curved cusps which decrease gradually towards lateral. Salivary glands as 2 separated, slightly triangular masses (Fig.338) just posterior to nerve ring; their ducts somewhat broad and sinuous, run on dorsal surface of buccal mass through nerve ring, in short distance after nerve ring penetrate in dorsal wall, aperture above described. Esophagus long, broad, thin walled. Anterior esophagus with pair of low, longitudinal folds in a side (Fig.342). Posterior esophagus narrower, inner surface smooth. Stomach (Fig.343) very large and long (about 1 whorl length). Esophagus insertion in middle level of ventral-left (inferior) surface, single duct to digestive gland at right (superior) to esophagus insertion, relatively small. Gastric shield thin, elliptical, small, located dorsal and slightly anterior to esophagus insertion. Stomach inner surface most smooth, single longitudinal fold in left (inferior) surface, from esophagus insertion (slightly dorsal to it) to

posterior gastric end. Stomach gradually narrows anteriorly, without clear separation with intestine and style sac. No style found. Digestive gland beige, covers some portions around stomach and about 1.5 whorls posterior to it. Intestine broad, with 3 loops anterior to stomach inside renal posterior chamber (Fig.337). Fecal pellets formed in first intestinal loop. Rectum and anus above described.

Genital system – ♂ : Testis pale beige, long and very small, located in columellar surface of digestive gland first 1.5 whorls. Vas deferens very narrow, runs along ventral surface of stomach. Seminal vesicle intensely coiled (Fig.344), starts about 1 whorl posterior to pallial cavity. Seminal vesicle abruptly finishes at some distance from pallial cavity, vas deferens becomes very narrow and runs towards right and anterior, at right from rectum. Prostate long and broad (Fig.344), walls thick glandular, entirely closed (tubular). Prostate posterior end just in pallial cavity posterior limit. Prostate anterior end just posterior to anus, abruptly narrows and crosses to pallial cavity floor, runs short distance and penetrates in penis base. Penis (Figs.330, 331, 345) long, large, curved in base and apex, slightly flattened, length about same than that of pallial cavity. Muscular tissue present in anterior region of penis base connecting it with adjacent integument. Penis tip pointed. Penis duct very narrow, slightly coiled in basal half, simple in distal half, runs closer to lateral penis margin. ♀ : Visceral organs (Fig.343) similar located than respective structures of males, including very small and narrow gonad. Ovary color pale cream. Visceral oviduct (Figs.333, 347) with bulged portion of about ¼ whorl followed by another portion of ¼ whorl narrow and coiled, just posterior to pallial cavity. Albumen gland small, cylindrical, as thick pallial continuation of visceral oviduct. Capsule gland large, elliptical, broad, dorso-ventrally flattened, located dorsal to rectum, connected with middle level of pallial oviduct by narrow, subterminal duct. Vaginal tube, after capsule gland duct, gradually expands, part dorsal to rectum. Aperture a longitudinal slit turned to right, posterior to anus. Inner surface of vaginal tube thick, with pair of longitudinal folds.

Nervous system (Figs.346) – Of typical epiathroid fashion, supra esophageal ganglion far from nerve ring. Anterior pedal nerve very broad. Statocysts with single and large statolyth (Figs.334, 346).

N.B. – All examined specimens possess several small pearls along visceral mass, irregular in size,

iridescent, most in larger blood sinus as renal chamber.

Measurements of shells (in mm) – MZSP 28273: ♀ , 14.8 by 7.6; MZSP 28281, ♂ 1, 10.6 by 6.1; ♂ 2, 9.1 by 5.6.

Distribution – Full range unknown, but includes at least NE Mexico.

Habitat – Terrestrial, on dry vegetation.

Material examined – (R.Pinto-da-Rocha and S.Casari cols.) MEXICO - YUCATAN: Uxmal, MZSP 28266, 12 specimens, MZSP 28273, 3 specimens, MZSP 28275, 5 shells (25/IX/1996); near Blankanché Cave, MZSP 28281, 7 specimens (24/IX/1996).

Discussion – This unnamed species is very characteristic of the genus, however, a more precise identification was not possible because of the large number of species and the taxonomic confusion in the group. The generic placement of this species is based on the key to genera of HENDERSON & BARTSCH (1921:54). Although, it looks similar to *Choanopoma terecostatum* Thompson, 1966 (from Chiapas, Mexico) in shell and operculum characters, but differs in its shallower suture. Despite there being relatively comprehensive revisions of the Annulariidae (e.g., BARTSCH, 1946), the anatomical knowledge of the group is still poor.

DISCUSSION OF THE CHARACTERS

SHELL

1. Spire: 0= high (about 2 times aperture length); 1= low (ampullariids, cyclophorids, *Larina*); 2= planispiral (*Marisa*) (CI: 50; RI: 66; additive).

This character can be considered additive due to ontogeny, since *Marisa* presents a low spire during early development, as seen in protoconch. But when treated as non-additive nothing changes, neither in result or indices.

2. Periostracum: 0= thin; 1= thick/ (viviparids) (CI: 100; RI: 100).

3. Suture: 0= deep; 1= shallow (plane) (*F. neritiformis*, *A. megastoma*) (CI: 50; RI: 0)

4. Sculpture: 0= absent (smooth); 1= axial ridges (cyclophorids, *Annularia*) (CI: 50; RI: 66).

5. Determinate growth: 0= absent; 1= present (*Annularia*, cerithioideans) (CI: 100; RI: 100).

The shell characters (1-5) are little more than 3.5% of the characters. The shell is the main structure analyzed in most literature, and is the most accessible structure that the malacologist has for

analysis. With this in mind, special attention was paid to searching for conchological characters, but most were deleted as autapomorphies. Of the 5 shell characters used, only 2 (characters 2 and 5) are non-homoplastic in this analysis.

The determinate growth (character 5), which became a non-architaenioglossan caenogastropods synapomorphy (node 7), was explored in detail by VERMEIJ & SIGNOR (1992). It consists of the formation of a differentiated peristome in the shell when the animal reaches the adult phase. Determinate growth is, however, also known in some Cyclophoroidea not included in this study.

OPERCULUM

6. Outline: 0= circular; 1= with an upper-inner projection(sub-pyriform) (ampullariids, viviparids) (CI: 50; RI: 80).

The plesiomorphic condition is that normally found in the vetigastropods, with rounded outline and multi- or paucispiral. Although somewhat circular, the ampullariids and viviparids have a modified outline, a projection in upper-inner quadrant. This is an apparent adaptation for fitting it tightly into the aperture, occluding this completely and hermetically.

7. Outer surface: 0= spiral; 1= concentric (ampullariids, viviparids, cyclophorids) (CI: 50; RI: 50).

The members of the three architaenioglossan families in the analysis modified the outer surface of the operculum from a spiral to a concentric growth pattern. This condition was apparently reverted in the remainder basal caenogastropods, in which the paucispiral operculum is the rule.

The concentric outer sculpture is also found, by convergence, in some other caenogastropods, such as some families of Cerithioidea, in Stromboidea and in all "higher" superfamilies.

8. Type: 0= corneous; 1= calcareous (cyclophorids, *Annularia*) (CI: 50; RI: 66).

The calcareous operculum is herein considered derived from the corneous one. This type resulted as a convergence between both terrestrial forms (cyclophorids and annulariids). However, calcareous opercula are known to occur in several outgroups, such as, *e.g.*, the vetigastropod Trochoidea (Trochidae = corneous; Turbinidae, Phasianellidae = calcareous). Moreover, the ampullariids have representatives (not included here) with calcareous operculum, as in genus *Pila* Röding, 1798.

HEAD-FOOT

9. Food groove: 0= absent; 1= present (viviparids) (CI: 100; RI: 100).

The food groove running on the head-foot, in the floor of the pallial cavity, is an adaptation for filter feeding. The groove runs close to the apex of the gill filaments and conducts mucus with particles towards the mouth, by means of cilia (COOK, 1949). Amazingly similar food grooves are found convergently in other filter-feeding caenogastropods, such as struthiolariids (Stromboidea), vermetids (Cerithioidea) and calyptraeids (Calyptraeidea). These taxa apparently lacking any close relationship. The viviparid food groove differs from those of the other filter-feeding groups in being taller, forming almost a carina, and in having a relation with the right siphon (or nuchal lobe). This latter structure conducts the food to the mouth.

10. Right siphon: 0= absent; 1= present (ampullariids); 2= with a fold to mouth (viviparids) (CI: 66; RI: 88; additive).

The additive optimization of this character is because of ontogeny, as very young viviparids (state 2), found inside the brood pouch, lack the fold to mouth. If this character is considered non-additive, the result is the same, but both indices change to 100.

11. Left siphon: 0= absent; 1= present (ampullariids, viviparids); 2= very long (*Marisa*, *P. crosseana*, *P. scalaris*, *P. curumim*, *P. lineata*, *P. bridgesi*, *P. sordida*, *P. canaliculata*) (CI: 40; RI: 75; additive).

The right and left siphons, also called nuchal lobes (PRASHAD, 1925; SCOTT, 1957) and pseudo-epipodia (PRASHAD, 1925), are prominent muscular flaps with the apparent function of controlling the water flow inside the pallial cavity. The left siphon is longer and works in the incurrent, and the right siphon in the excurrent flow (ANDREWS, 1965b).

In some ampullariids, the left siphon is very extensive, becoming sometimes twice as long as the shell. Its tip may be extended from the water surface, capturing air (PRASHAD, 1925:120; DEMIAN, 1965; pers.obs.). Their presence and length have also been considered by BERTHOLD (1991) and BIELER (1993, characters 37-38), and have been utilized for separating genera long ago (BINNEY, 1867:2).

Due to their similarity, the head-foot siphons of the ampullariids and viviparids were tentatively considered homologues. However, the siphons of both groups differ in some details of their bases,

with the viviparids having the base divided by a median, tall fold (clearer in the right siphon). This fold is maybe an adaptation for conducting the food to the mouth, and is lacking or inconspicuous in the ampullariids. Considering the cladogram obtained in this analysis, the siphons should have arisen in node 4 and reverted in node 7. However, another equally parsimonious optimization exists, convergence between nodes 6 and 10 (viviparids and ampullariids respectively). The first hypothesis is shown in the cladogram.

The ampullariid and viviparid siphons are clearly a modification of the head-foot, which differentiates them from the siphons of the "higher" caenogastropods. In these groups, the siphons are clearly a modification of the pallial edge (ANDREWS, 1965b:86).

The character 11 was considered additive because the state 2 is potentially a state 1 modification. The tree is the same if the character was considered non-additive, the indices, however, change to CI: 50 and RI: 81.

12. Ommatophore in tentacles; 0= absent; 1= present (all species) (CI: 100; RI: 100).

The ommatophore is here defined as a secondary stalk for the eyes, positioning them away from the main axis of the cephalic tentacles. In the archaeogastropods, the ommatophore, when present, is normally located close to, but separated from the tentacle. In the architaenioglossans, as well as in the other caenogastropods that possess this structure, the ommatophore is part of the cephalic tentacle. Although, in the 2 basal branches (cyclophorids and ampullariids) the ommatophore is located on the tentacle base, while in the other caenogastropods it is located more distally.

13. Pedal furrow of pedal glands: 0= anterior margin only; 1= entire foot margin (*Neocyclotus prominulus*); 2= also along sole, on median line (*Annularia*) (CI: 100; RI: 100; non-additive).

Pedal glands are expected to be found in all gastropods. In the caenogastropods, beyond this, possess an additional furrow lying at anterior margin of the foot, into which the anterior mucus glands open. This furrow probably is used for spreading the mucus along the foot sole. Beyond this adaptation, 2 additional modifications to the foot furrow were detected, as noted above, resulting as autapomorphies.

14. Columellar muscle: 0= 1.5 whorls; 1= $\frac{3}{4}$ whorl (cyclophorids); 2= $\frac{1}{3}$ whorl (ampullariids except *Marisa*) (CI: 100; RI: 100; non-additive).

See comments after character 17.

15. Columellar muscle number: 0= 2; 1=1 (all species) (CI: 100; RI: 100).

The single columellar muscle is a derived condition from the double one found in archaeogastropods. However, it is known that the state 1 is shared with a few members of the caenogastropod sister-taxon, the Heterobranchia.

16. Pair of snout tentacles: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).

The snout tentacles are long projections of the lateral edges of the structure anterior surface, being almost as long as the cephalic tentacles. PRASHAD (1925) described them for *Pila*, calling them labial palps or anterior tentacles. These tentacles are a notable ampullariid synapomorphy, and have also been considered by BERTHOLD (1991) and BIELER (1993, character 1). Analogous structures are also found in some heterobranchs, such as the nudibranchs.

PALLIAL CAVITY

17. Pallial cavity length: 0= 1 whorl; 1= 1.5 whorls (viviparids); 2= less than $\frac{1}{2}$ whorl (ampullariids except *Marisa*) (CI: 100; RI: 100; non-additive).

The viviparids, because of their filter-feeding adaptations, developed a very long pallial cavity (state 1). Most ampullariids (node 12), on the other hand, presents a very short cavity (state 2), maybe a consequence of the spherical shell. This shortness is also reflected in the columellar muscle length (character 14).

18. Osphradium form and type: 0= small, circular; 1= long, ridge-like (viviparids, *Annularia*, cerithioideans); 2= elliptical (ampullariids); ?= cyclophorids (CI: 100; RI: 100; non-additive).

The osphradium commonly found in the archaeogastropods and in the heterobranchs (which have it) is in form of a small node. This state was modified in the ingroup: the cyclophorids lost it; the ampullariids developed an elliptical, bipectinate fashion (state 2); while the viviparids, as well as the remaining caenogastropods, have a long, ridge-like osphradium (state 1).

19. Osphradium leaflets: 0= absent; 1= present (ampullariids); 2= small projections on right side only (*Notopala spp*, *Larina*) (CI: 100; RI: 100; non-additive).

20. Osphradium: 0= sessile; 1= on a stalk (*P. crosseana*, *P. bridgesi*, *P. sordida*, *P. canaliculata*, *A. megastoma*); 2= on ctenidial vein (*Notopala spp*, *Larina*) (CI: 66; RI: 85; non-additive).

The osphradium is a sensory organ of olfaction, important in aquatic species. In caenogastropods, particularly, this structure is normally complex and large if compared to those of other molluscs. In terrestrial forms, the osphradium is generally reduced (*e.g.*, annulariids), or missing (*e.g.*, cyclophorids). The vestigial osphradium of *Annularia* sp., despite its small proportions, is long, which suggests the tentative attribution to the state 1 in the character 18.

The osphradium of the ampullariids has been classified as bipectinate. Bipectinate osphradia are also found in other caenogastropods, such as, *e.g.*, cerithiids (Cerithioidea), strombids (Stromboidea), and “higher” caenogastropods (Calyptraeidea, Naticoidea, Cypraeoidea, Tonnoidea, Neogastropoda), as I have observed. However, the ampullariid bipectinate osphradium is a quite different from these other caenogastropods in being located on a stalk, and in having a conspicuous longitudinal fold uniting both sides of the filaments. Those differences suggest that the bipectinate condition of the ampullariid osphradium may be due to convergence, and that this kind of modification, for increasing the surface of this sensory organ, may be a common feature among caenogastropods. Only the osphradium short length have been considered by BERTHOLD (1991) and BIELER (1993, character 2). PRASHAD (1925:95, 143) has described the osphradium of *Pila* and is a quite similar to the South American species studied here.

No vestige of an osphradium was found in the examined cyclophorids. This is the reason for putting question marks on the matrix in all osphradial characters of the cyclophorids. However, it is expected that additional studies on ontogeny, and on more species, will bring new revelations.

21. Gill: 0= present; 1= absent (cyclophorids, *Annularia*) (CI: 50; RI: 66).

The terrestrial, air-breeding species, lost the gill. However, a vestige of its original blood supply, with an afferent vessel on the right and an efferent (homologue to the ctenidial) vessel on the left, is found in annulariids and cyclophorids. The collateral circulation between these 2 vessels is markedly increased, to form a lung.

22. Gill anterior end: 0= posterior from mantle border; 1= on mantle border (viviparids); ?= no gill (CI: 100; RI: 100).

23. Gill outline: 0= elliptical; 1= narrow and curved (ampullariids except *P. curumim*) (CI: 50; RI: 85).

24. Gill filaments: 0= triangular; 1= rounded (*P. curumim*) (CI: 100; RI: 100).

25. Gill filament tip: 0= central; 1= at right (*F. neritiniiformis*, *P. scalaris*, *P. curumim*, *P. lineata*, *P. canaliculata*, *A. megastoma*, *Viviparus* spp., cerithioideans) (CI: 25; RI: 57).

The gill of the viviparids has an additional function beyond respiration, as it is also used for filter feeding. For this task, the viviparid gill obviously presents modifications, mainly an enlargement of the total length and of the filaments. The ampullariid gill, on the other hand, due to the compression of the lung (which additionally helps in the respiration), is narrow, and normally curves around the lung sac. The unusual fashion of the ampullariid gill have been considered by BERTHOLD (1991) and BIELER (1993, character 4), and was described in more detail by PRASHAD (1925:96-98) for *Pila* and by LUTFY & DEMIAN (1965) for *Marisa cornuarietis*.

Once more, because of the absence of the structure in the terrestrial forms, the gill characters have been coded with a question mark on the matrix for the cyclophorids and annulariid.

26. Ctenidial vein: 0= single; 1= double (*P. lineata*, *P. sordida*, *P. canaliculata*) (CI: 33; RI: 0).

Beyond the development of the lung (see comments after character 29), the ctenidial vein of the above *Pomacea* species is double in its middle and anterior parts.

27. Distance gill-rectum: 0= broad; 1= very close (*Pomacea* spp, *A. megastoma*, *F. neritiniiformis*) (CI: 100; RI: 100).

28. Endostyle: 0= absent; 1= present at right of gill (viviparids) (CI: 100; RI: 100).

The name “endostyle” is used as an analogy to the structure in the Cephalochordata, and has been used in the literature on filter-feeding gastropods. The endostyle is an additional glandular ridge parallel to the gill, normally present in filter-feeding caenogastropods, such as struthiolariids (Stromboidea), turitellids-vermetids (Cerithioidea) and calyptraeids (Calyptraeidea). In these taxa, the endostyle is different in being located along the left edge of the gill, and is apparently developed from a modification of the local mucus cells of the mantle.

As the viviparids are filter-feeding animals, they also developed a glandular ridge, here called an endostyle (Fig.304: en). However, the viviparid endostyle is unlike those of above mentioned taxa in being located along the right edge of the gill (instead of in

left side), and in being apparently developed from a modification of the gill filaments. This is suggested because of the location of the structure between the filaments and the afferent gill vessel, as well as the presence of successive septa in the endostyle, each one corresponding to a gill filament.

29. Lung sac: 0= absent; 1= present and short (ampullariids); 2= present and very long (*Marisa*) (CI: 100; RI: 100; additive).

It is intuitive to deduce the evolution of the gill-less pallial cavity of air-breathing snails such as the cyclophorids and annulariids (*e.g.*, CEI, 1942). In fact the lung vessel present in both groups running on the left margin of the pallial cavity is probably homologous to the ctenidial vein, since it is located in a similar position and is connected to the auricle. However, the derivation of the net of lung vessels from the vessels and sinuses of the gill is still not clear. The pallial cavity of *Cyclophorus* (TIELECKE, 1940) is similar to the cyclophorids examined herein. Some studies on the pallial blood vessel circulation (*e.g.*, TIELECKE, 1940) shows that the circulation pattern in *I. tupy* and *A. blanchetiana* is normal for the family, and *N. prominulus* could present a derived condition. This species has the vessel homologous to the ctenidial vein running along the left edge of the lung inserting in the kidney, instead of the auricle.

The ampullariid lung differs from that in any other terrestrial gastropod, normally formed in the pallial cavity by the loss of the gill and an enlargement of the mantle vessels (see comments after character 21). The ampullariid lung is surrounded on the right by the gill and is restricted to the left region of the pallial cavity, posterior to the osphradium.

The ampullariid lung is a sac with muscular walls, its inner surface has a net of transverse brood vessels, protruding inside it. A pneumostome, with muscular edges, is the aperture of the lung sac, and is located in its anterior-left region, turned to the base of the left siphon. BERTHOLD (1991) noted that some ampullariids lack musculature surrounding the pneumostome, which may be the plesiomorphic condition, and this was considered by BIELER (1993) as character 36. The lung sac is a conspicuous synapomorphy present in all species of the family, and has also been considered by BERTHOLD (1991) and BIELER (1993, character 3).

The analysis of the morphology of the lung sac reveals that the blood inside its vessels came from the marginal vessel located along the anterior and left edges of the organ. The origin of this vessel is

almost in the anterior end of the afferent ctenidial vessel, and afterwards, it crosses above the anterior region of the gill. This arrangement suggests that the lung sac afferent vessel may be derived from the afferent ctenidial vessel. Details of the histology of the lung are found in LUTFY & DEMIAN (1965).

The blood situated in the lung sac vessels flows to the ctenidial vein, which supplies both, the gill and the lung (ANDREWS & LITTLE, 1972: fig.1d; this study). In some species (character 26), the ctenidial vein is duplicated in its anterior and middle regions, differentiating a lung efferent vessel. However, PRASHAD (1925) has described for *Pila* a totally duplicated vessel, *i.e.*, a pulmonary and ctenidial vein, wholly separated from the anterior region until they reach the auricle (see his figs.10, 12, and fig. 1 of pl.18). This condition is assumed to be the more derived state. The additional afferent vein of *Pomacea canaliculata* has been advocated as a development of a horizontal division of the efferent ctenidial vein (ANDREWS, 1965b). A study on the respiratory mechanism of an ampullariid (*Marisa cornuarietis*) was provided by DEMIAN (1965). BROOKS (1907) and BROOKS & MCGLONE (1908, pls.1-7) have reported the embryological appearance of the ampullariid lung, and suggested an origin from the gill.

The long lung sac of *Marisa* is perhaps an adaptation to the planispiral shell, and is suggested that it has been derived from the short lung sac, present in other ampullariids. For this reason, the 3 states of character 29 are considered additive. However, nothing changes if the character is not considered additive. The lung of *Pomacea* has been regarded as more highly organized than that of other genera (ANDREWS, 1965b: 88), this is true in relation to *Marisa*, but this does not differentiate the genus from *Felipponea*, *Pomella* and *Asolene*; anyway, this character could be another basing the node 12.

30. Hypobranchial gland: 0= thick; 1= thin, inconspicuous (ampullariids, *Notopala spp.*, *Larina*, *Annularia*, cyclophorids) (CI: 33; RI: 33).

The hypobranchial gland is normally well developed in caenogastropods, particularly in aquatic taxa. However, most ingroup species have a thin, inconspicuous hypobranchial gland, practically represented only by the mantle mucosa. ANDREWS (1965b) demonstrated that hypobranchial gland is present in *Pomacea canaliculata*, but only distinguishable in sections, and is unusual in covering the rectum and genital ducts. Further studies are necessary to determine, though, if the

caenogastropod hypobranchial gland is actually homologous to the hypobranchial gland of the archaeogastropods.

Cyclophorids have modified the hypobranchial gland for an accessory excretory gland (ANDREWS & LITTLE, 1972, 1982). This feature is commented in the character 44.

The basal gland, present in the base of the male penis shield of the ampullariids, has been referred to as hypobranchial gland. This nomenclature is not followed here because the gland is only present in the males. Additionally, nothing else suggests a homology of this gland with the ordinary hypobranchial gland, normally located between the gill and the rectum.

CIRCULATORY SYSTEM

31. Pericardium: 0= visceral and pallial; 1= also connected to pallial floor (ampullariids) (CI: 100; RI: 100).

32. Ampulla in anterior aorta: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).

The ampullariids have the two modifications in the heart explored in the characters 31 and 32. The ampulla at the origin of the anterior aorta (Figs.154, 179:am) is of particular interest for future physiological studies. This structure is almost as large as the ventricle, differing by its thinner walls, and by its location just after the origin of the posterior aorta. The ampulla is a long known ampullariid feature (*e.g.*, PRASHAD, 1925: fig.10), and has also been taken into consideration by BERTHOLD (1991) and BIELER (1993, characters 5, 40).

The development of an ampulla have been advocated as an adaptation to accommodating the blood forced into the heart during the retraction of the animal into its shell (ANDREWS, 1965b).

33. Intestinal loop inside pericardium: 0= absent; 1= present (*Larina*, *Notopala spp.*) (CI: 100; RI: 100). Normally there is a structural correlation between the pericardial cavity and the kidney cavity, particularly with the posterior renal chamber (when 2 chambers are present). The Australian viviparids *Notopala* and *Larina* are derived in have lost the membrane that separates both the pericardium and the posterior renal chamber. This state forms a wide cavity in which the heart and intestinal loops stay together.

EXCRETORY SYSTEM

34. Number of kidneys: 0=2; 1=1 (all species) (CI: 100; RI: 100).

Most archaeogastropods possess a pair of kidneys, as well as a pair of pericardial structures and pallial organs. The caenogastropods, on the other hand, lost totally the (post-torsional) right structures, including the kidney. However, it is known that the loss of the right structures is a derived condition shared with the heterobranchs, the caenogastropods sister-taxon, and also some sparse archaeogastropod taxa.

35. Renal tissue: 0= solid glandular mass in pallial cavity roof; 1= solid glandular mass confined in a separated chamber (ampullariids); 2= a thin layer of gland and vessels (viviparids) (CI: 100; RI: 100; non-additive).

36. Renal lobes: 0= single: 1= 2 (all species) (CI: 100; RI: 100).

37. Intestinal loops in kidney chamber connected by a mesentery: 0= absent; 1= present (ampullariids, *Annularia*) (CI: 100; RI: 100).

The clear mesentery present in some ingroup species, connecting the intestinal loops inside the posterior renal chamber to its dorsal-right surface, is an interesting feature, mainly relative to the discussion of the coelomatic condition of molluscs, as it suggests a true coelom. BERTHOLD (1991) and BIELER (1993, character 18) have considered a "repeatedly coiled" intestine as an ampullariid feature, however, but did not mention an association with the kidney. On the other hand, BOUVIER (1888, figs.2, 7) BURNE (1898) and PRASHAD (1925) have reported the coiled intestine inside the renal chamber. The ampullariid kidney function has been investigated by LITTLE (1968), but no information on the function of the intestinal loops was reported.

38. Anterior septate chamber: 0= absent; 1= present, with two equal-sized series of septa (*Marisa*); 2= present, with two asymmetrical series of septa (remainder ampullariids) (CI: 100; RI: 100; additive).

The anterior chamber has been reported by BOUVIER (1888, fig.3) and PRASHAD (1925, fig.13), and was also considered by BERTHOLD (1991) and BIELER (1993, character 6). Some histological features of this kidney region are found in PRASHAD (1925:124).

The anterior chamber has been referred as "ureter" by some authors (*e.g.* THIENGO, 1987, fig.8). This terminology can suggest any homology with the ureter of the viviparids, however, based on investigations on the structure of viviparids (JOHANSSON, 1950), ANDREWS (1965b: 88) have

suggested that this hypothesis is not upheld. Another current name for the anterior renal chamber is "lamellar renal organ" (BURNE, 1898). The additive optimization is based on ontogeny, since very young specimens of all ampullariids possesses state 1. However, nothing changes if the character was considered non-additive.

39. Connection between longitudinal fold of renal anterior chamber with nephrostome edge: 0= absent, 1= present (ampullariids, except *Marisa*) (CI: 100; RI: 100).

40. Nephrostome: 0= in middle region of membrane between kidney and pallial cavity; 1= close to posterior end of pallial cavity (cyclophorids); 2= inside ureter (viviparids); 3= connected by an anterior chamber (ampullariids) (CI: 100; RI: 100; non-additive).

The position of the nephrostome of the ampullariids has been shown and discussed by BURNE (1898).

41. Closed ureter: 0= absent; 1= present (viviparids) (CI: 100; RI: 100).

42. Communication between kidney and ureter; 0= absent; 1= an open pore (viviparids); 2= a muscular papilla (*Notopala spp*, *Larina*) (CI: 100; RI: 100; additive).

43. Urinary gutter: 0= absent; 1= a furrow along right margin of pallial cavity and head (cyclophorids); 2= a fold along rectum and pallial gonoducts (ampullariids) (CI: 100; RI: 100; non-additive).

PRASHAD (1925), DEMIAN (1965) and LUTFY & DEMIAN (1965) have called the urinary gutter of ampullariids as "epitaenia".

44. Collar vessel: 0= inserted in kidney; 1= inserted in auricle (*A. blanchetiana*, *I. inca*) (CI: 100; RI: 100).

The ingroup taxa are all non-marine gastropods. Adaptations to freshwater (ampullariids, viviparids) or terrestrial (cyclophorids, annulariids) environments certainly demand modifications of the kidney, because this organ must conserve electrolytes (freshwater forms) and water (terrestrial forms). These extra efforts, if compared with marine groups, certainly brings effects in the morphology. This has presumably resulted in the complexity of the ingroup kidneys, outlined in characters 35-44.

Although the members of each ingroup family have similar kidney modifications, each family is very different from each other. All taxa have two chambers, a posterior, with intestinal loops and usually connected to pericardium, and another anterior, in pallial cavity. The cyclophorids differs

in having the posterior chamber lacking visible glands, and an almost solid anterior chamber. The ampullariids have a dorsal renal lobe in the posterior chamber and the anterior chamber has two series of transverse glandular septae. The viviparids resemble the cyclophorid arrangement, but the anterior chamber is solid.

The urine transportation from the nephrostome to the exterior also involves further modifications. The ampullariids and the cyclophorids have a urinary gutter, formed by a fold running along the right edge of the pallial cavity, from the nephrostome to the region behind the head (character 43). The viviparids, on the other hand, developed a tubular ureter (character 41), which conducts the urine from the nephrostome to the region close to the mantle border; this ureter runs attached to the rectum and its pore is close to the anus.

Most of the ingroup kidney structures have obscure functions, and are an interesting area for further investigation. ANDREWS & LITTLE (1972) performed a discussion on of the excretory system of architaenioglossans, comparing their anatomy and physiology (their fig.6, p.410). The authors described a large hypobranchial gland in all examined species (no one from South America), composed by subepithelial tubular glands, secreting purines, phospholipids and mucus. Such a gland is absent, at least as a clear organ, in the examined species, except *Incidostoma tupy*, in which it is small and lies covered ventrally by posterior portion of rectum [Fig.262, middle-superior region, between rectum (rt)]. Further and wider discussion on the excretory strategies, in a comparative scenario, is provided by ANDREWS (*e.g.*, 1979, 1981).

DIGESTIVE SYSTEM

BUCCAL MASS

45. Jaws: 0= pair of small plates; 1= very large (ampullariids); 2= plated fused in median line (cyclophorids); 3= absent (*Annularia*) (CI: 100; RI: 100; non-additive).

The enlargement of the ampullariid jaws has been also considered by BERTHOLD (1991) and BIELER (1993, character 11).

46. Dorsal chamber of buccal mass: 0= deep; 1= shallow (*Annularia*, cerithioideans) (CI: 100; RI: 100).

47. Dorsal folds of buccal mass: 0= low, inconspicuous; 1= broad, tall (all species); 2= with transverse furrows (ampullariids) (CI: 100; RI: 100; additive).

The dorsal chamber (character 46) is located in the dorsal wall of the buccal mass, opposite the odontophore, and may be an adaptation to avoid radular auto-injury. It is particularly large in the archaeogastropods. In the caenogastropods, however, there are a pair of broad and somewhat tall folds (character 47), and the dorsal chamber is reduced. These states have been regarded as notable synapomorphies of the ingroup (*e.g.*, Fig.160: df, dc). Heterobranchs, on the other hand, apparently lack both the folds and chamber, with the dorsal wall of the buccal mass more muscular and with the inner surface simpler. The dorsal folds had been also reported by PRASHAD (1925), and called a "buccal gland on the roof of the buccal cavity".

The additive optimization is based on ontogeny, since young specimens of ampullariids lack transverse furrows, acquiring them early in development. However, the result and indices are the same if the character is considered non-additive.

ODONTOPHORE

48. Mj: 0= diffuse; 1= 2 broad bands (all species) (CI: 100; RI: 100).

49. M1a: 0= absent; 1= present (cyclophorids) (CI: 100; RI: 100).

50. M1b: 0= absent; 1= double (*N. prominulus*); 2= single mass (*A. blanchetiana*, *I. inca*) (CI: 100; RI: 100; non-additive).

51. M2 as pair of retractor muscles of buccal mass: 0= absent; 1= present (viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100).

The m2 of the 3 above mentioned groups work as retractors of the buccal mass (retractor of "pharynx"). The pair is dissimilar to that called m2 of ampullariids, which is an abductor of the jaw plates, and is not considered homologous.

52. Ma: 0= absent; 1= present and single (cyclophorids); 2= multiple (ampullariids) (CI: 100; RI: 100; non-additive).

PRASHAD (1925, fig.4) described 3 pairs of here denominate 'ma' for *Pila*, calling them anterior dorsolateral muscles; while BROWN & BERTHOLD (1990), describing *Lanistes neritoides*, called madible adductors.

53. M3: 0= absent; 1= pair with dorso-ventral fibers (*N. prominulus*); 2= single, with transverse (latero-lateral) fibers (*P. scalaris*, *P. curumim*, *P. lineata*, *P. bridgesi*, *P. sordida*, *Annularia*); 3= both (H-fashion) (*Marisa*, *P. crosseana*, *F. neritiformis*, *P. canaliculata*, *A. megastoma*) (CI: 60; RI: 80; non-additive).

An m3 is also present in *Pila*, according to PRASHAD (1925, fig.5), which he called "superficial muscles of the ventral surface of the buccal mass".

54. M4 pair: 0= composed by several muscles; 1= composed by 2 pairs of muscular layers surrounding odontophore cartilages (all species); 2= a single pair of large mass surrounding odontophore cartilages (viviparids; *Annularia*, cerithioideans) (CI: 100; RI: 100; additive).

The additive optimization is a try for testing if the large mass fashioned m4 is a modification (fusion) of the 2 layered m4 of 2 more basal branches. However, the result and indices do not change if the character was optimized as non-additive. This result is compatible with the suggestion, but further studies are surely necessary.

55. M4 connection with tissue on middle region of radula (to): 0= absent; 1= via m9 (ampullariids); 2= present (viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100; non-additive).

Although in part of the viviparids (*Larina* and *Notopala*) a pair of m9 muscles is found (divided in some separated fibers), they have a connection between the m4 pair with the above referred tissue. Then, these species are coded in the state 2.

56. Ventral and dorsal branches of m4 pair: 0= not connected anteriorly; 1= connected anteriorly (viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100).

57. Ventral tensor muscle of radula: 0= present; 1= very reduced (m11) (all species) (CI: 100; RI: 100).

58. Dorsal tensor muscle of radula: 0= weak; 1= strong (m4 + m5) (all species) (CI: 100; RI: 100).

59. M5 pair: 0= connected with odontophore cartilages; 1= on m4 (all species) (CI: 100; RI: 100).

60. M5 pair form: 0= short and broad; 1= long and thin (all species) (CI: 100; RI: 100).

61. M6: 0= edging most of medial surface of odontophore cartilages; 1= edging less than 2/3 of this surface (all species) (CI: 100; RI: 100).

62. M6: 0= narrow and thin; 1= broad and thick (all species) (CI: 100; RI: 100).

63. M7: 0= absent; 1= present (all species) (CI: 100; RI: 100).

64. M7a pair (inserted in m5): 0= absent; 1= present (*Viviparus* spp) (CI: 100; RI: 100).

65. M2 as abductor of jaw plates: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).

See comments after character 51.

66. Approximator muscles of cartilages: 0= present; 1= absent or part of m4 (all species) (CI: 100; RI: 100).
67. M9: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).
68. M10 insertion in odontophore ventral surface: 0= posterior; 1= anterior (all species) (CI: 100; RI: 100).
69. M10a: 0= absent; 1= present (viviparids) (CI: 100; RI: 100).
70. M10c: 0= absent; 1= present (cyclophorids) (CI: 100; RI: 100).
71. M11: 0= broad, as ventral tensor muscle of radula; 1= narrow (all species) (CI: 100; RI: 100).
72. M12: 0= absent; 1= present (ampullariids, *Viviparus* spp, cerithioideans) (CI: 33; RI: 71).
73. M14: 0= absent; 1= present (*Annularia*) (CI: 100; RI: 100).
74. Number of main cartilages: 0= more than 1 pair; 1= single pair (all species) (CI: 100; RI: 100).
75. Pair of accessory cartilages: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).

The odontophore muscles and structures are an important source of comparative data (characters 48-75). The architaenioglossans present an interesting link between the archaeogastropod and other caenogastropod odontophores in several characters. An example is the pair of m4 muscles. This muscle is the largest pair from the caenogastropod odontophore, surrounding almost the entire cartilages, and apparently works as the main tensor of the subradular membrane. Analyzing the archaeogastropod odontophore, nothing similar to m4 is found. Apparently, the caenogastropod m4 is a combination of several pairs of archaeogastropod muscles, such as the several pairs that connect the cartilages to the subradular membrane (character 54), and also the pairs that connect the anterior with the posterior cartilages (character 66). The two first branches of the caenogastropods, the Cyclophoroidea and the Ampullarioidea, have the m4, composed by two layers (m4 and m4a). This state is here interpreted as an intermediate step to a single-layered and thick m4, derived from several pairs of muscles.

The odontophore cartilages (character 74) are present, in general, as more than one pair in the archaeogastropods, mostly as two pairs (anterior and posterior pairs). However, all caenogastropods (including the architaenioglossans) have a single pair. This pair is homologue to the anterior pair of archaeogastropod cartilages, according to the

analysis of some muscles, such as, *e.g.*, the horizontal muscle (m6).

A possible function of the muscles and odontophore is suggested elsewhere (SIMONE, 2001), the odontophore of the caenogastropods, including those of architaenioglossans, differs from the archaeogastropod and heterobranch odontophore in having no apparent gliding between the radula and the cartilages, provided, in those taxa, by the ventral and dorsal tensor muscles (characters 57, 58) working alternately. In the caenogastropods, the muscles apparently work pulling and stretching the subradular structures (membrane and cartilage) and the entire odontophore works grinding the food.

Most of the comparative analyses and the polarization of the odontophore characters (48-75) are based on comparisons with the archaeogastropods. Although some heterobranchs were examined, their odontophore apparently has other, still unclear, modifications, any comparative analysis is still premature.

The present discussion on odontophore features is still superficial. Further analysis will be done in the final stage of the project, when all caenogastropod superfamilies will be analyzed and each muscle will be discussed.

The ampullariids developed a secondary pair of thin cartilages (Figs.166-167:oa), this pair of cartilages is probably a modification of the subradular membrane. These cartilages connect the ventral and dorsal branches of the pair m4. Analyzing their location, it is clear that the secondary cartilages are new acquisitions. The cyclophorids have nothing uniting both referred branches of the m4, while the remainder caenogastropods (including viviparids) both branches are united with each other (character 55). PRASHAD (1925) performed a detailed study on the odontophore of *Pila globosa* and have described two pairs of cartilages. What he called "superior cartilages" are apparently what is called here subradular cartilage (*e.g.*, figs.163, 286: sc). This structure is shown as very thick (his figs 6, 8, 9), but he referred to them as very thin in the text (PRASHAD 1925:102). Then, PRASHAD's "superior" cartilages are not related to the accessory cartilages described herein, suggesting that *Pila* lacks this attribute. He called the ordinary odontophore cartilages as "lateral" cartilages.

RADULA

76. Subradular cartilage: 0= narrow; 1= broad (all species) (CI: 100; RI: 100).

The subradular cartilage (sc) is most probably secreted by the subradular membrane (br), and is a transparent, chitinous pair of expansions of the radula, in buccal cavity. The subradular cartilage is a specialization of the cartilage that covers the inferior surface of the radular ribbon, which links the teeth.

The subradular cartilage is present in the archaeogastropods, but is narrow. In caenogastropods, the structure is broad, entirely covering the buccal surface of the subradular membrane that, otherwise, would be exposed directly to the buccal cavity, accessible to injuries. The heterobranchs apparently also have a broad subradular cartilage, but it is still unclear its state in the basal taxa.

77. Radular sac length: 0= long; 1= short (about same length of buccal mass) (ampullariids) (CI: 100; RI: 100).

The short length of the radula in ampullariids has also been considered by BERTHOLD (1991) and BIELER (1993, character 12).

78. Rachidian form: 0= narrow; 1= broad (ampullariids); 2= tall and curved (viviparids) (CI: 100; RI: 100; non-additive).

79. Rachidian cusps: 0= few (0-3); 1= multicuspid (ampullariids, viviparids, cerithioideans) (CI: 50; RI: 75).

80. Rachidian basal broad cusp pair: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).

81. Rachidian tip: 0= broad; 1= pointed (*A. blanchetiana*; *I. inca*; *Annularia*) (CI: 50; RI: 50).

82. Lateral teeth number: 0= several (about 5); 1= 1 (all species) (CI: 100; RI: 100).

83. Lateral teeth tip: 0= multicuspid; 1= 1-2 cusps (*A. megastoma*, *F. neritiformis*, cyclophorids, *Annularia*) (CI: 25; RI: 40).

84. Lateral teeth shape: 0= different from rachidian; 1= tip tends to be similar shaped to rachidian (all species) (CI: 100; RI: 100).

85. Marginal teeth number: 0= many (more than 10); 1= 2 (all species) (CI: 100; RI: 100).

86. Marginal teeth shape: 0= similar to each other; 1= different (all species) (CI: 100; RI: 100).

In the current literature, radular characters have generally been more important than those of the shell and operculum in comparative analyses. Several radular characters were in fact searched in present study, but they were eliminated because resulted as autapomorphies. Only the characters

77-86 are suitable, and were polarized mainly based on the analysis on the archaeogastropods. In those taxa, the typical radula is rhipidoglossate, with a central (rachidian), about 5 lateral, and many marginal teeth. Nearly all caenogastropods, however, have a taenioglossate radula (or a kind of radula derived from it), including the architaenioglossans. The taenioglossate radula has only 7 teeth per row: a central or rachidian, a pair of lateral, and two pairs of marginal teeth.

SALIVARY GLANDS

87. Aperture in dorsal wall of buccal mass: 0= middle; 1= anterior (viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100).

88. Salivary glands: 0= absent; 1= present as 2 separated masses (all species); 2= a single fused mass (ampullariids, *Annularia*) (CI: 66; RI: 88; additive).

The additive optimization of this character is based on ontogeny, since, as well as is known, the ontogeny of the salivary glands starts as 2 separated masses. The apparent fusion is normally due to enlargement. If the character was considered non-additive, nothing changes in the result, only the RI changes to 87.

89. Type: 0=glandular; 1= tubular (*Notopala* spp, *Larina*) (CI: 100; RI: 100).

Salivary glands are present in other classes of the mollusks, but there are several archaeogastropod taxa lacking them (SASAKI, 1998). The polarization of salivary glands characters (87-89) is mainly based on the archaeogastropods that possess them. The salivary glands are particularly well developed in caenogastropods. Additionally, they developed salivary ducts, a character also shared with heterobranchs.

The salivary aperture in the caenogastropods is distinct in opening generally in the anterior region of the dorsal folds of buccal mass (character 47), (character 87) in the taxa allocated after the node 5.

ESOPHAGUS

90. Position of esophagus origin: 0= in lateral-dorsal region of odontophore; 1= in its posterior region (all species) (CI: 100; RI: 100).

The typical shape of the archaeogastropod foregut is a "V", with the mouth at the base, and the arms are the odontophore and the esophagus respectively. This differs from the arrangement typically found in the caenogastropods, where the esophagus is more or less continuous with the

buccal mass. In this case, the esophagus is inserted in the posterior-dorsal region of the odontophore. The caenogastropod fashion is considered derived, although appears to be shared with some heterobranchs.

91. Anterior esophagus: 0= with a pair of pouches; 1= a simple tube (viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100).

92. Esophageal pouches: 0= a simple diverticulum; 1= covered with papillae (cyclophorids); 2= with a dorsal fold (ampullariids) (CI: 100; RI: 100; non-additive).

93. Special pair of blood vessels connected to esophageal pouches: 0= absent; 1= present (ampullariids, cyclophorids) (CI: 100; RI: 100).

The cyclophorids and the ampullariids have a pair of prominent pouches connected to the lateral surface of the anterior esophagus. Their inner surface connects with the adjacent esophageal cavity. Important branches of the anterior aorta irrigate both pouches. Something similar, but lacking the distinct blood vessels, is found in vetigastropods and neritimorphs, and other archaeogastropods (SASAKI, 1998: 150; pers.obs.). The presence of esophageal pouches is considered plesiomorphic, however, it is possible that they are not homologous structures, because they differ in several details as referred above. The esophageal pouches with demarcated esophageal gland have been considered by BERTHOLD (1991) and BIELER (1993, character 16). PRASHAD (1925: 109, fig.4) described short and rounded esophageal pouches for *Pila*, which differ from the species studied here. PRASHAD (1925:116, fig.11) described the arterial system in the foregut in more detail, and showed a small pair of vessels irrigating the pouches.

94. Middle esophagus: 0= narrow; 1= bulging (ampullariids except *Marisa*); 2= very narrow (*Notopala* spp, *Larina*) (CI: 100; RI: 100; non-additive).

95. Esophageal insertion in stomach: 0= in posterior region; 1= in middle region (cyclophorids, *Annularia*, cerithioideans) (CI: 50; RI: 75).

The insertion of the esophagus in the posterior region of the stomach (state 0) is "U"-shaped, as happens in most archaeogastropods. The esophageal insertion in the middle region of the stomach (state 1) is apparently associated with gastric enlargement, and resulted in convergence between the cyclophorids (first branch) and the remainder of the basal caenogastropods (represented by node 7).

STOMACH

96. Gastric caecum: 0= developed; 1= small, only internal (*Viviparus* spp); 2= absent (remainder species) (CI: 66; RI: 50; additive).

A homologous structure to the archaeogastropod gastric caecum is not found in the ingroup species. However, the viviparids have a septum that surrounds a small chamber, and possesses a folded inner surface. This small chamber was initially interpreted as a caecum vestige (as denoted by the above states).

The gastric caecum was apparently lost in the caenogastropods and, if the small viviparid chamber is homologous to that, it is a reversion. Nevertheless, it is likely that this structure is a new viviparid acquisition. For testing this hypothesis, the character was considered additive. The result is the same if it was considered non-additive. Both indices, however, change to 100. This may be an indication that the *Viviparus* structure may be a new acquisition. PONDER & LINDBERG (1997) argue that gastric caecum is a vetigastropod apomorphy.

97. Stomach walls: 0= thin; 1= dorsal half muscular (*Marisa*, *P. crosseana*, *P. scalaris*, *F. neritiformis*); 2= almost entirely muscular (remainder of ampullariids) (CI: 100; RI: 100; additive).

98. Stomach transverse muscular septum: 0= absent; 1= present (ampullariids); 2= bending inwards (*P. lineata*, *P. bridgesi*, *P. canaliculata*, *A. megastoma*) (CI: 66; RI: 90; additive).

The ampullariid stomach is unusual in being highly muscular (character 97), working as a gizzard. Additionally, the stomach developed a muscular transverse septum (character 98). This septum divides the stomach of most ampullariids into 2 chambers, a larger dorsal chamber with muscular walls, and a ventral chamber with thin walls, bearing the ducts to digestive gland. This septum is also present in the genus *Pila* (PRASHAD, 1925). The characters 97 and 98 are optimized as additive because of the ontogeny, since state 1 precedes 2 during development. The result is the same if both states were considered non-additive, only the RI of the character 98, changes from 90 to 85.

99. Gastric muscle: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).

The gastric muscle, an ampullariid synapomorphy, is apparently reported for the first time. Its origin is in the shell columella, just posterior to that of the columellar muscle; and it runs dorsally and anteriorly, and penetrates the stomach wall just

anterior to the ventral gastric chamber. After this, the gastric muscle fibers spread like a fan along the gastric muscular walls, and divide the stomach into esophageal and intestinal branches.

The gastric muscle is small in *Marisa*, and broad and thick in the remainder of the studied ampullariids. Nothing is known about its occurrence in other ampullariid genera, as it is not reported in the consulted literature.

The gastric muscle probably works as a base for the musculature of the gastric wall. But, further investigations are necessary to clarify the function of this muscle, as well as the remainder of the complex structures of the ampullariid stomach, some of which are explored in characters 97-99. The ampullariid stomach is a rich source of characters for comparative analysis, but has been poorly explored. BERTHOLD (1991) and BIELER (1993) considered only a single character (17): 2 median stomach grooves.

100. Ducts to digestive gland: 0= 2; 1= 1 (cyclophorids, *Annularia*, *Notopala* spp.); 2= several (ampullariids) (CI: 50; RI: 77; non-additive).

The plesiomorphic number of the ducts to the digestive gland, as shown by most archaeogastropods, is a pair. One of them is in the esophageal insertion, and the other in the stomach ventral surface, close to the intestinal origin. However, the number and location of the ducts are highly variable. A duct may reduce and even disappear (state 1). On the other hand, the duct may multiply, as in the case of the ampullariids (state 2). The analysis of the location of the several ducts to the digestive gland in the ampullariids suggests that they are derived from both original ducts, with both becoming close together on the ventral gastric surface. This is suggested because there are ducts turned both, anteriorly and posteriorly. Notwithstanding, it is possible that the esophageal duct could be missing, and all ducts are a result of the division of the gastric duct only. This could probably be resolved with further studies on ontogeny.

101. Style sac: 0= present; 1= absent (ampullariids, viviparids, cyclophorids) (CI: 50; RI: 50).

Despite the absence of a gastric style sac in the archaeogastropods (the main outgroups), its presence in the caenogastropods is regarded as plesiomorphic. This polarization is based on the presence of style sacs in other classes, notably the bivalves. Thus loss is assumed in the archaeogastropod taxa, as well as the architaenioglossans. Its presence in the remaining

caenogastropods is interpreted as a reversion. On the other hand, it is possible that the caenogastropod style sac is an extraordinary convergence with those of bivalves.

INTESTINE

102. Intestinal loop close to kidney-pericardium region, in left part of visceral mass: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).

103. Dorsal chamber of intestinal region close to pericardium: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).

104. Ventral chamber of intestinal region close to pericardium: 0= absent; 1= simple (ampullariids); 2= complex (*P. lineata*, *P. canaliculata*, *A. megastoma*) (CI: 66; RI: 91; additive).

The ampullariids have an intestinal region near the pericardium, which contain 1 to several small, blind-sacs. Apparently the region is reported for the first time. These chambers are disposed from longitudinally to transversally, and the aperture of each is normally turned proximally (contrary to the flow). Sometimes, the transverse chamber has its origin in the longitudinal chamber aperture. The term "complex" is used for that state with several small sub-chambers.

The formation and function of the intestinal chambers are unknown and interesting goal for further investigations.

PRASHAD (1925) have reported an intestinal "caecum" for *Pila globosa*, being a short blind sac in which he tried to find a crystalline style. Looking at his fig.2 (p.99) the topology of the caecum is comparable to the topology of the intestinal chambers, however, the aperture of this caecum is close to the stomach in his fig.7 of pl.17. The homology of these structures remains unclear.

105. Intestinal loops in visceral mass: 0= several; 1= a single "S" (ampullariids, viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100).

106. Intestinal loops localization: 0= immerse in digestive gland; 1= free from digestive gland (ampullariids, viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100).

107. Intestinal loop in haemocoel: 0= present; 1= absent (all species) (CI: 100; RI: 100).

Unlike the archaeogastropods and heterobranchs, the caenogastropods tend towards a reduction of the midgut, in favor of the development of the foregut, even in herbivorous groups. Most archaeogastropods and heterobranchs have a

several-looped intestine, mostly immersed in the digestive gland, then, in visceral mass. The caenogastropods, on the other hand, including the architaenioglossans, have the midgut "Z"-shaped (an angle is the stomach and the other the pericardial or renal loop. In the cases of several looped caenogastropod intestines, the loops are inside the kidney or in the pallial cavity.

The haemocoel of the caenogastropods is separated from the visceral cavity by a thin septum. This obstructs the passage of visceral structures, what does not happen in other gastropods. In some archaeogastropod groups, such as vetigastropods and neritimorphs, there is an intestinal loop almost touching the buccal mass. Nothing similar is found in the ingroup, however, SASAKI (1998: 151) considered the condition of ampullariids comparable to archaeogastropods.

108. Intestinal region passing through kidney: 0= with single or two loops; 1= several looped (*P. scalaris*, *P. curumim*, *P. lineata*, *P. bridgesi*, *P. sordida*, *P. canaliculata*, *A. megastoma*, *Marisa*) (CI: 50; RI: 87).

The intestinal loops inside the renal chamber of the ampullariids are here apparently explored for comparative purposes for the first time. There is uniformity of the loops shape in samples of the same species, and there are conspicuous differences among species. Those differences certainly are useful for species distinction. Some ampullariids have complex renal intestinal loops that, besides their interest in systematics, are an interesting subject for further physiological analyses.

109. Fecal pellets: 0= absent; 1= present (all species) (CI: 100; RI: 100).

Fecal pellets were also explored as phylogenetic character by previous authors (PONDER & LINDBERG, 1997; SASAKI, 1998) and are also the goal of comparative studies (MOORE, 1931). In the present study, fecal pellets resulted as a notable synapomorphy of the Caenogastropoda, differing from the archaeogastropods and heterobranchs that, characteristically, have a single continuous fecal strip. Fecal pellets are also convergently found in some Polyplacophora and in amphibolids (Pulmonata) (PONDER & LINDBERG, 1997).

GENITAL SYSTEM

♂

110. Testis: 0= along visceral mass; 1= restrict to posterior region of visceral mass (cyclophorids) (CI: 100; RI: 100).

111. Seminal vesicle: 0= absent; 1= present (*Annularia*, cerithioideans) (CI: 100; RI: 100).

The seminal vesicle is a differentiated glandular portion of the anterior region of the visceral vas deferens, in general convolute and iridescent because of presence of spermatozoids. The vesicle is absent in the architaenioglossans, but remarkably present in remainder caenogastropods. PRASHAD (1925:127, fig.15) reported a "vesicula seminalis" for the ampullariid *Pila*, but of different fashion and topology, certainly a new acquisition.

112. Prostate: 0= absent; 1= present in pallial region (all species) (CI: 100; RI: 100).

The prostate is a broad glandular portion of the caenogastropod pallial vas deferens. The gland may be opened (a furrow), as in the cerithioideans, or closed (a tube), as in architaenioglossans and annulariids. The prostate gland most probably secretes the spermatophore. The prostate of the Australian viviparids (*Notopala*, *Larina*) is difficult to be seen because of the pallial positioned testis. According to the literature (e.g., ANNANDALE & SEWELL, 1921), the prostate lies in the wall below the food groove and is actually difficult to be seen.

113. Pallial vas deferens: 0= a furrow; 1= partially closed (cyclophorids); 2= entirely closed (tubular) (ampullariids, viviparids, *Annularia*) (CI: 50; RI: 60; additive).

The vas deferens is mostly absent in archaeogastropods (except Neritimorpha), and highly modified in the heterobranchs (running free into haemocoel). Those facts in part preclude the analysis of the structure in the ingroup. However, the 3 states are presently aligned in a single ordered evolutionary trend based on the ontogeny, which the 3 states appear successively during the development of the state 3-bearing groups. The result is the same if they were optimized as non-additive, both indices, however, change to 66.

114. Vas deferens aperture: 0= in posterior end of pallial cavity; 1= in dorsal end of right cephalic tentacle (viviparids); 2= in penis tip (ampullariids, *Annularia*); 3= in penis base (cyclophorids) (CI: 75; RI: 85; non-additive).

The character has connection with the degree of closure of the pallial vas deferens, in such the states 0 and 1-2 are extremes (entire open and entire closed respectively), with the state 3 as intermediary.

115. Ejaculatory tube as a long muscular portion

of vas deferens immersed in integument, and protruding into pallial floor and haemocoel: 0= absent; 1= present (viviparids) (CI: 100; RI: 100).

116. Right cephalic tentacle modified as copulatory organ, with vas deferens running along it: 0= absent; 1= present (viviparids) (CI: 100; RI: 100).

117. Special cavity for retraction of right cephalic tentacle tip: 0= absent; 1= present (*Viviparus* spp) (CI: 100; RI: 100).

The characters 115-117 and the state 2 of the character 114 explore the modification of the male pallial genital structures of viviparids, which are very different from any other gastropod. The pallial vas deferens runs in the floor of the pallial cavity, immerse in the integument, mostly surrounded by thick muscular walls disposed concentrically in many layers, protruding into the haemocoel. The right cephalic tentacle is also modified as a copulatory organ, or a penis-like structure. Although this kind of modification of the right tentacle is convergently found in several cocculiniforms and some neritimorphs, the viviparid modification is unique in having a closed duct running along its inner region. Besides, several viviparid species have special features of the copulatory tentacle, which are characteristic of the species and genera, as explored in the character 117 and others that were autapomorphic.

118. Exophalic penis (behind right tentacle): 0= absent; 1= present (cyclophorids, *Annularia*) (CI: 50; RI: 66).

119. Papilla on exophalic penis tip: 0= absent; 1= simple (*N. prominulus*); 2= double (*A. blanchetiana*, *I. inca*) (CI: 100; RI: 100; non-additive).

The cyclophorid exophalic penis (characters 118-119) is extraordinarily similar in shape and location to the exophalic penis found in the higher caenogastropods, such as most mesogastropods and neogastropods. They are here considered homologues. But, according to the tree, the cyclophorid structure is convergent. More complex penises have been described for other cyclophorids, having even retractile terminal papilla, e.g., in *Murdochia pallidum* (MORTON, 1952).

The penis of annulariids is apparently homologous to those of higher caenogastropods. However, THOMPSON (1978) referred to the penis as of pallial origin and innervated by the left pleural ganglion.

120. Penis sac: 0= absent; 1= present, with a broad

and short penis (ampullariids); 2= present, with a very long, convolute penis (*P. crosseana*, *P. canaliculata*, *A. megastoma*) (CI: 66; RI: 90; additive).

The ordered optimization is based on the ontogeny, since young specimens of taxa with state 2 penis have a state 1-like one. The result does not change if the character was considered non-additive, only the RI changes to 87.

121. Penis duct highly convolute: 0= no; 1= yes (*P. crosseana*, *A. megastoma*, *P. sordida*, *P. canaliculata*, *P. lineata*) (CI: 33; RI: 60).

122. Penis shield: 0= absent; 1= present (ampullariids) (CI: 100; RI: 100).

123. Penis shield tip: 0= absent; 1= simple (ampullariids); 2= glandular (*P. curumim*, *P. lineata*, *P. bridgesi*, *P. sordida*, *P. canaliculata*, *A. megastoma*) (CI: 100; RI: 100; non-additive).

124. Penis shield middle region: 0= simple; 1= with a flap (ampullariids).

125. Penis shield middle-right gland: 0= absent; 1= present (*Marisa*, *F. neritiformis*, *P. curumim*, *P. lineata*, *P. bridgesi*, *P. sordida*, *P. canaliculata*) (CI: 25; RI: 57).

126. Penis shield gland in tip: 0= no gland; 1= far from middle flap (*P. curumim*, *P. lineata*), 2= close to flap (*P. canaliculata*, *P. bridgesi*, *P. sordida*, *A. megastoma*) (CI: 100; RI: 100; non-additive).

Despite the fact the 3 states are considered non-additive, the position of the taxa on the tree suggests that they actually may be additive. If considered additive, nothing changes, neither in result or indices.

127. Penis shield base: 0= without gill; 1= with gill (*Marisa*, *P. curumim*, *P. lineata*, *P. bridgesi*, *A. megastoma*) (CI: 25; RI: 40).

The ampullariid modifications of the male pallial genital structures (characters 120-127) are unlike those of other gastropods. The pallial vas deferens runs along the right edge of the pallial cavity, along the side rectum, as it is found in other caenogastropods, however this is the only similarity. Close to the anus, the vas deferens crosses to a penis sac (character 120), which is half solid and half hollow. The hollow portion contains a convolute and slender penis. The penis may be shorter and broad, or very long, with a filiform apical region (character 120). The duct of the penis may or not be highly convolute (character 121). The penis is protruded protected by a special structure of the mantle border – the

penis shield (characters 122-127). The penis shield is very large, sometimes more than half the volume of the pallial cavity. It is retracted inside this cavity, except during copulation. The penis shield is much more complex than the penis itself, and has several valuable characters for comparative analysis. Although most of the characters are autapomorphies in the present study, some of them are explored in the characters (123-127). Male genital characters have been also considered by BERTHOLD (1989, 1991) and BIELER (1993, characters 7, 48-58). Maybe due to the invasion of freshwater (ampullariids and viviparids) and the terrestrial (cyclophorids) habitats, the architaenioglossans are highly modified in their male genital system. They possess highly specialized features not found in any other gastropod. On the other hand, no close correlation between these major groups is possible, showing that most probably these structures evolved independently.

BERTHOLD (1991) and BIELER (1993, characters 8-9) also considered two other male features as ampullariid synapomorphies: the presence of eupyrene and atypical sperm anchored by nurse cells, and reduction of the spermatophore.

♀

128. Pallial oviduct: 0= absent; 1= present and opened (a glandular furrow) (cerithioideans); 2= closed (a glandular tube) (ampullariids, viviparids, cyclophorids, *Annularia*) (CI: 66; RI: 0; additive). The pallial oviduct is present in neritimorphs amongst the archaeogastropods, in all heterobranchs and all caenogastropods. Possibly it is an indicative of a close relationship among those three groups. Some archaeogastropods, however, have an inconspicuous furrow running from the female genital aperture (*e.g.*, cocculiniformians), which is an analogous the structure. In caenogastropods, the pallial oviduct can be open (as a furrow), this condition is found only in the cerithioideans; or closed (tubular), found in the other groups. It is suggested that the open condition is a step between the inconspicuous furrow and the closed state. Though, according to the tree, the open condition of the cerithioideans is a reversion. If the character was optimized as unordered, nothing changes in the result, but both indices become 100. The indices of the whole cladogram become the following: length: 249 (instead 252), CI: 77 (instead 76), RI: 91 (same).

129. Brood pouch: 0= absent; 1= present as part of oviduct (viviparids) (CI: 100; RI: 100).

The viviparid brood pouch (or uterus), contains capsules with young specimens from 1 to 4 whorls. These young specimens are born already well-formed, justifying the name of the type genus of the family.

130. Pallial oviduct localization: 0= in pallial floor; 1= entirely at right of rectum (all species) (CI: 100; RI: 100).

The position of the pallial oviduct in caenogastropods differentiates it from the pallial oviducts of other groups that possess this structure (the heterobranchs and neritiforms). In these groups, the pallial oviduct runs partially or totally in the pallial floor. Obviously, in several caenogastropods, when the pallial oviduct is mature, acquiring enormous proportions, a part of it also attaches to the floor of the cavity, but it always arises from the pallial roof.

131. Albumen gland: 0= absent; 1= loop of visceral oviduct (cyclophorids); 2= a compact mass (ampullariids); 3= a posterior glandular sac (*Notopala* spp, *Larina*) (CI: 100; RI: 100; non-additive).

The albumen glands of the different architaenioglossan taxa are doubtless not homologous. Most probably they are independent acquisitions from different portions of the pallial oviduct.

132. Bursa copulatrix: 0= absent; 1= present, connected to visceral oviduct (*N. prominulus*); 2= present, opening in pallial cavity (*A. blanchetiana*, *I. inca*) (CI: 100; RI: 100; non-additive).

The bursa copulatrix is unusual in the cyclophorids, in which (state 2) it opens directly to the pallial cavity. The pallial oviduct thus has two apertures: a posterior one (the bursa) and an anterior one (the capsule gland). The plesiomorphic condition of the bursa connected to the pallial oviduct and not directly connected to the pallial cavity is present in some cyclophorids, such as *Cyclophorus perdix tuba* (Tielecke, 1940), and *Cyclobrandia beauianus* (Petit) (THOMPSON, 1967). THOMPSON (1969) has reported a more variable condition of the bursa aperture, in a study on Mexican and Central American cyclophorids, which he also called a seminal receptacle.

133. Capsule gland: 0= absent; 1= present (all species); 2= with a complex, sometimes spiral inner duct (ampullariids) (CI: 100; RI: 100; additive).

The additive optimization is based on ontogeny. Young ampullariid specimens possess a very simple

capsule gland duct. However, nothing changes if the character was considered unordered.

134. Inner blind-sac glandular chamber in capsule gland: 0= absent; 1= present (cyclophorids) (CI: 100; RI: 100).

Based on the morphological disparity and different localization, the capsule glands (character 133-134) of the different groups are possibly not homologous. The gland of the ampullariids is very large, and surrounds most structures of the pallial oviduct. Its duct is complex, sometimes spiral or with series of blind-sac, flat chambers. The gland of the cyclophorids is U-shaped, with a branch as a blind sac.

135. Female pore: 0= not developed (pallial oviduct absent or opened); 1= a slit (cyclophorids, *Annularia*); 2= a papilla (ampullariids, viviparids) (CI: 50; RI: 50).

The additive optimization is based on comparison, since state 2 appears to be a modification of state 1. The ontogeny also corroborates this optimization as I have observed in young specimens. However, nothing changes in the result or indices if the character was considered non-additive.

136. Vaginal tube: 0= absent; 1= origin in anterior end of pallial oviduct (ampullariids); 2= origin in middle level of pallial oviduct (*F. neritiformis*, *P. bridgesi*, *P. sordida*, *A. megastoma*) (CI: 50; RI: 83; additive).

The vaginal tube is long and has thick-glandular walls. It runs parallel to the rectum and connects the capsule gland to the female pore. This happens in two different ways as mentioned above. The additive condition is based on the ontogeny as I have observed, because the species, that have state 2 in the mature stage have state 1 in immaturity. The result is the same if the character was considered non-additive, the single change is RI: 75.

The pallial oviduct structures have been referred here by names, based on the nomenclature found in the literature and on topology. However, there is no uniformity of the designations and there is few taxa studied on the function of each portion (ANDREWS, 1964, 1965a; PRINCE, 1967). The nomenclature employed here is thus provisional.

137. Brood strategy: 0= absent (eggs free); 1= inside pallial oviduct (viviparids); 2= a jelly mass laid out of water (ampullariids) (CI: 100; RI: 100; non-additive).

The reproductive strategies of the viviparids and ampullariids are unusual for gastropods. In the former, the viviparous strategy raising the name of the type genus (*Viviparus*) (see FALNIOWSKI et al., 1996). In the latter, the strategy is to fix the capsules out of the water, despite the aquatic condition.

CENTRAL NERVOUS SYSTEM

138. Nerve ring position: 0= surrounding mouth; 1= in middle level of buccal mass (ampullariids, cyclophorids); 2= posterior to buccal mass (viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100; additive).

The nerve ring position in the archaeogastropods and heterobranchs is characteristically anterior to the buccal mass. Notwithstanding, most caenogastropods have the nerve ring posterior to the buccal mass. In the ampullariids and cyclophorids, however, the position of the nerve ring is intermediate, *i.e.*, located in the middle level between the anterior and posterior ends of the buccal mass. According to the tree, the location of these two groups is intermediate between the plesiomorphic condition found in the outgroups (nerve ring anterior to buccal mass) and the apomorphic one of the remainder of the caenogastropods, viviparids included. The result shows the tendency to a posterior positioned nerve ring, present since the basal taxa.

The additive condition of the states is based on ontogeny. In caenogastropods the buccal mass arises posterior to the nerve ring, and gradually passes through it during the development, positioning anterior to it (BALL *et al.*, 1997). However, if considered non-additive, the result and indices do not change.

139. Position of pleural ganglia: 0= close to pedal ganglia (hypoathroid); 1= close to cerebral ganglia (epiathroid) (viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100).

140. Connective pedal-pleural ganglia: 0= very short; 1= long, separated from pedal-cerebral connective (viviparids); 2= long, running close to pedal-cerebral connective (*Annularia*, cerithioideans) (CI: 100; RI: 100; non-additive).

These characters (139-140) have correlations to the hypo- and epiathroid conditions of the nerve ring, explored by previous authors in

comparative and phylogenetic studies (*e.g.*, HASZPRUNAR, 1988, PONDER & LINDBERG, 1997, 1998). HASZPRUNAR (1988:394-398) commented extensively about the subject and referred to the viviparid nerve ring as of dystenoid type, the same designation given by BOUVIER (1888) and ANNANDALE & SEWELL (1921:236). This type is hypoathroid on the left side and epiathroid on the right side (HASZPRUNAR, 1988:395, fig.3c).

The hypoathroid condition of the cyclophorids is a long known feature (TIELECKE, 1940, figs.19-20). A similar condition is found in the ampullariids (BURNE, 1899; PRASHAD, 1925:fig.17).

The nerve ring of the viviparid species studied here, show that they can be considered as epiathroid, since both pleural ganglia are located close to the cerebral ganglia (Figs.349-352). However, unlike the normal fashion of the epiathroid nerve ring, present in the other caenogastropods, the viviparid pedal connectives to the other two pairs of ganglia are separated from one another in a V-shaped fashion (Figs.300, 348-352). In the normal epiathroid condition both pair of connectives run close and parallel to each another. However, the viviparid pedal ganglia are apparently modified in a long fashion (ANNANDALE & SEWELL, 1921: figs.8-9; FRETTER & GRAHAM, 1962, fig.161), lacking clear boundaries. The pedal ganglia are apparently diffused along a wide length, becoming unclear where the pleuro-pedal connective and the anterior pedal nerve start. This fashion precludes the exact classification of the viviparid nerve ring.

Additionally, an interesting difference between the two groups of examined viviparids, *i.e.*, the European *Viviparus* and the Australian *Notopala-Larina*, was found. Like the other architaenioglossans, but unlike the higher caenogastropods, the cerebral commissure is distinct and relatively long, but the *Viviparus* fashion is longer than that of the *Notopala*, in such both cerebral ganglia are closer (Figs.348, 350:cc). The viviparid pedal ganglia are distinct in being antero-posteriorly long, but those of *Notopala* have a wider and more distinct pedal commissure than those of *Viviparus*. The connectives between the pedal ganglia with the other two pair of ganglia are shorter and broader in *Notopala* than in *Viviparus* species,

but in both cases they are separated from each other dorsally, as referred above. In both viviparid groups the pedal ganglia have a dorsal narrow and long region in such connectives to the other two pairs of ganglia insert, this region is shorter in *Notopala* than in *Viviparus* species; this dorsal region is singular in confusing with the connectives, becoming difficult to interpret where is the division between the connectives and the ganglia.

Interpreting the cladogram obtained in the present study, the epiathroid condition of the nerve ring appeared at node 5, including the viviparids (character 139). However, the connectives apparently evolved in two different ways. These ways can be seen as steps of a single evolutionary trend, as also suggested by HASZPRUNAR (1988:395). This last hypothesis is explored in character 140. This character was optimized both, as additive or non-additive, and nothing changed in the result or in the indices.

BERTHOLD (1991) and BIELER (1993) have considered other nerve ring attributes as ampullariid synapomorphies, such as presence of pleurosupraintestinal zygois, subintestinal ganglion fused with right pleural ganglion, presence of pleural commissure, and pedal and pleural ganglia fused on both sides (BIELER, 1993, characters 19-22).

141. Statocysts: 0= with several statoconia; 1= with single statolith (*Annularia*) (CI: 100; RI: 100). Although state 1 resulted as an *Annularia* autapomorphy, it is a state found in many higher caenogastropods. Thus, the character is maintained and will be used in future comparisons.

142. Buccal ganglia: 0= close to nerve ring; 1= separated, far from nerve ring (all species) (CI: 100; RI: 100).

143. Buccal ganglia position: 0= close to median line; 1= lateral (viviparids, *Annularia*, cerithioideans) (CI: 100; RI: 100).

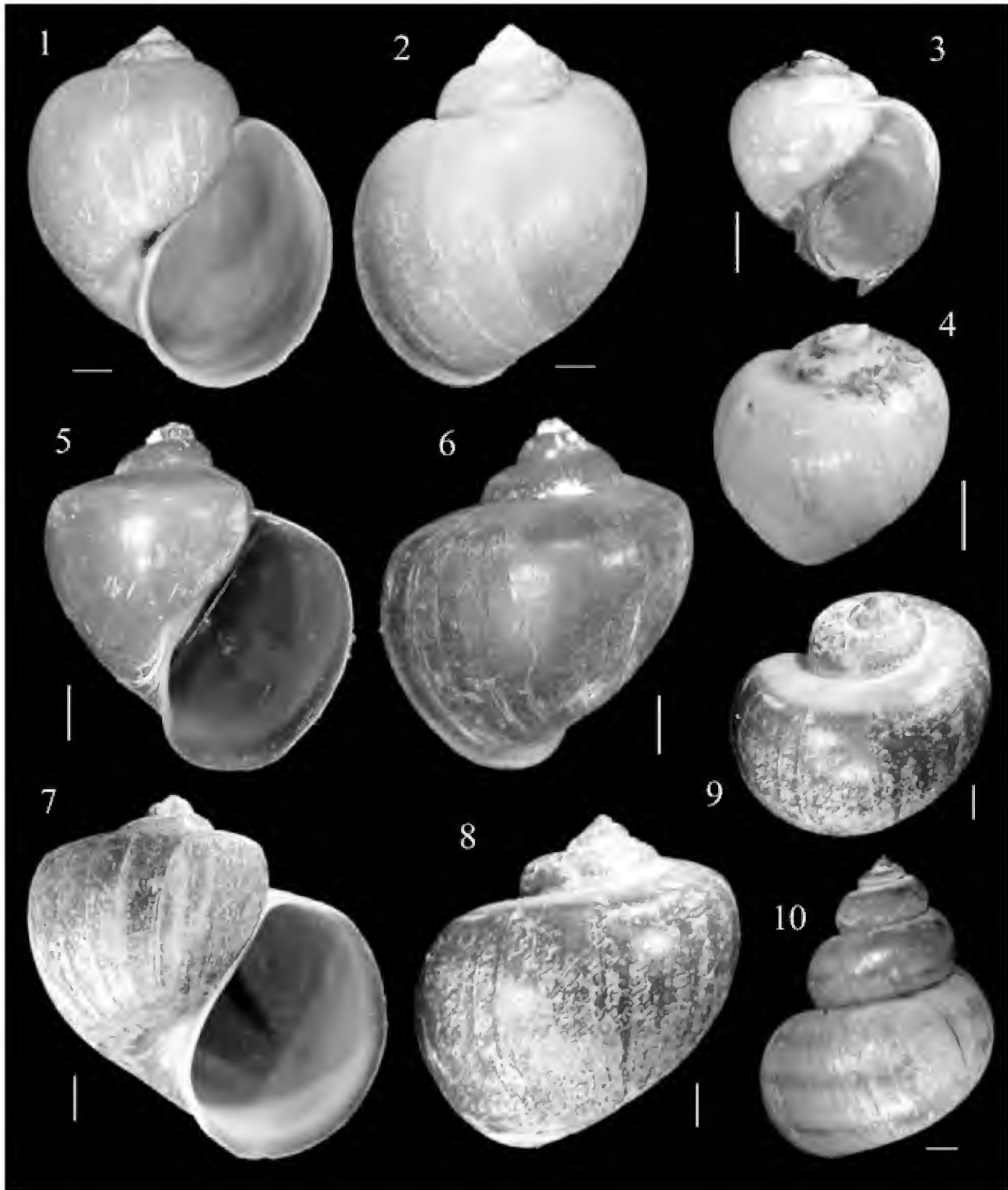
The buccal ganglia, as reported by SASAKI (1998), are not distinct in the archaeogastropods, being represented by a thickening of the buccal nerve, and located close to the nerve ring. In the caenogastropods, the pair of buccal ganglia becomes well delimited, and is located at some distance from the nerve ring, closely attached to the posterior region of buccal mass.

MATRIX OF CHARACTERS

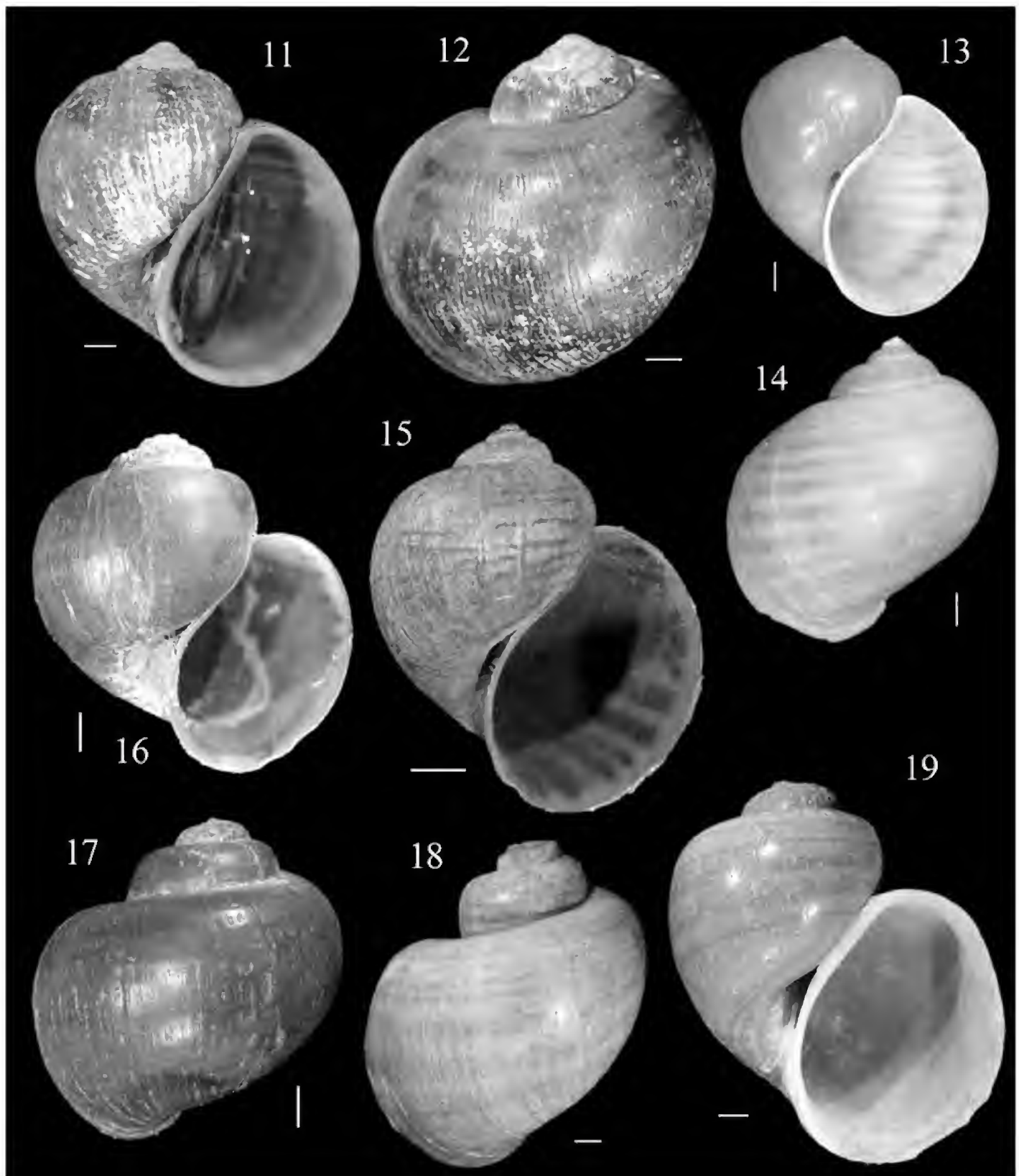
Table 1. Matrix of characters and their states, including 2 outgroups in last lines.

CHARACTER TAXON	1	2	3	4	5	6	7									
	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12	
<i>P.crosseana</i>	10000	11001	21021	12211	00100	01011	11012	11213	00201	02100	02311	01111	11101	11100	11	
<i>P.canaliculata</i>	10000	11001	21021	12211	00101	11011	11012	11213	00201	02100	02311	01111	11101	11100	11	
<i>P.scalaris</i>	10000	11001	21021	12210	00101	01011	11012	11213	00201	02100	02211	01111	11101	11100	11	
<i>P.lineata</i>	10000	11001	21021	12210	00101	11011	11012	11213	00201	02100	02211	01111	11101	11100	11	
<i>P.curumim</i>	10000	11001	21021	12210	00011	01011	11012	11213	00201	02100	02211	01111	11101	11100	11	
<i>Marisa</i>	20000	11001	21001	10210	00100	00021	11012	11103	00201	01100	02311	01111	11101	11100	11	
<i>Asolene</i>	10100	11001	11021	12211	00101	01011	11012	11213	00201	02100	02311	01111	11101	11100	11	
<i>Felipponea</i>	10100	11001	11021	12210	00101	01011	11012	11213	00201	02100	02311	01111	11101	11100	11	
<i>P.bridgesi</i>	10000	11001	21021	12211	00100	01011	11012	11213	00201	02100	02211	01111	11101	11100	11	
<i>P.sordida</i>	10000	11001	21021	12211	00100	11011	11012	11213	00201	02100	02211	01111	11101	11100	11	
<i>Neocyclotus</i>	10010	01100	01111	00?00	1????	00001	00010	100?1	00102	01111	01110	01111	11100	10101	10	
<i>Aperostoma</i>	10010	01100	01011	00?00	1????	00001	00010	100?1	00112	01112	01010	01111	11100	10101	10	
<i>Incidostoma</i>	10010	01100	01011	00?00	1????	00001	00010	100?1	00112	01112	01010	01111	11100	10101	10	
<i>V.contectus</i>	01000	11012	11001	01100	01001	00100	00011	100?2	11000	01100	10022	11111	11110	10110	11	
<i>V.acerosus</i>	01000	11012	11001	01100	01001	00100	00011	100?2	11000	01100	10022	11111	11110	10110	11	
<i>N.ampullaroid</i>	01000	11012	11001	01122	01000	00101	00111	100?2	12000	01100	10022	11111	11100	10110	10	
<i>N.essigntone.</i>	01000	11012	11001	01122	01000	00101	00111	100?2	12000	01100	10022	11111	11100	10110	10	
<i>Larina</i>	11000	11012	11001	01122	01000	00101	00111	100?2	12000	01100	10022	11111	11100	10110	10	
<i>Annularia</i>	00011	00100	01201	00100	1????	00001	00010	110?0	00003	11100	10222	11111	11100	10100	10	
<i>Cerithioidea</i>	00001	00000	01001	00100	00001	00000	00010	100?0	00000	11100	10022	11111	11100	10100	11	

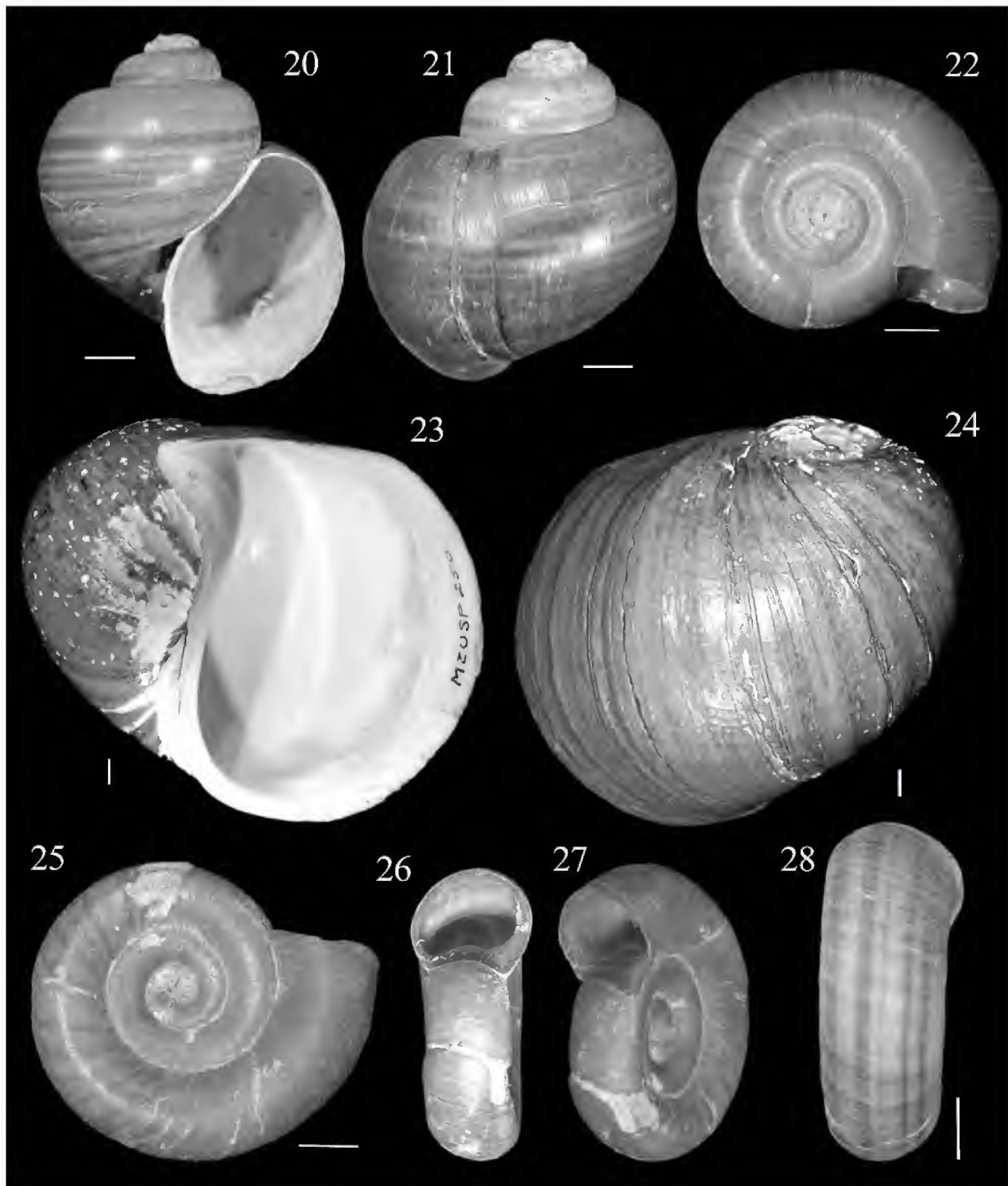
CHARACTER TAXON	7	8	9	10	11	12	13	14							
	345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	123
<i>P.crosseana</i>	011	11111	01011	10201	02110	21112	11111	11010	00220	00002	11110	00201	20202	12100	010
<i>P.canaliculata</i>	011	11111	01011	10201	02110	22212	11121	11110	00220	00002	11211	20201	20202	12100	010
<i>P.scalaris</i>	011	11111	01011	10201	02110	21112	11111	11110	00220	00001	01110	00201	20202	12100	010
<i>P.lineata</i>	011	11111	01011	10201	02110	22212	11121	11110	00220	00001	11211	11201	20202	12100	010
<i>P.curumim</i>	011	11111	01011	10201	02110	22112	11111	11110	00220	00001	01211	11201	20202	12100	010
<i>Marisa</i>	011	11111	01011	10201	02100	21012	11111	11110	00220	00001	01111	01201	20202	12100	010
<i>Asolene</i>	011	11111	01111	10201	02110	22212	11121	11110	00220	00002	11210	21201	20202	22100	010
<i>Felipponea</i>	011	11111	01111	10201	02110	21112	11111	11010	00220	00001	01111	0?201	20202	22100	010
<i>P.bridgesi</i>	011	11111	01011	10201	02110	22212	11111	11110	00220	00001	01211	21201	20202	22100	010
<i>P.sordida</i>	011	11111	01011	10201	02110	22112	11111	11110	00220	00001	11211	20201	20202	22100	010
<i>Neocyclotus</i>	010	10000	01111	10101	01101	20001	10000	01011	00130	00110	01000	00201	11111	00100	010
<i>Aperostoma</i>	010	10000	11111	10101	01101	20001	10000	01011	00130	00120	01000	00201	12111	00100	010
<i>Incidostoma</i>	010	10000	11111	10101	01101	20001	10000	01011	00130	00120	01000	00201	12111	00100	010
<i>V.contectus</i>	010	10210	01011	11101	1??00	10000	10001	11010	01211	11000	01000	00211	00102	01211	011
<i>V.acerosus</i>	010	10210	01011	11101	1??00	10000	10001	11010	01211	11000	01000	00211	00102	01211	011
<i>N.ampullaroid</i>	010	10210	01011	11111	1??20	20001	10001	11010	01211	10000	01000	00211	30102	01211	011
<i>N.essigntone.</i>	010	10210	01011	11111	1??20	20001	10001	11010	01211	10000	01000	00211	30102	01211	011
<i>Larina</i>	010	10210	01011	11111	1??20	20000	10001	11010	01211	10000	01000	00211	30102	01211	011
<i>Annularia</i>	110	10000	11111	11201	1??01	20001	00001	11010	11220	00100	01000	00201	00101	00212	111
<i>Cerithioidea</i>	010	10010	01011	11101	1??01	20000	00001	11010	11000	00000	01000	00101	00100	00212	011



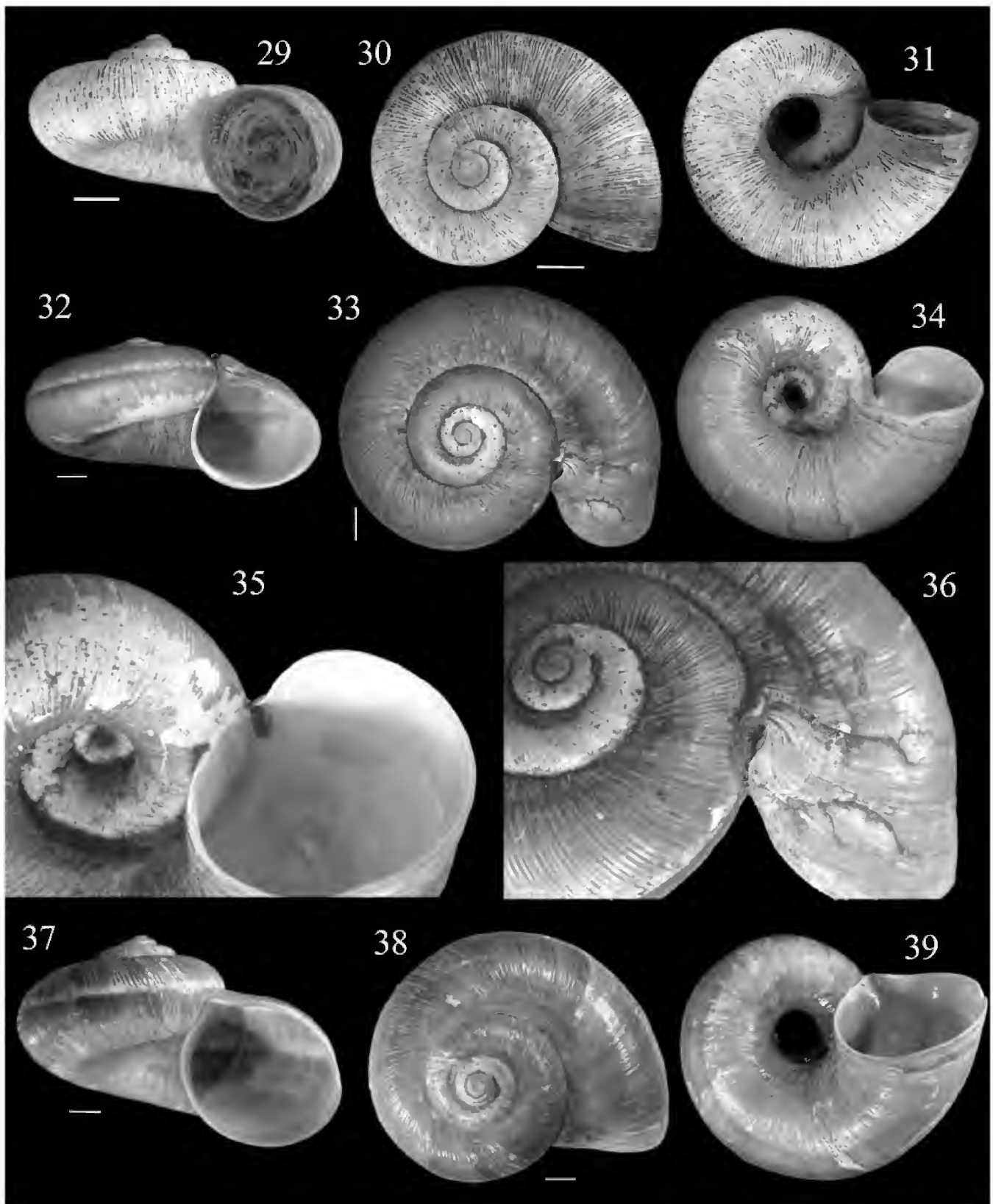
Ampullariid shells: fig.1-2- *Pomacea crosseana*, frontal and dorsal views, MZSP 20158 (♀ 4); fig.3-4- *Pomacea curumim*, frontal and dorsal views, holotype MZSP 30760. *Pomacea scalaris* MZSP 29590, fig.5-6- ♂, frontal and dorsal views, fig.7-9- ♀ 2, frontal, dorsal and apical views; fig.10- *Viviparus contectus*, MZSP 29402. Scale bars: (1-2, 5-9) = 5mm, (3-4) = 2mm, (10) = 3mm



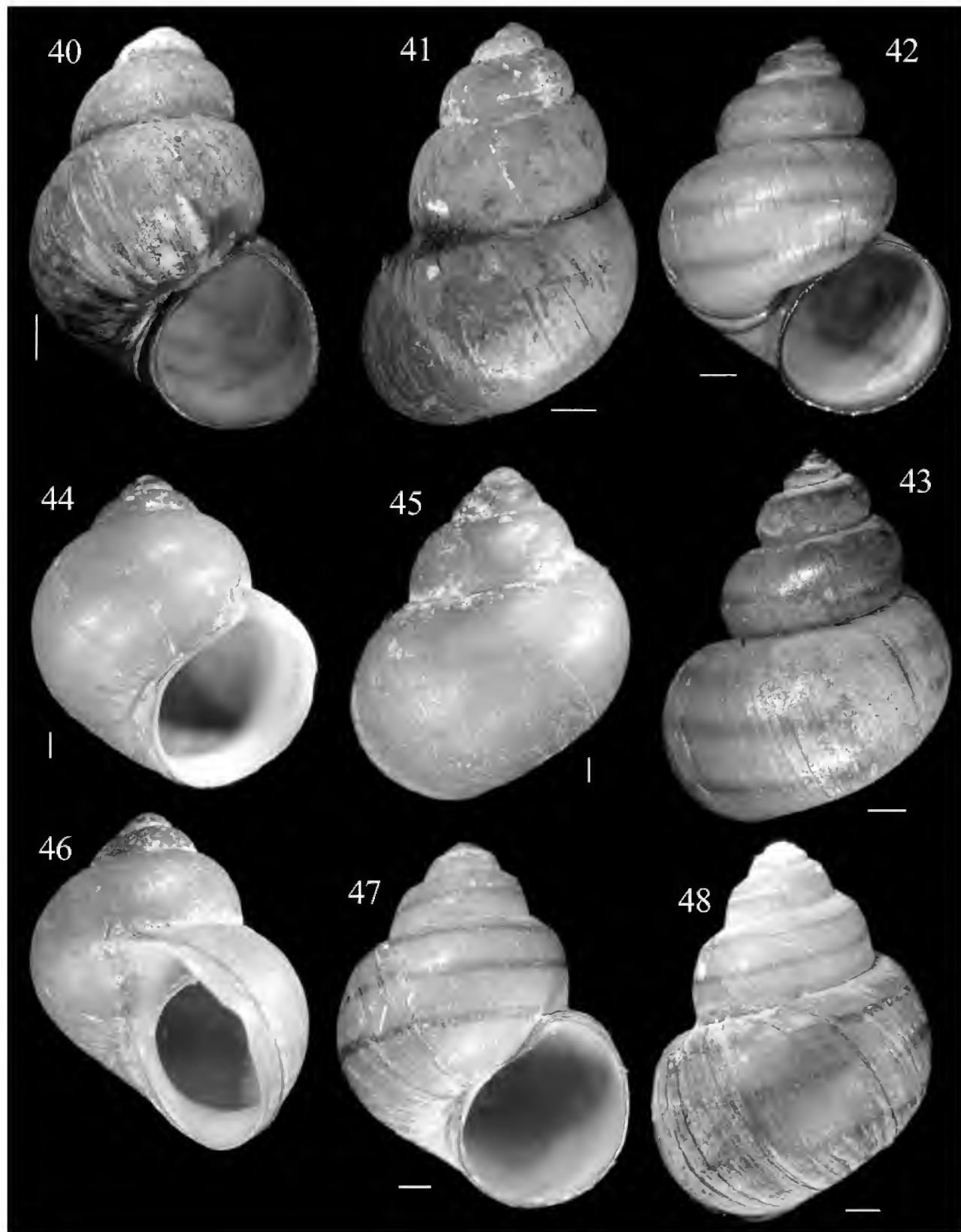
Ampullariid shells: fig.11-12- *Pomacea canaliculata*, MZSP 29633, frontal and dorsal views; fig.13-15- *Pomacea lineata*, fig.13-14- MZSP 26684, frontal and dorsal views, fig.15- MZSP 31147 (from Fernando de Noronha Archipelago), frontal view; fig.16-17- *Pomacea sordida*, MZSP 32195, frontal and dorsal views; fig.18-19- *Pomacea bridgesi*, MZSP 27880, dorsal and frontal views. Scale bars = 5mm.



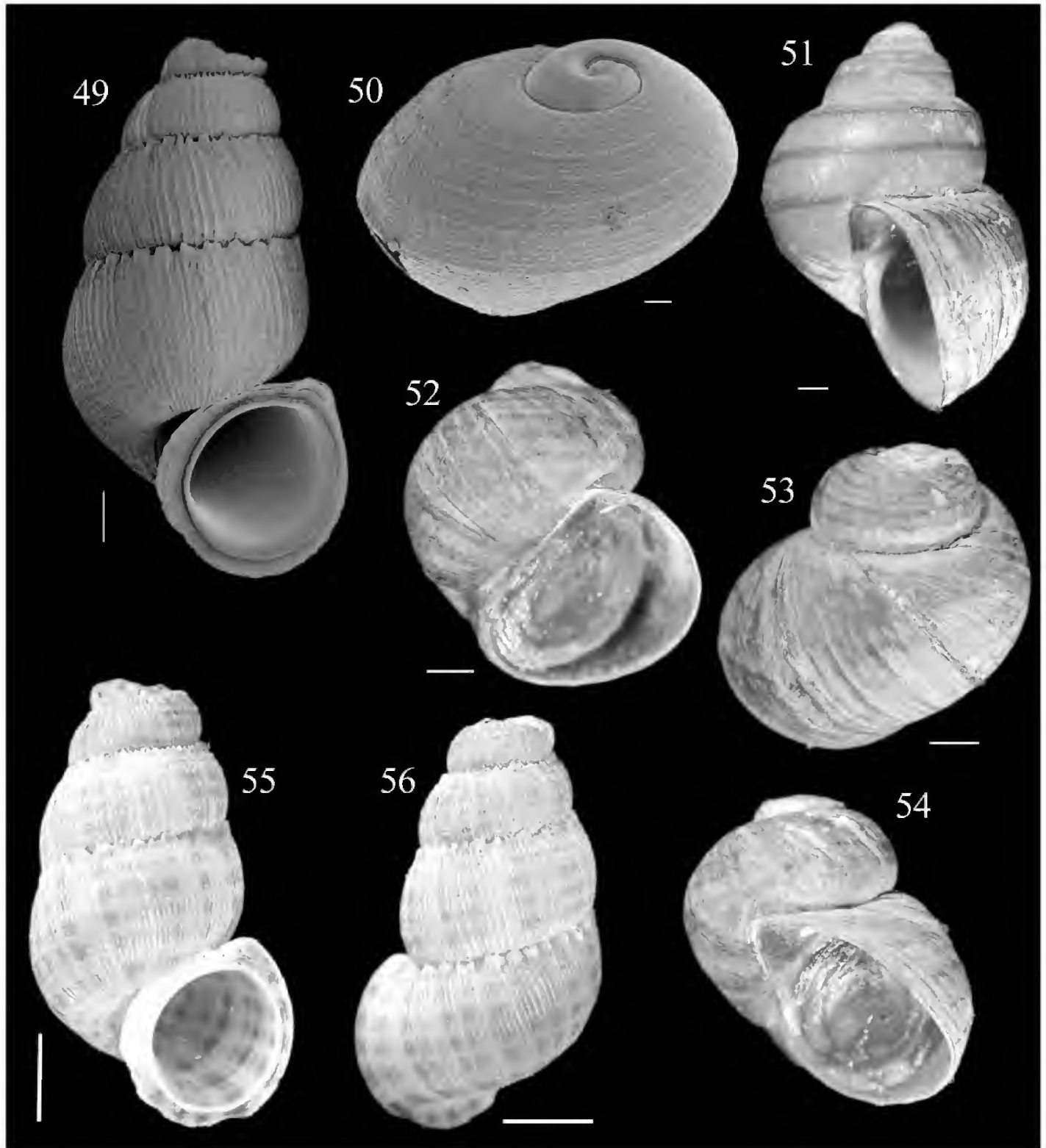
Ampullariid shells: fig.20-21- *Pomacea bridgesi*, MZSP 32196, frontal and dorsal views; fig.22- *Marisa planogyra*, MZSP 29674, specimens with uniform color, right view; fig.23-24- *Asolene megastoma*, MZSP 250, frontal and dorsal views; fig.25-28- *Marisa planogyra*, MZSP 29674, fig.25-27- specimen with uniform color (same than figure 22), left, frontal and oblique views; fig.28- specimen with bands in color, dorsal view. Scale bars = 5mm.



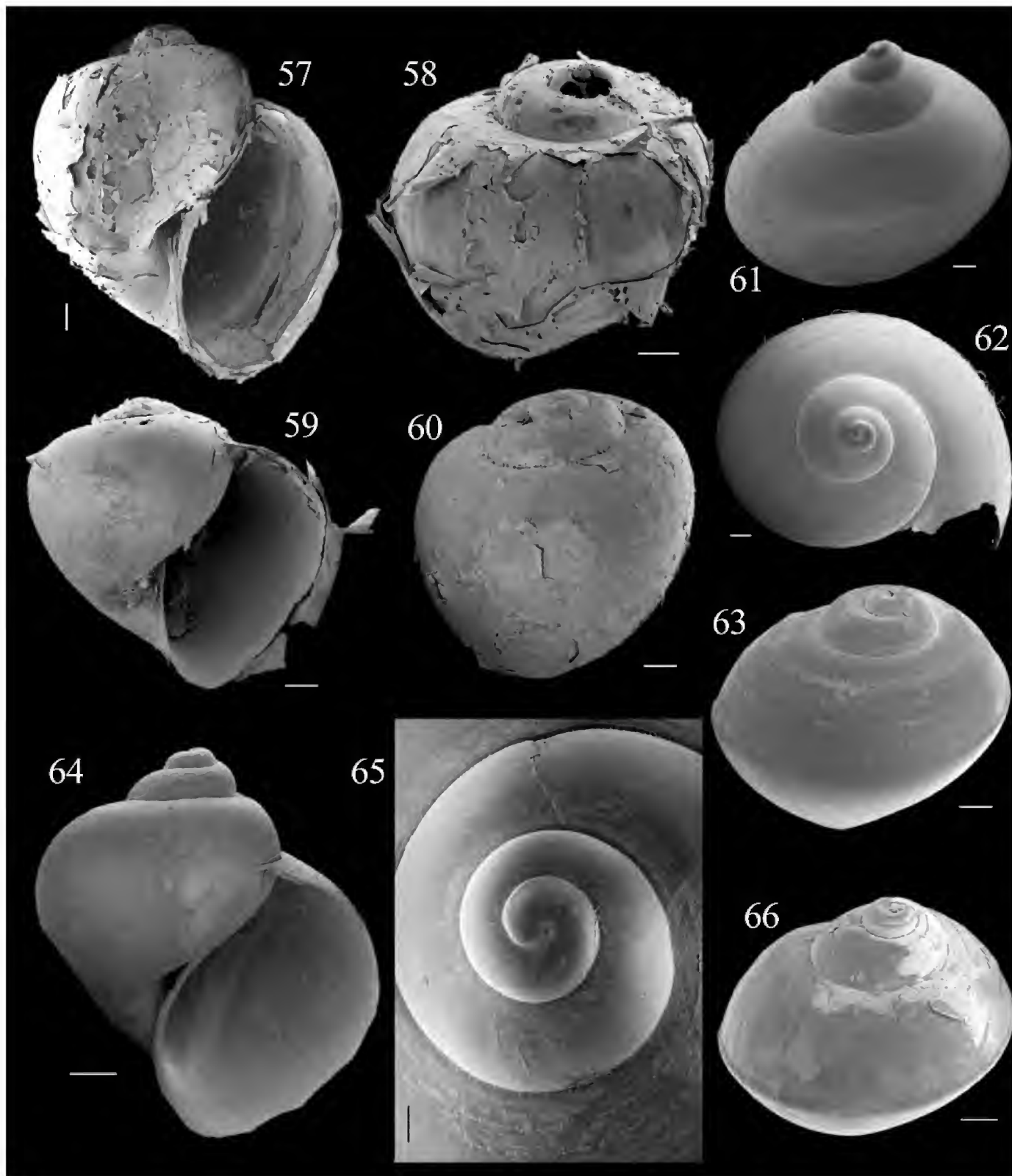
Cyclophorid shells: figs.29-31- *Neocyclotus prominulus*, MZSP 24546, frontal, apical and umbilical views. *Incidostoma tupy*, holotype, MZSP 29560, fig.32-34- frontal, apical and umbilical views, fig.35- detail of aperture, inner view, fig.36- same, dorsal view; fig.37-39- *Aperostoma blanchetiana* frontal, apical and umbilical views. Scale bars: (29-31, 37-39) = 2mm, (32-36) = 3mm.



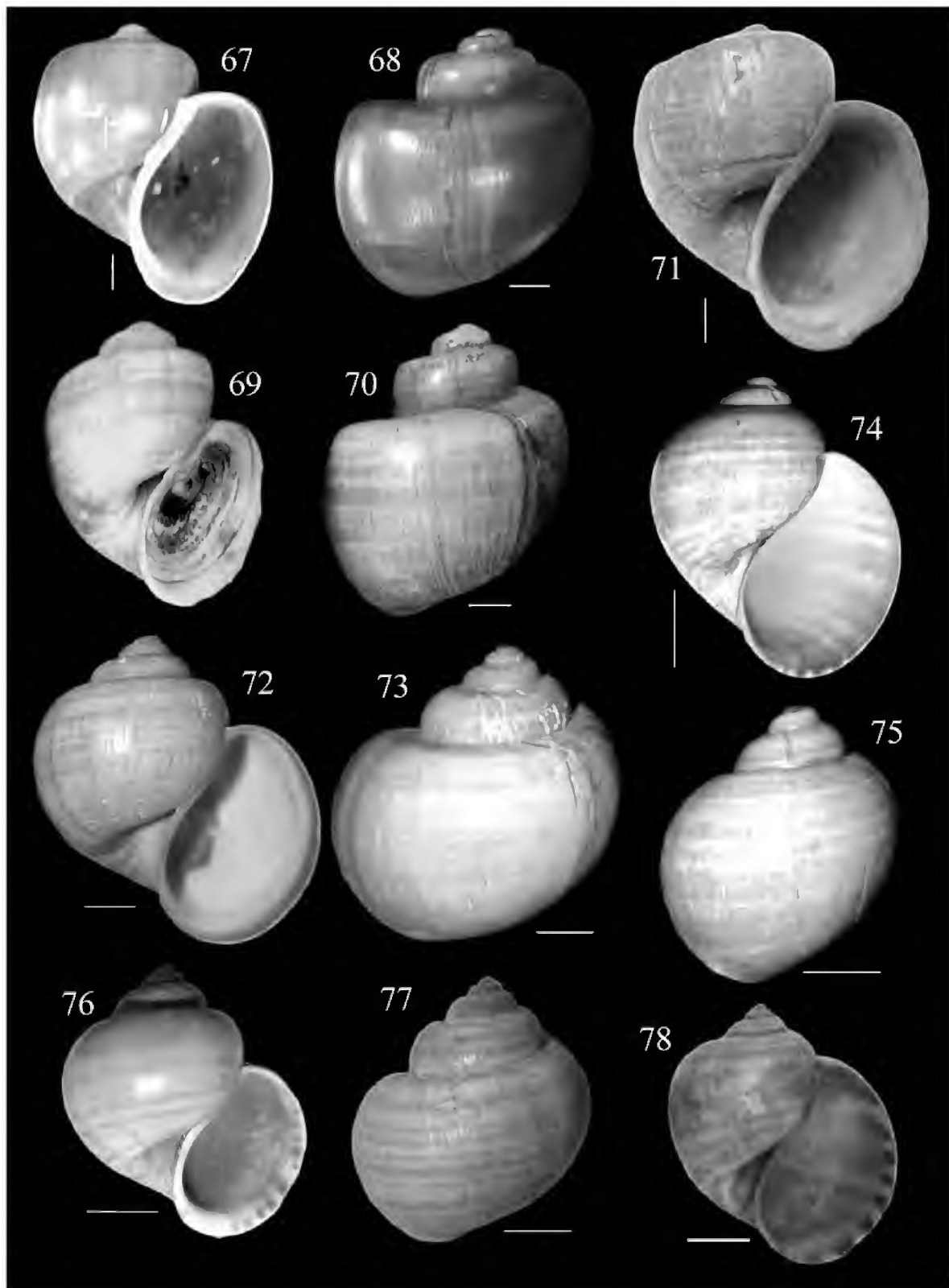
Viviparid shells: fig.40-41- *Viviparus acerosus*, MZSP 29403, frontal and dorsal views; fig.42-43- *Viviparus contectus*, MZSP 29402, frontal and dorsal views; fig.44-46- *Notopala ampullaroides*, AMS 202766 (♀ 1), frontal, dorsal and lateral-left views; fig.47-48- *Notopala essintonensis*, AMS 153577 (♀ 1), frontal and dorsal views. Scale bars: (40-41) = 5mm, (42-43) = 3mm, (44-48) = 2mm.



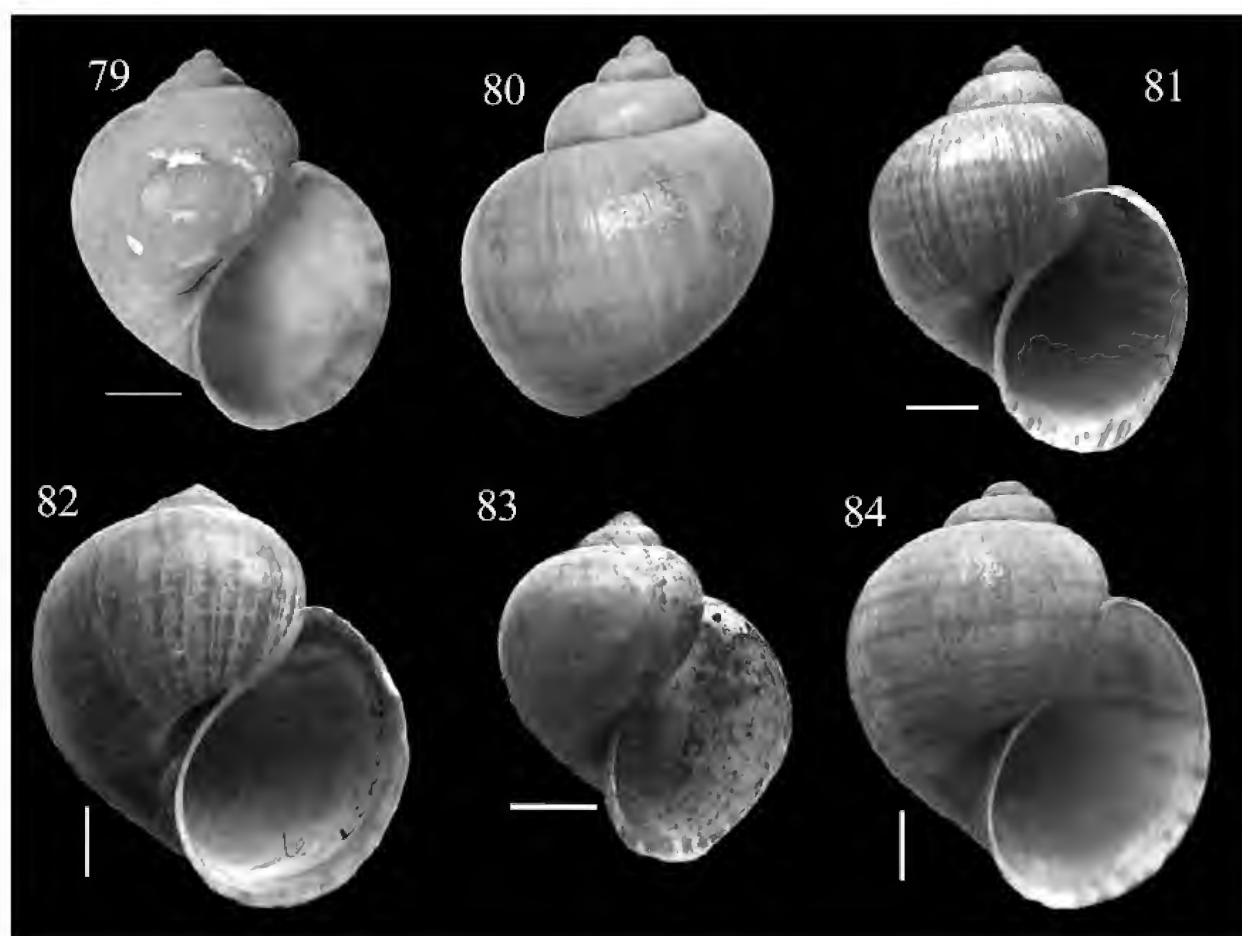
Shells: fig.49- *Annularia* sp, MZSP 28266, SEM, frontal view; fig.50- *Larina* cf *strangei*, AMS 338590, SEM, young specimen extracted from brood pouch, dorsal view; fig.51- *Notopala essingtonensis*, AMS 153577, lateral-left view; fig.52-54- *Larina* cf *strangei*, AMS 338590, frontal, dorsal and lateral-left views; fig.55-56- *Annularia* sp., MZSP 28266, frontal and dorsal views. Scale bars: (49) = 1mm, (50-56) = 2mm.



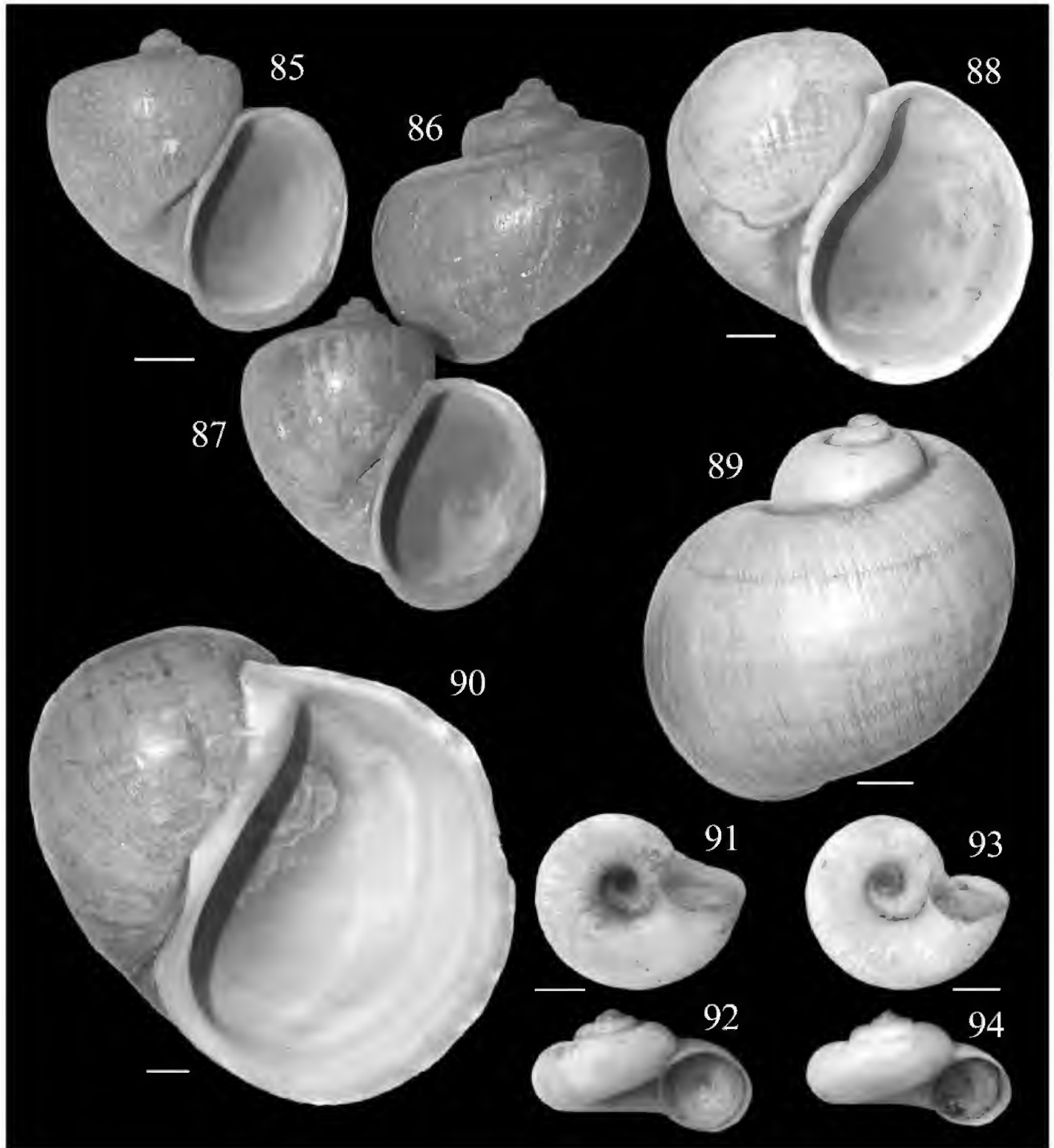
Shells in SEM: *Pomacea curumim*, paratypes, fig.57-58- specimens with intact periostracum, frontal and dorsal views; fig.59-60- specimen with most periostracum removed, frontal and dorsal views; fig.61-62- *Viviparus contectus*, young specimen removed from brood pouch, dorsal and apical views; fig.63- *Notopala ampullaroides*, young specimen removed from brood pouch, dorsal view; fig.64-65- *Pomacea lineata*, MZSP 31147 (from Fernando de Noronha Archipelago); fig.64- young specimen, frontal view; fig.65- same, detail of apex, apical view; fig.66- *Notopala essingtonensis*, young specimen removed from brood pouch, dorsal view. Scale bars: (57-60) = 0.6mm, (61-62) = 0.5mm, (63, 65-66) = 0.4mm, (64) = 1mm.



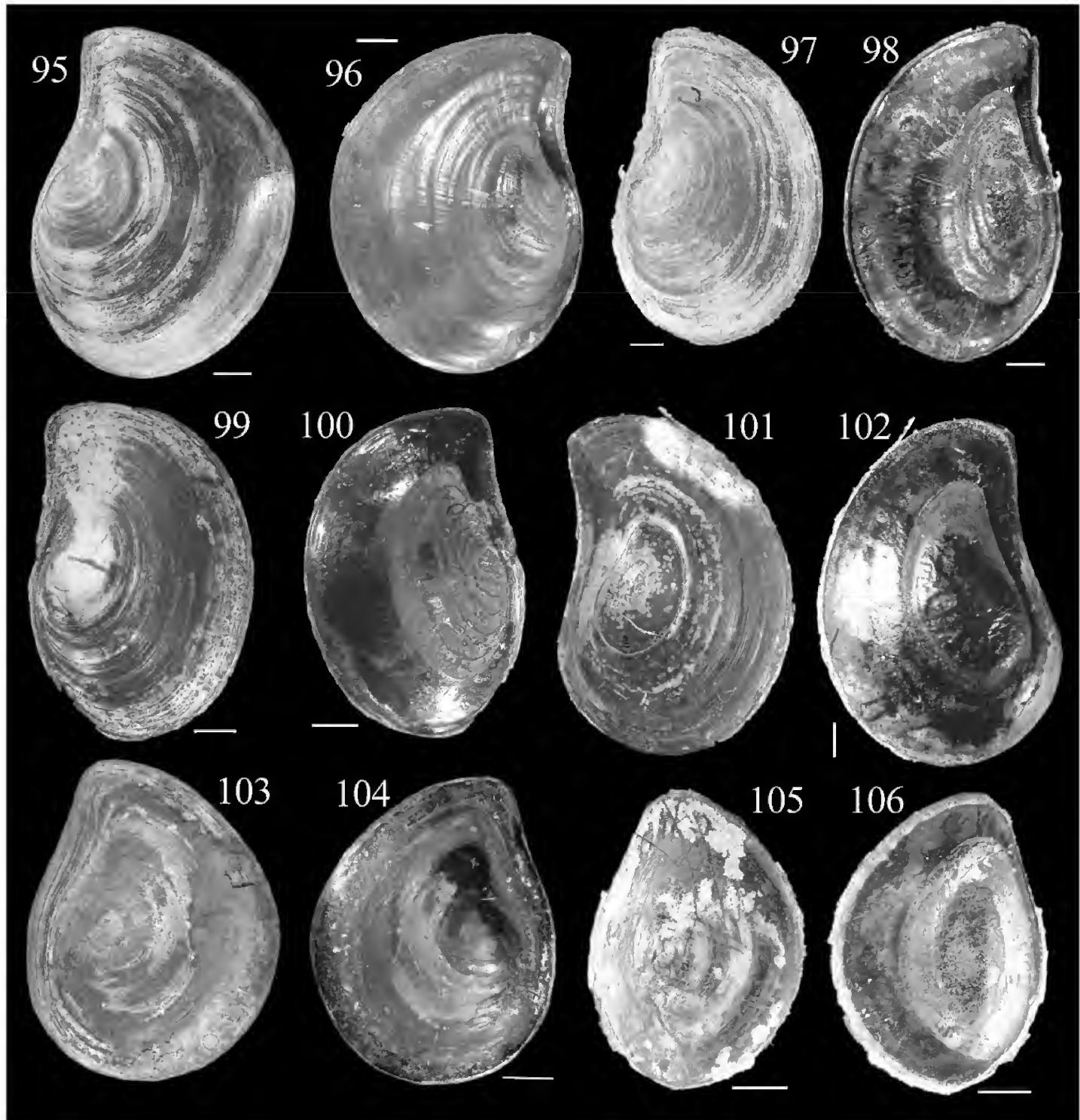
Some shell TYPES: *Pomacea bridgesi* syntypes, BMNH, fig.67-68- specimen 1, frontal and dorsal views, fig.69-70- same for specimen 2; fig.71- *P. bridgesi*, MNHN, labeled as "*Ampullaria scalaris* var *B major viridescens*" Orbigny, 1835, frontal view, Bolivie; fig.72-73- *P. sordida*, BMNH, holotype of *Ampullaria melanocheila* Reeve, frontal and dorsal views; fig.74-75- *P. lineata*, BMNH, holotype of *Ampullaria testudinea* Reeve, frontal and dorsal views; fig.76-77- *P. lineata*, MNHN, syntype 1 (of 2), Brazil, frontal and dorsal views; fig.78- *P. lineata*, MNHN, syntype 1 (of 2) of *Ampullaria physis* Hupé, 1857, frontal view. Scale bar = 10mm.



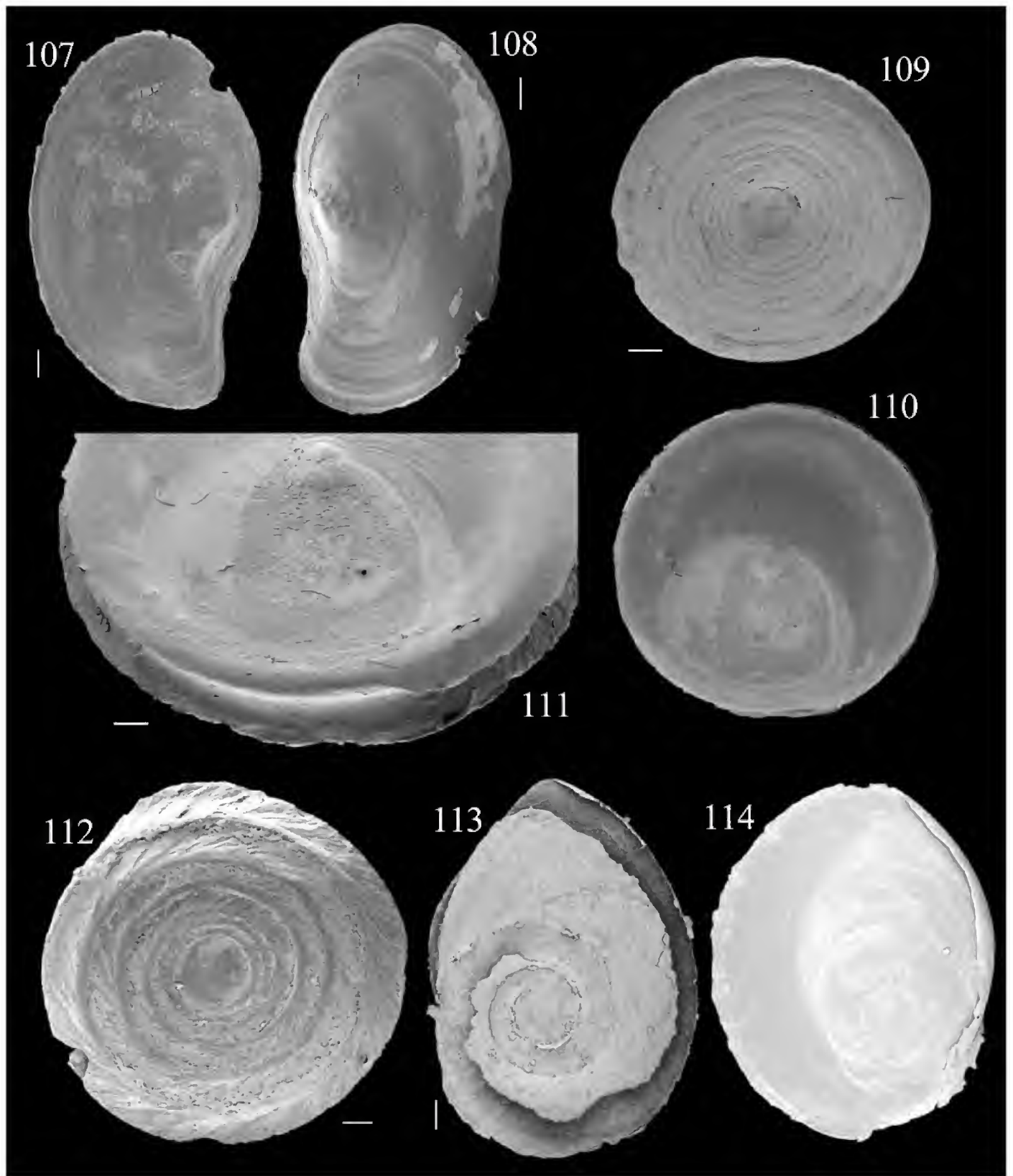
Pomacea lineata TYPES: fig.79-80- MNHN, syntype 2 (of 2, see figs.76-77), Brazil, frontal and dorsal views; fig.81-82- ZSM, Spix's types of *Pomus lineatus fasciatus*, Bahia; fig.83-84- ZSM, Spix's types of *Pomus fingulinus*, Bahia. Figs.81-84 courtesy of Silvana Thiengo (Fundação Oswaldo Cruz, Rio de Janeiro). Scale bars = 10mm.



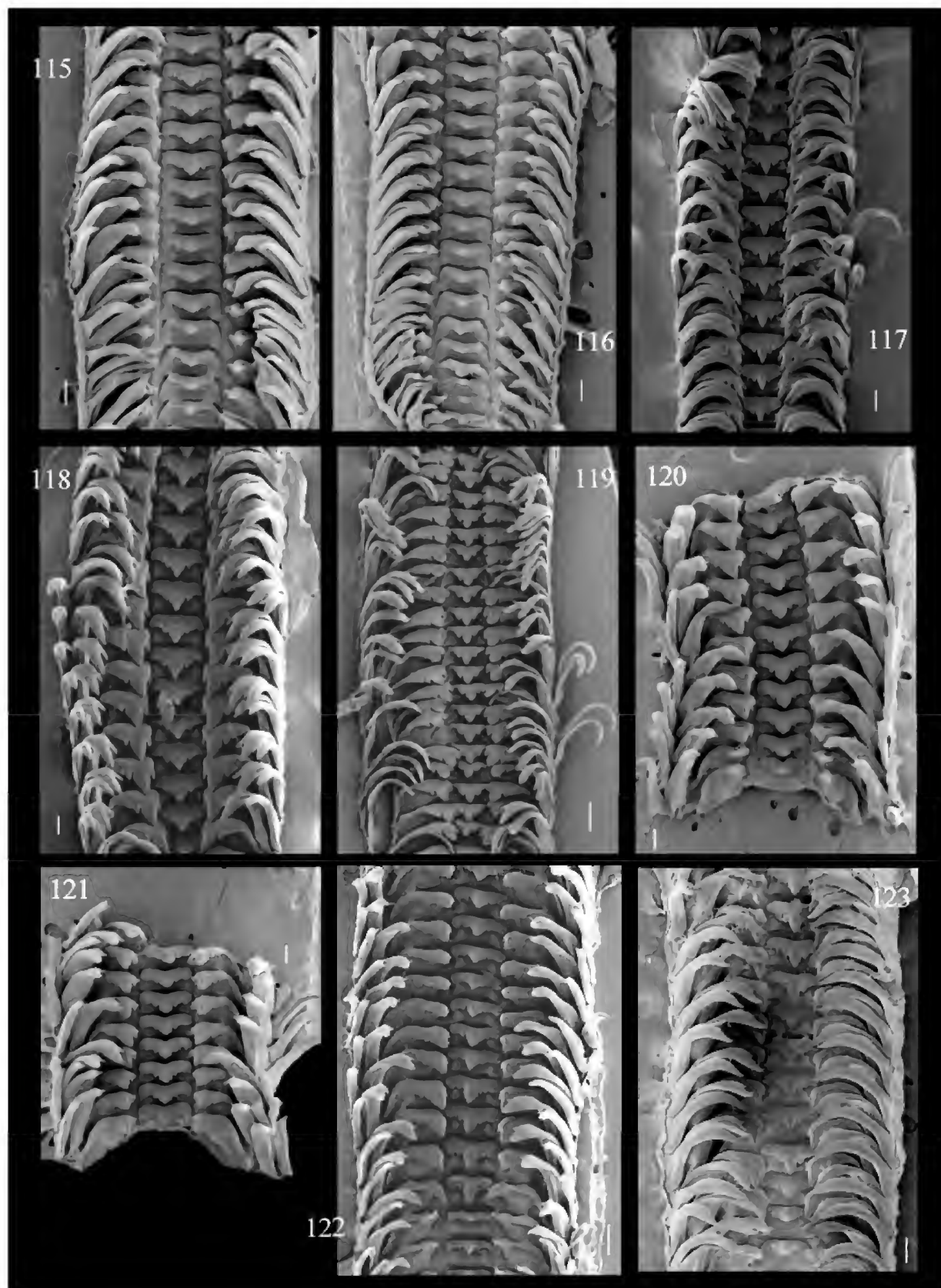
Some shell TYPES: fig.85-87- *Pomacea scalaris*, 3 syntypes, MNHN, Bolivia; fig.88-89- *P. canaliculata*, MNHN, Rio de la Plata, syntypes of *Pila insularum* Orbigny, fig.88- frontal view of syntype 1, fig.89- dorsal view of syntype 2; fig.90- *Asolene megastoma*, MNHN, probable type of *Ampullaria neritoides* Orbigny, Rio Uruguay, frontal view. *Neocyclotus prominulus*, MNHN, 2 probable syntypes of *Cyclostoma prominula* Fer. in Orbigny, Brazil, coll. Deshayes, fig.91-92- specimen 1, umbilical and frontal views, fig.93-94- same for specimen 2. Scale bars: (85-90) = 10mm, (91-94) = 3mm.



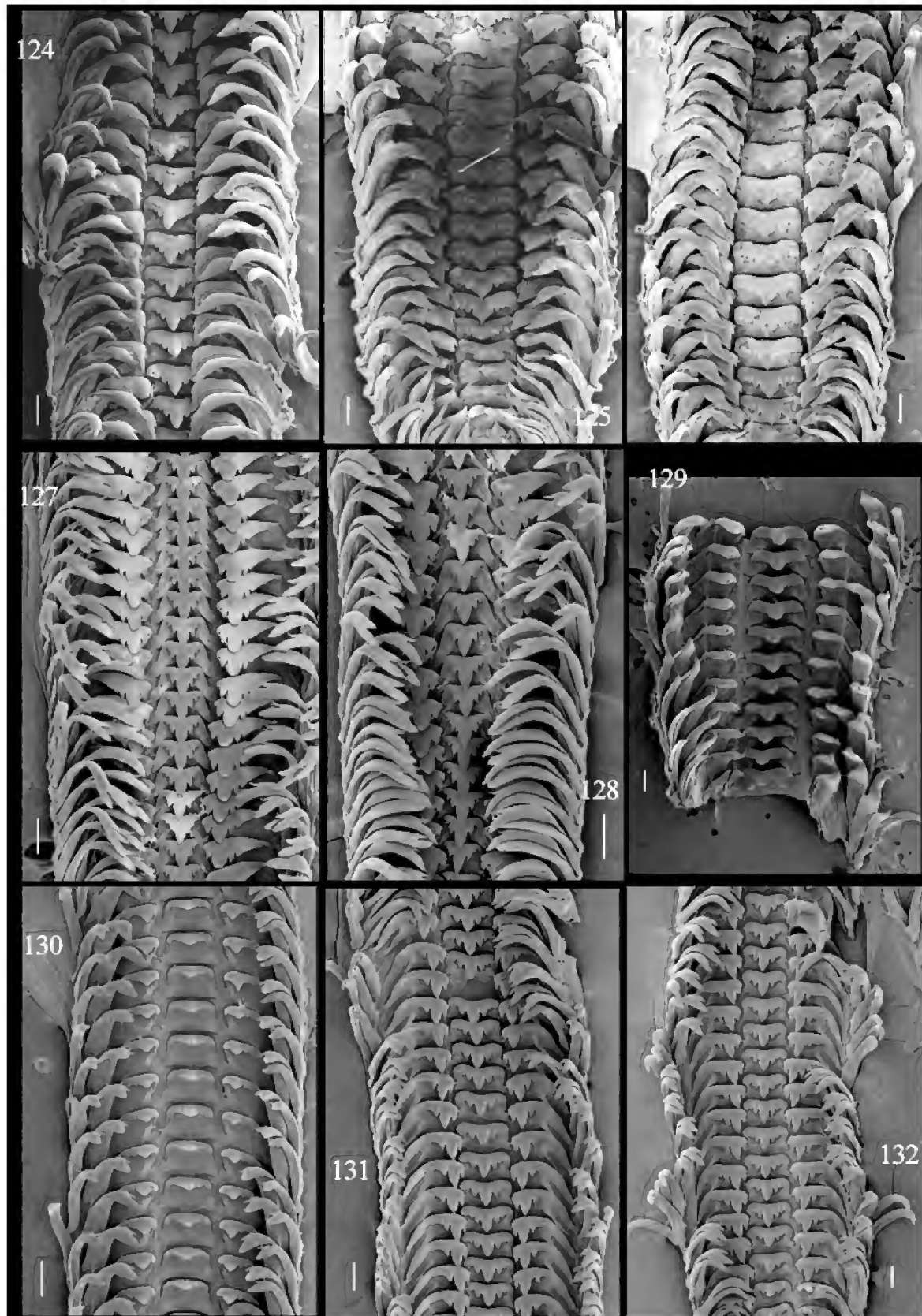
Opercula: fig.95-96- *Pomacea lineata*, outer and inner views; fig.97-98- *Pomacea crosseana*, outer and inner views; fig.99-100- *Pomacea sordida*, outer and inner views; fig.101-102- *Marisa planogyra*, outer and inner views; fig.103-104- *Viviparus acerosus*, outer and inner views; fig.105-106- *Notopala ampullaroides*, outer and inner views. Scale bars: (95-100, 103-104) = 3mm, (101-102, 105-106) = 2mm.



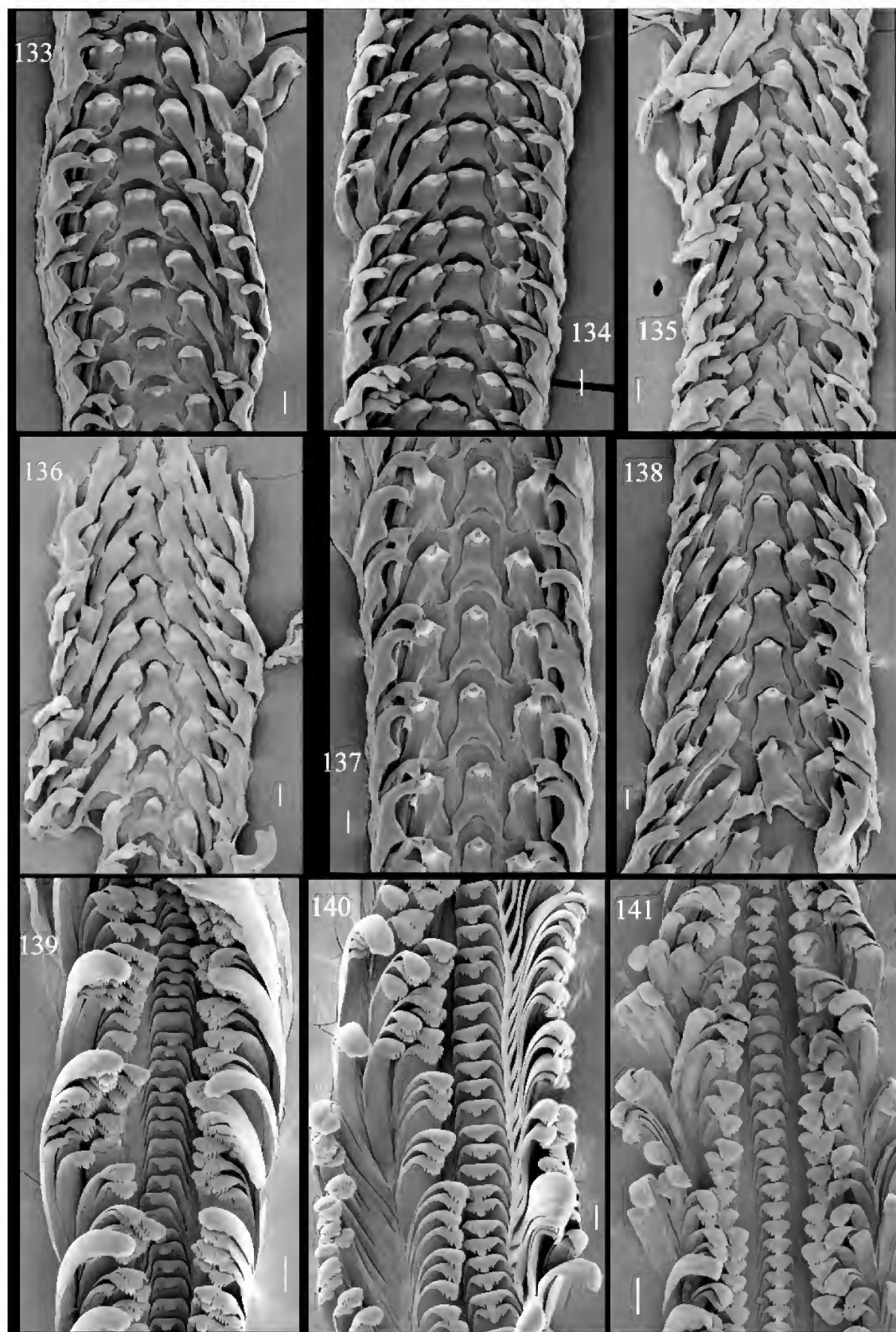
Opercula in SEM: fig.107-108- *Pomacea curumim*, outer and inner views; 109-111, *Neocyclotus prominulus*; fig.109-110- outer and inner views; fig.111- detail of border, inner-slightly oblique view; fig.112- *Aperostoma blanchetiana*, outer view; fig.113-114- *Annularia sp.*, outer and inner views. Scale bars: (107-108, 111, 113-114) = 0.3mm, (109-110, 112) = 0.5mm.



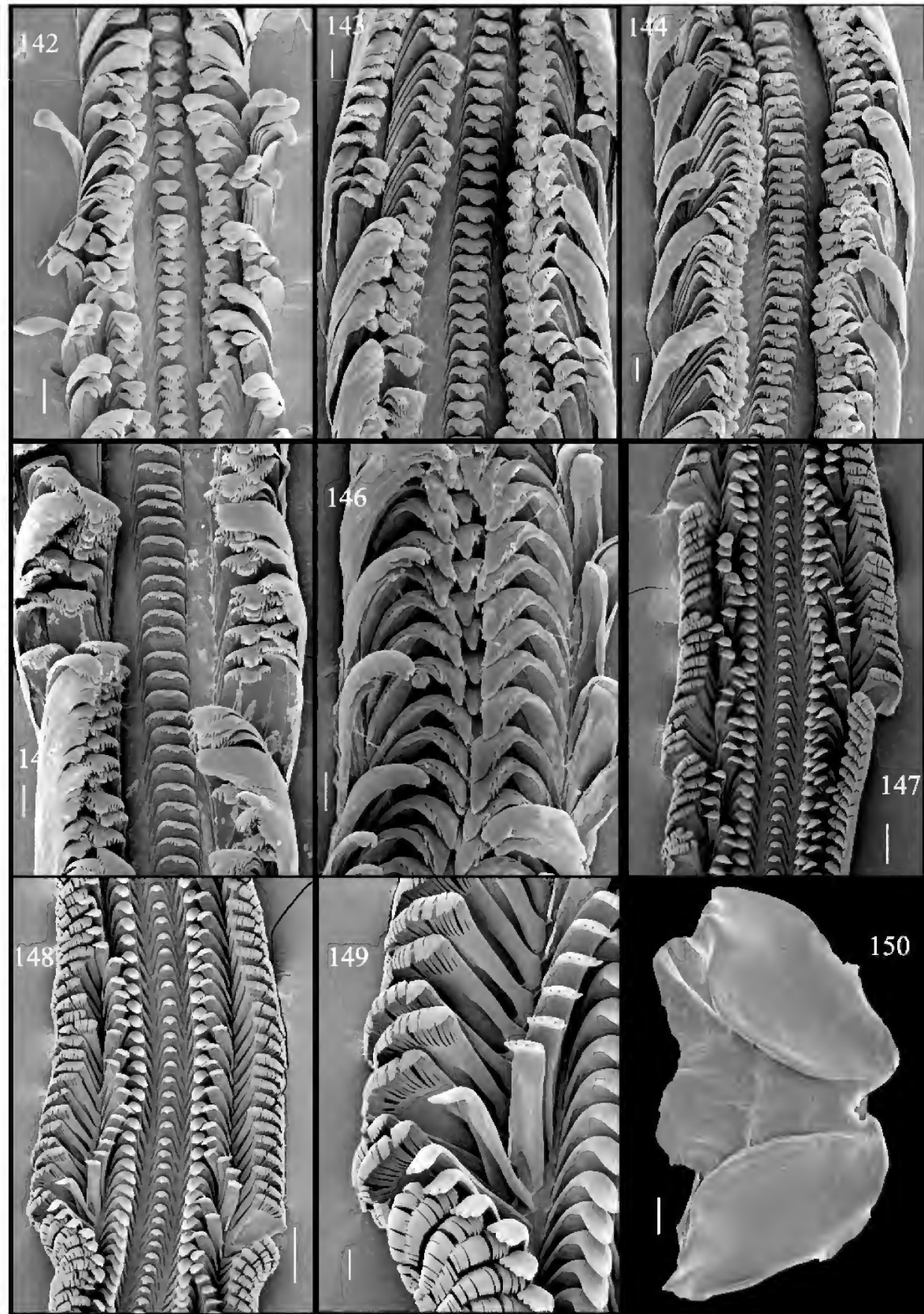
Pomacea radulae in SEM: fig.115-116- *Pomacearosseana*; fig.117-118- *P.curumim*; fig.119- *P.scalaris*; fig.120-121- *P.canaliculata*; fig.122- *P.lineata*; fig.123- *P.sordida*. Scale bars: (115-116, 119-123) = 200 μ m, (117-118) = 60 μ m.



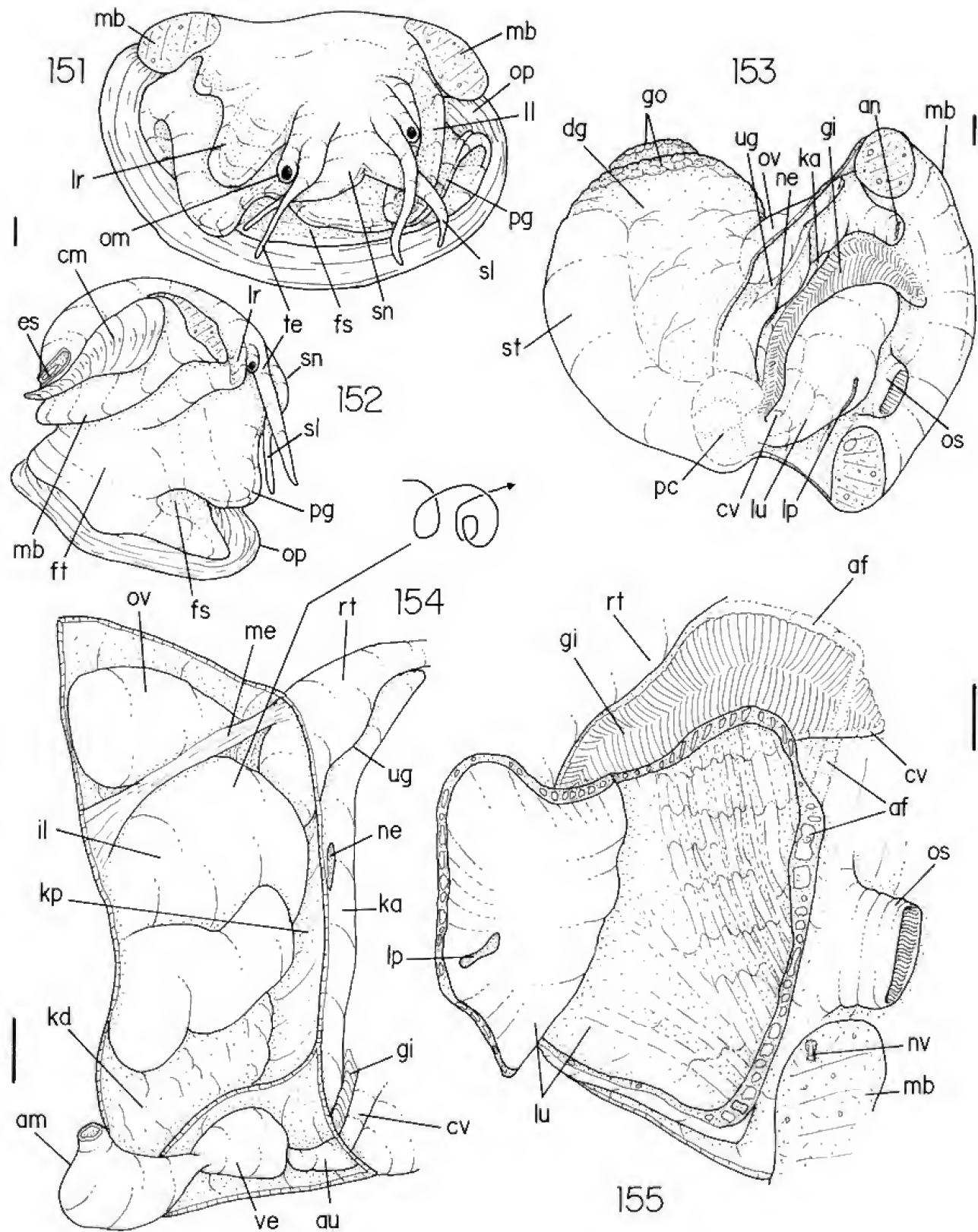
Ampullariid radulae in SEM: fig.124- *Pomacea sordida*; fig.125-126- *P. lineata* (from Fernando de Noronha Archipelago); fig.127-128- *P. bridgesi*; fig.129- *Asolene megastoma*; fig.130- *Felipponea neritiformis*; fig.131-132- *Marisa planogyra*. Scale bars: (124-128, 130) = 200 μ m, (129) = 400 μ m, (131-132) = 100 μ m.



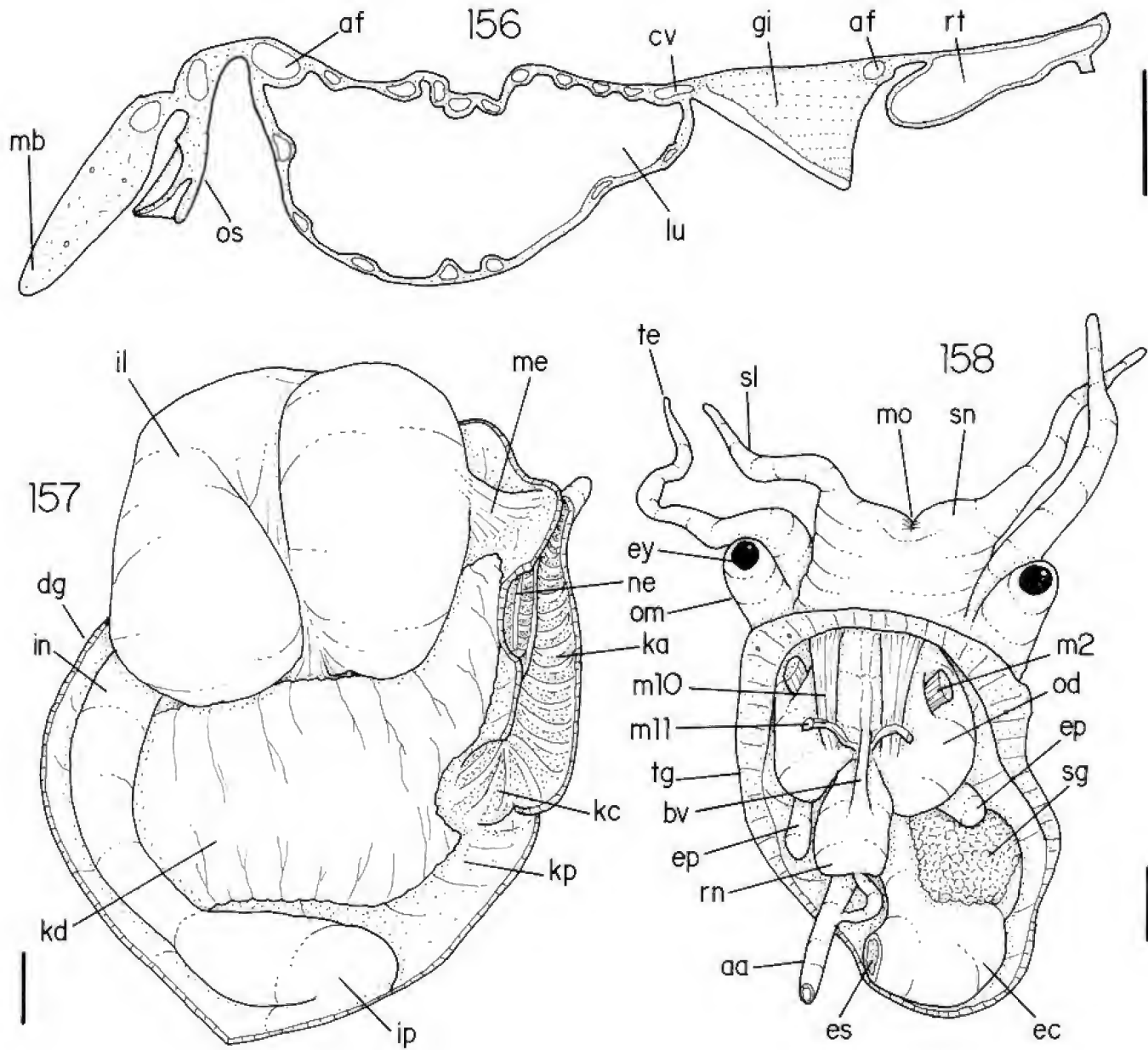
Radulae in SEM: fig. 133-134- *Neocyclotus prominulus*; fig. 135-136- *Incidostoma typy*; fig. 137-138- *Aperostoma blanchetiana*; fig. 139-140- *Viviparus acerosus*; fig. 141- *Viviparus contectus*. Scale bars: (133-134, 137-138) = 30 μ m, (135-136, 140) = 60 μ m, (139, 141) = 100 μ m



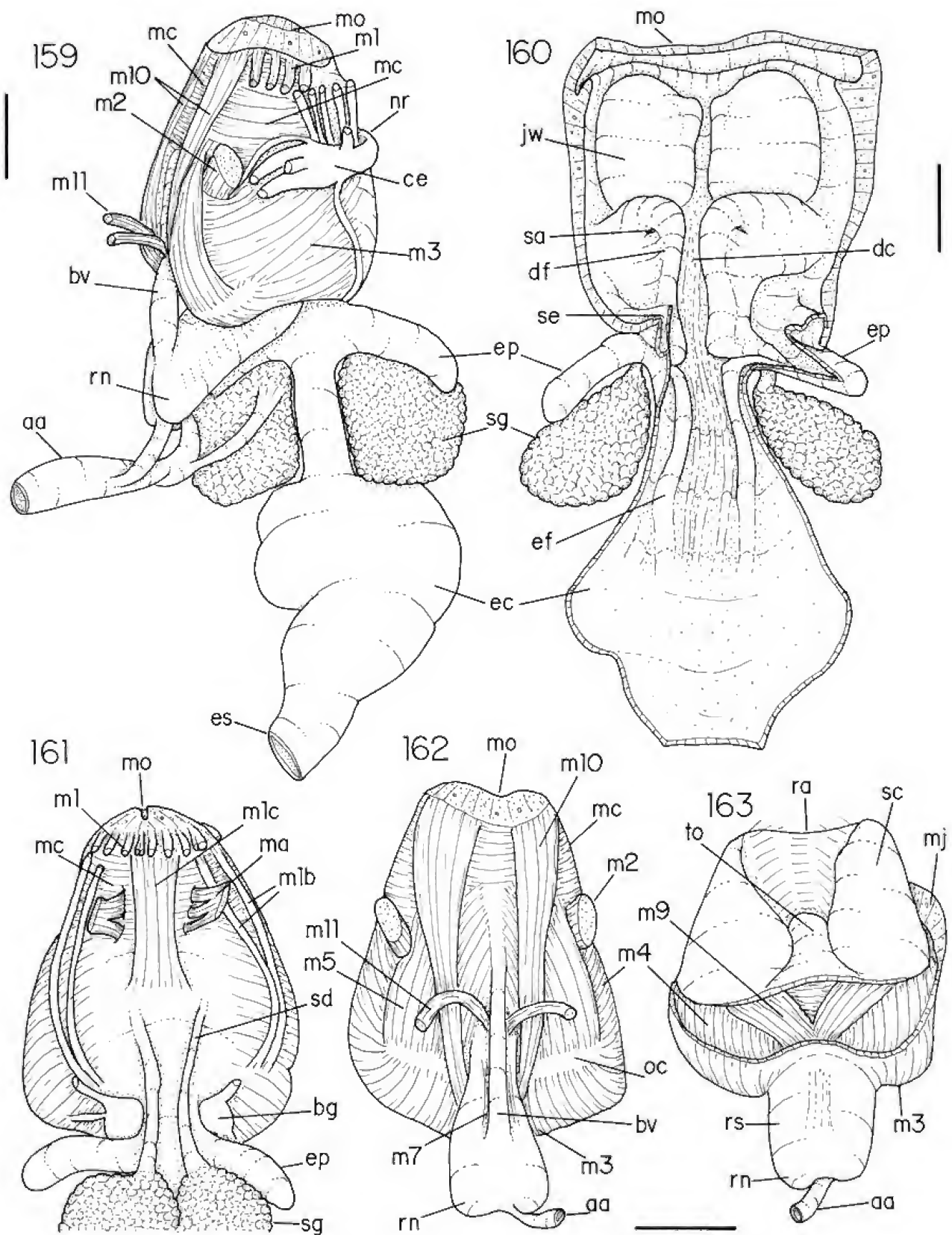
Hard structures (radula, except if indicated) in SEM: fig.142- *Viviparus contectus*; fig.143-144- *Notopala ampullaroides*; fig.145- *Notopala essingtonensis*; fig.146- *Larina cf strangei*; fig.147-148- *Annularia* sp.; fig.149- same, detail; fig.150- *Pomacea crosseana*, jaws. Scale bars: (142, 147-148) = 100 μ m, (143-146) = 40 μ m, (149) = 20 μ m, (150) = 200 μ m.



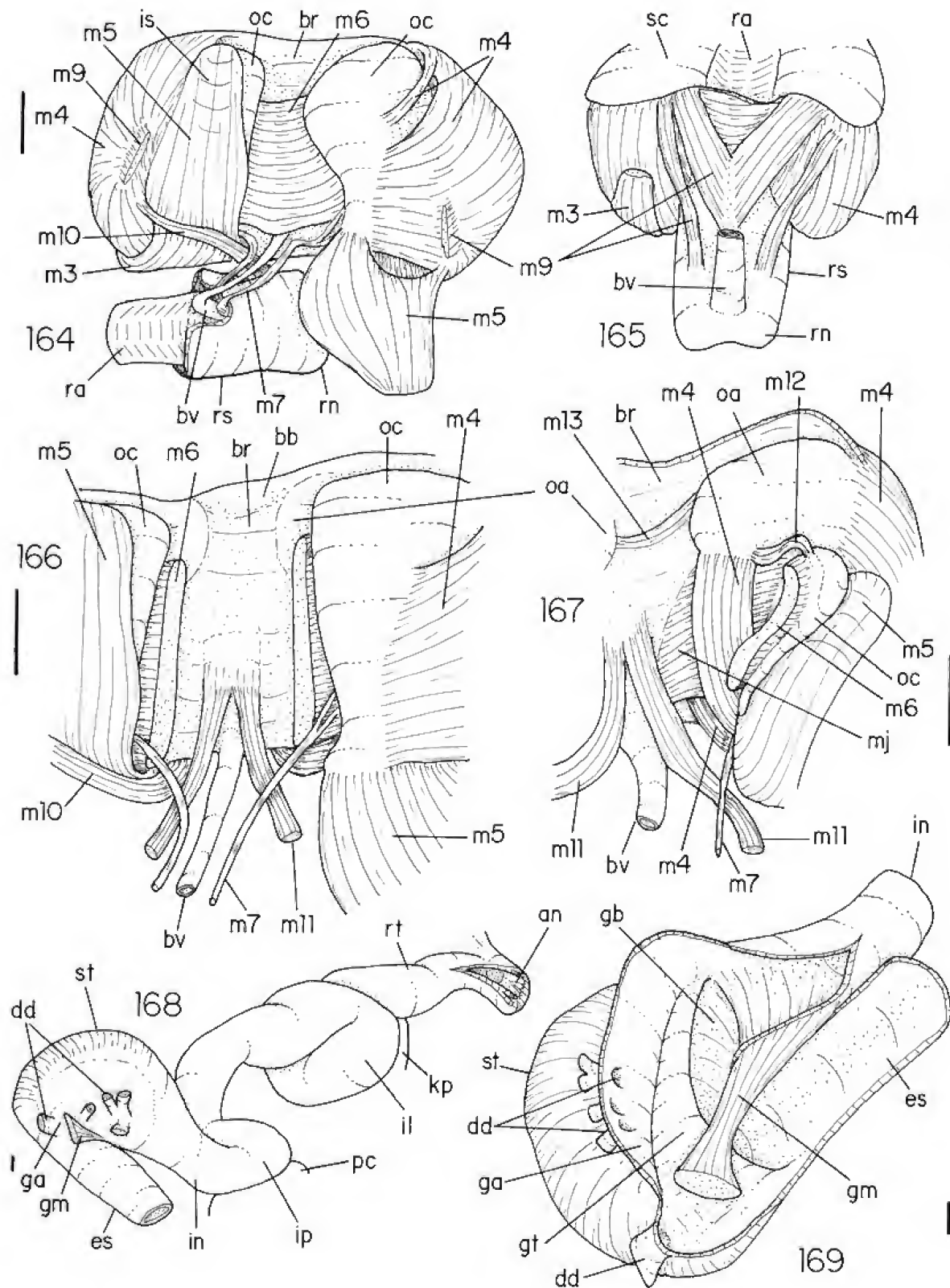
Pomacea crosseana anatomy: fig.151- head-foot, ♀, frontal view; fig.152- same, lateral-right view; fig.153- pallial cavity roof in inner-ventral view, and visceral mass; fig.154- anterior region of visceral mass and adjacent portion of pallial cavity, ventral view, ventral walls of pericardium and kidney removed, an schematic representation of in situ intestinal loops inside kidney shown in a separated detail; fig.155- detail of pallial cavity in region of lung, ventral wall of lung most removed and deflected posteriorly (to left in fig.). Scale bars = 2mm.



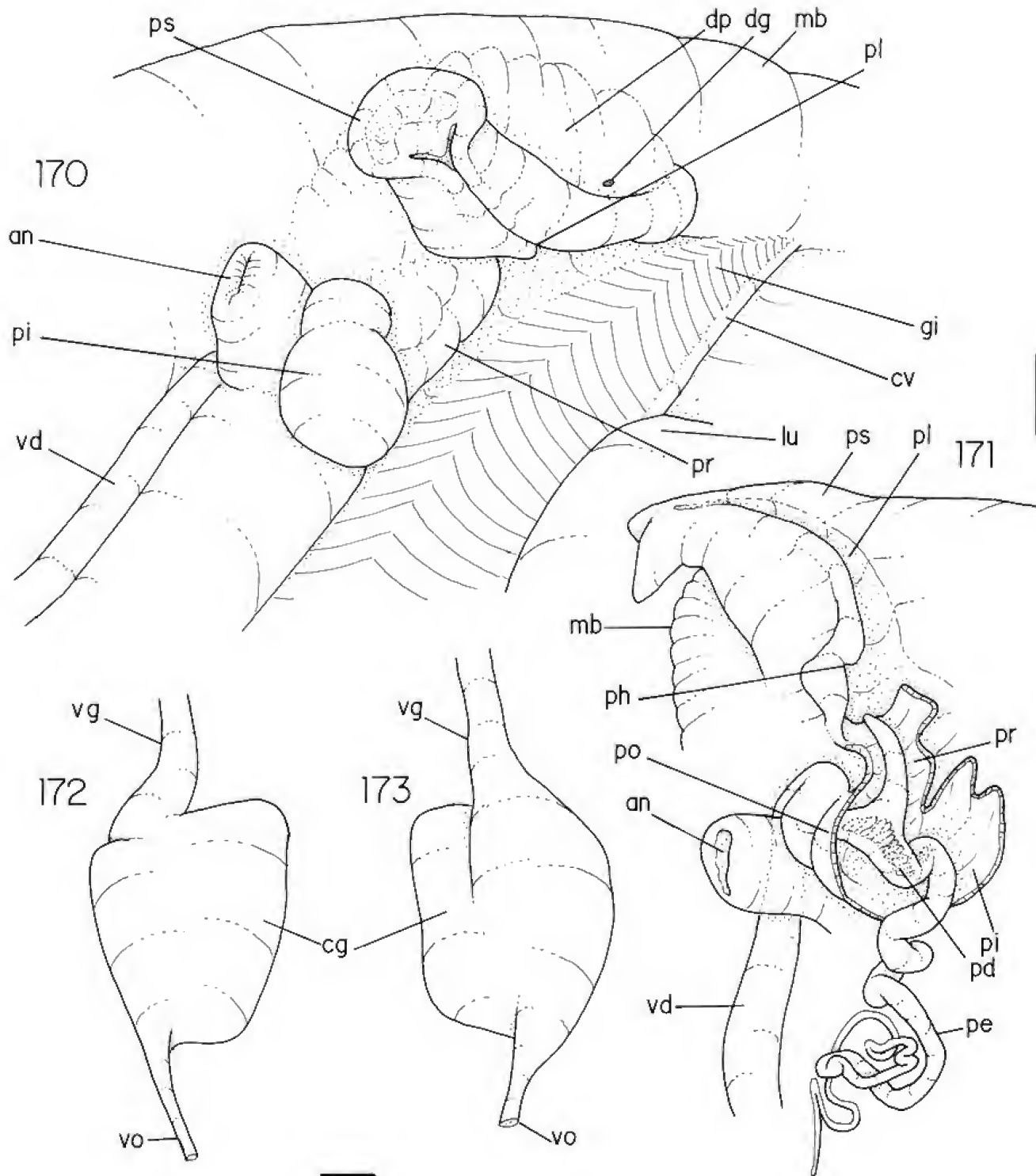
Pomacea crosseana anatomy: fig.156- pallial cavity roof, transversal section in middle region of osphradium; fig.157- kidney, ventral view, ventral wall removed, intestinal loops deflected, anterior lobe (ka) opened longitudinally; fig.158- head and haemocoel, ventral view, foot removed. Scale bars = 2mm.



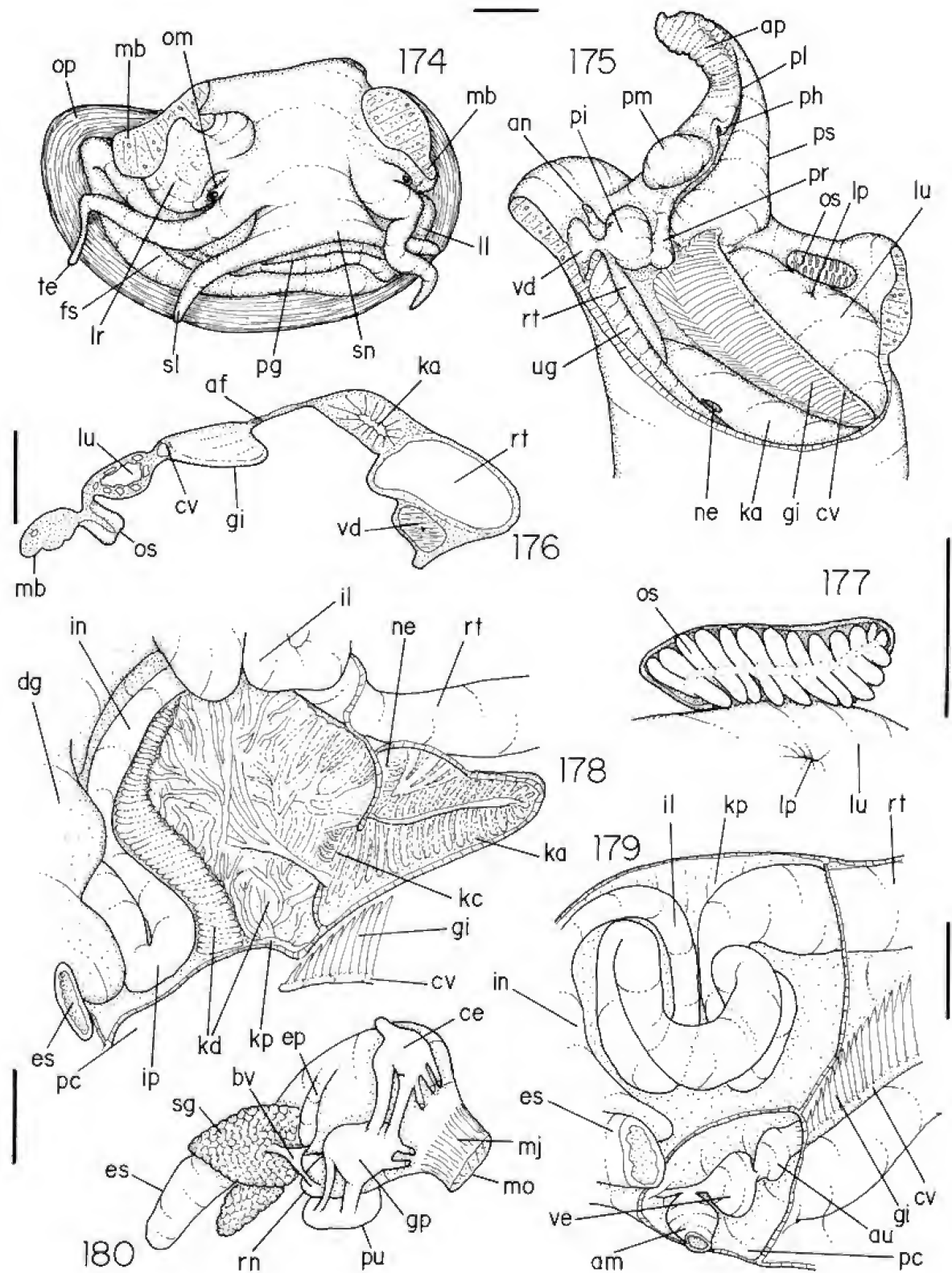
Pomacea crosseana anatomy: fig.159- foregut, buccal mass in lateral-left view, remainder structures in ventral view; fig.160- same, ventral view, odontophore removed, esophagus and left esophageal pouch (right in fig.) opened longitudinally; fig.161- buccal mass, dorsal view; fig.162- same, ventral view; fig.163- same, dorsal view, dorsal wall and esophagus removed. Scale bars = 2mm.



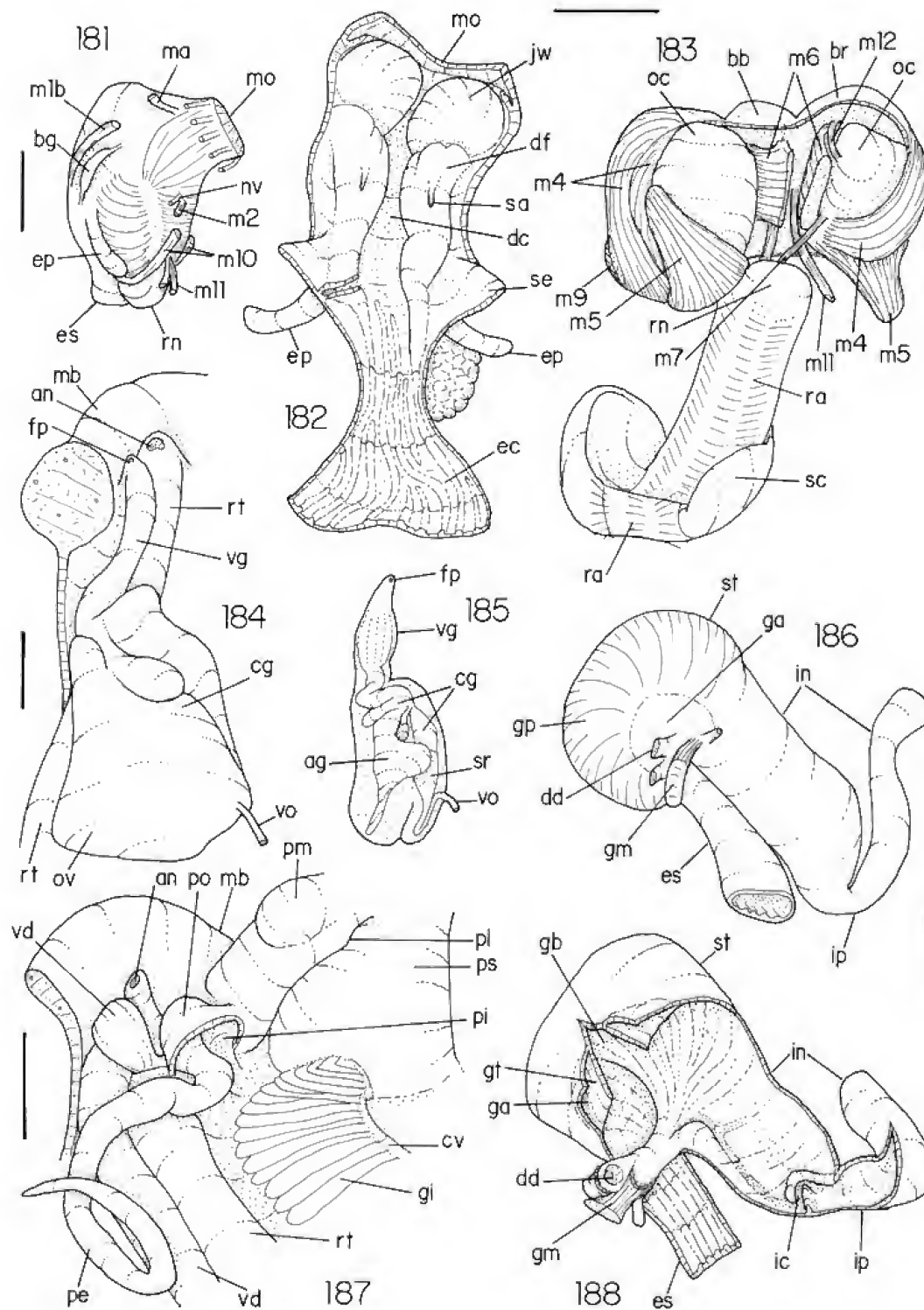
Pomacea crosseana anatomy: fig.164- odontophore, dorsal view, radular ribbon deflected and only partially shown, both cartilages and right m5 deflected; fig.165- same, dorsal view, detail of its posterior region with radular ribbon and subradular cartilage in situ; fig.166- detail of fig.164, with horizontal muscle (m6) sectioned longitudinally and deflected; fig.167- same, only right hemi-odontophore shown, odontophore cartilage (oc) deflected to show its opposed side; fig.168- middle and hindgut seen as in situ, ventral view; fig.169- stomach, ventral view, esophageal portion opened longitudinally, ventral gastric wall sectioned and deflected. Scale bars = 1mm.



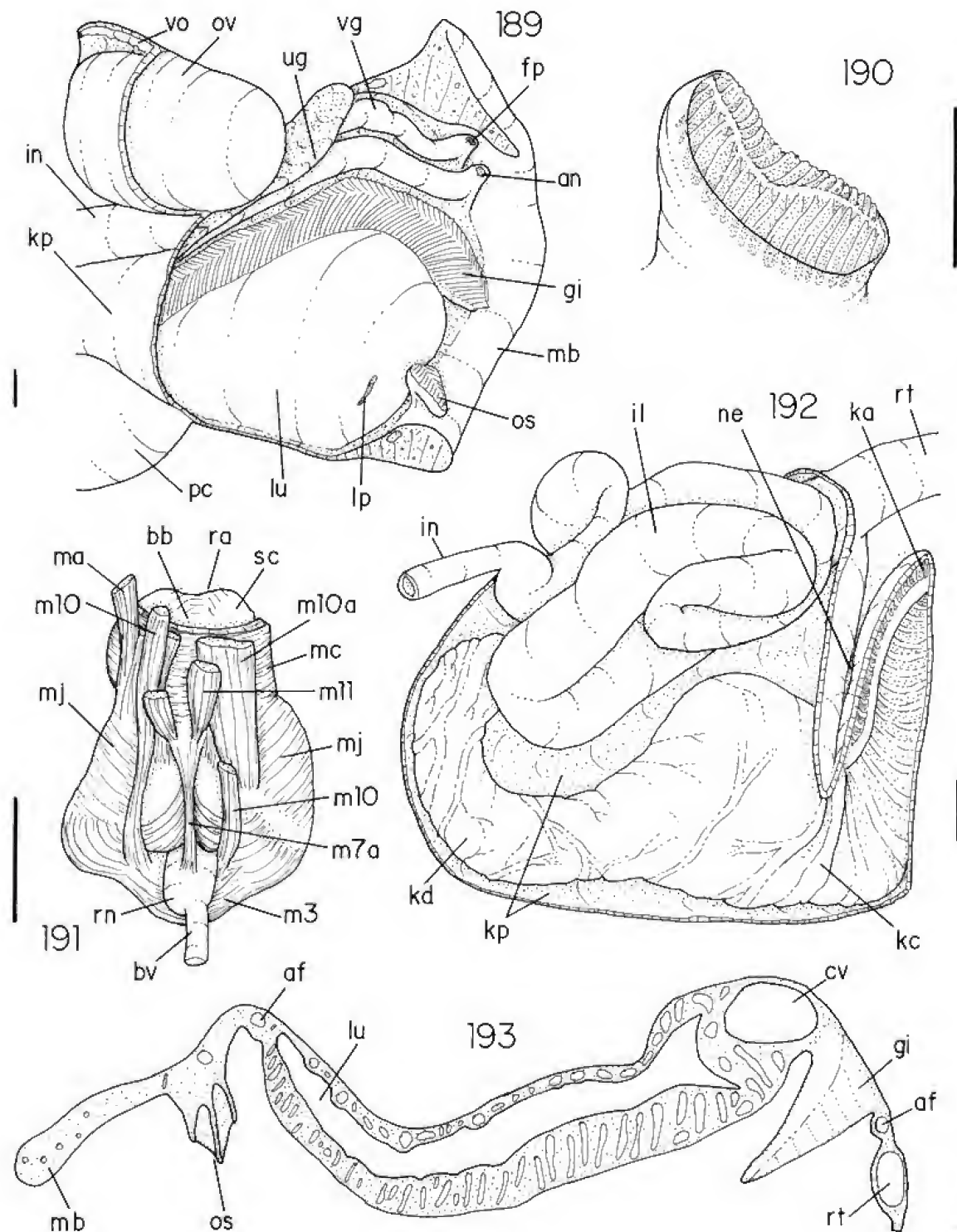
Pomacearosseana anatomy: fig.170- detail of pallial cavity in region of penis shield; fig.171- same, with penis shield deflected externally, penis sac opened, penis stretched; fig.172-173- pallial oviduct, ventral and dorsal views. Scale bars = 1mm.



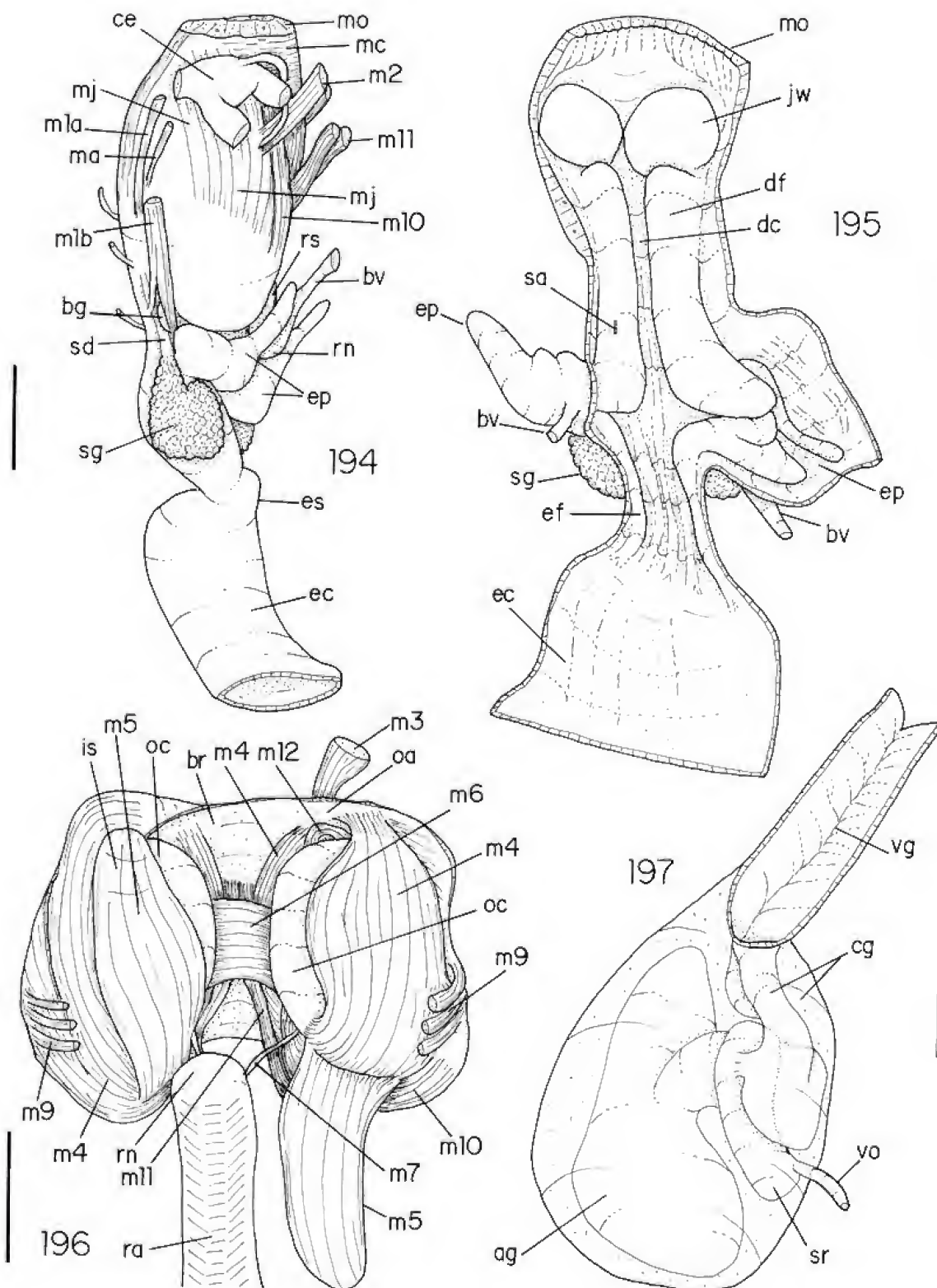
Pomacea curumim anatomy: fig.174- head-foot, ♀, frontal view; fig.175- pallial cavity roof, ♂, inner-ventral view, penis shield deflected outside; fig.176- pallial cavity roof, transversal section in middle region of osphradium; fig.177- detail of osphradium and adjacent region, ventral view; fig.178- kidney, ventral view, ventral wall removed, intestinal loops deflected, anterior lobe (ka) opened longitudinally; fig.179- anterior region of visceral mass and adjacent region of pallial cavity, ventral view, ventral walls of kidney and pericardium removed, special attention to fashion of renal intestinal loops; fig.180- foregut, lateral-right view. Scale bars = 1mm.



Pomacea curumim anatomy: fig.181- buccal mass, lateral-right view; fig.182- foregut, ventral view, odontophore removed, esophagus opened longitudinally right dorsal fold (left in fig.) sectioned in the level of esophageal pouch; fig.183- odontophore, dorsal view, radular ribbon extracted and deflected, both cartilages deflected, left cartilage in slightly apical view, horizontal muscle (m6) sectioned longitudinally and part deflected, left m5 also deflected; fig.184- pallial oviduct and adjacent structures of pallial roof, ventral view; fig.185- same, seen as a transparent structure; fig.186- midgut, ventral view as in situ; fig.187- right-anterior region of pallial cavity roof, male, penis shield deflected, penis sac opened and penis stretched; fig.188- midgut most opened longitudinally, ventral view, ventral gastric wall deflected, its transversal septum (gt) partially sectioned. Scale bars = 1mm.



Pomacea scalaris anatomy: fig.189- pallial cavity roof and anterior region of visceral mass, female, ventral view, oviduct deflected; fig.190- detail of osphradium, ventral view; fig.191- buccal mass, ventral view; fig.192- kidney, ventral view, ventral wall removed, intestinal loops deflected, anterior lobe (ka) opened longitudinally; fig.193- pallial cavity roof, transversal section in middle region of osphradium. Scale bars = 2mm.



Pomacea scalaris anatomy: fig.194- foregut, lateral-right view; fig.195- same, ventral view, odontophore removed, esophagus and left esophageal pouch (right in fig.) opened longitudinally; fig.196- odontophore, dorsal view, radular ribbon removed, deflected and only partially shown, both cartilages and right m5 deflected; fig.197- pallial oviduct, ventral view, seen as a transparent structure. Scale bars = 2mm.

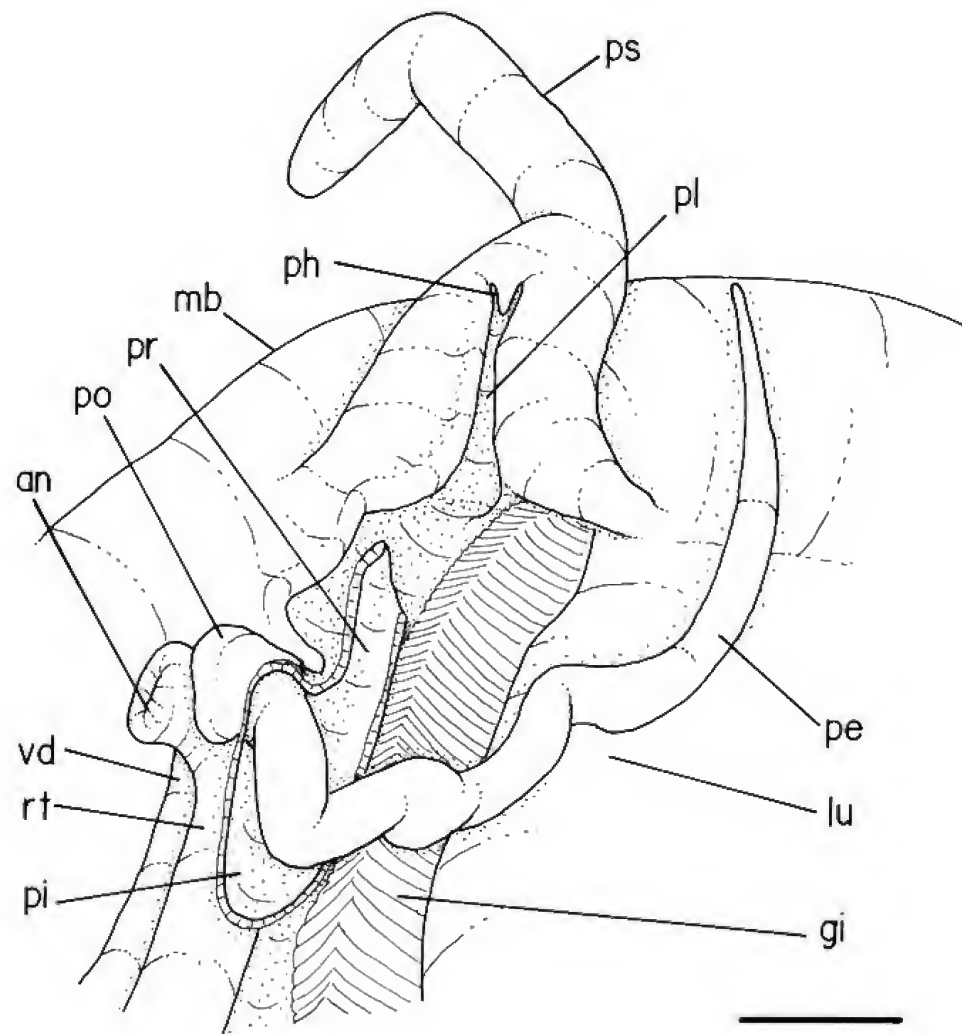
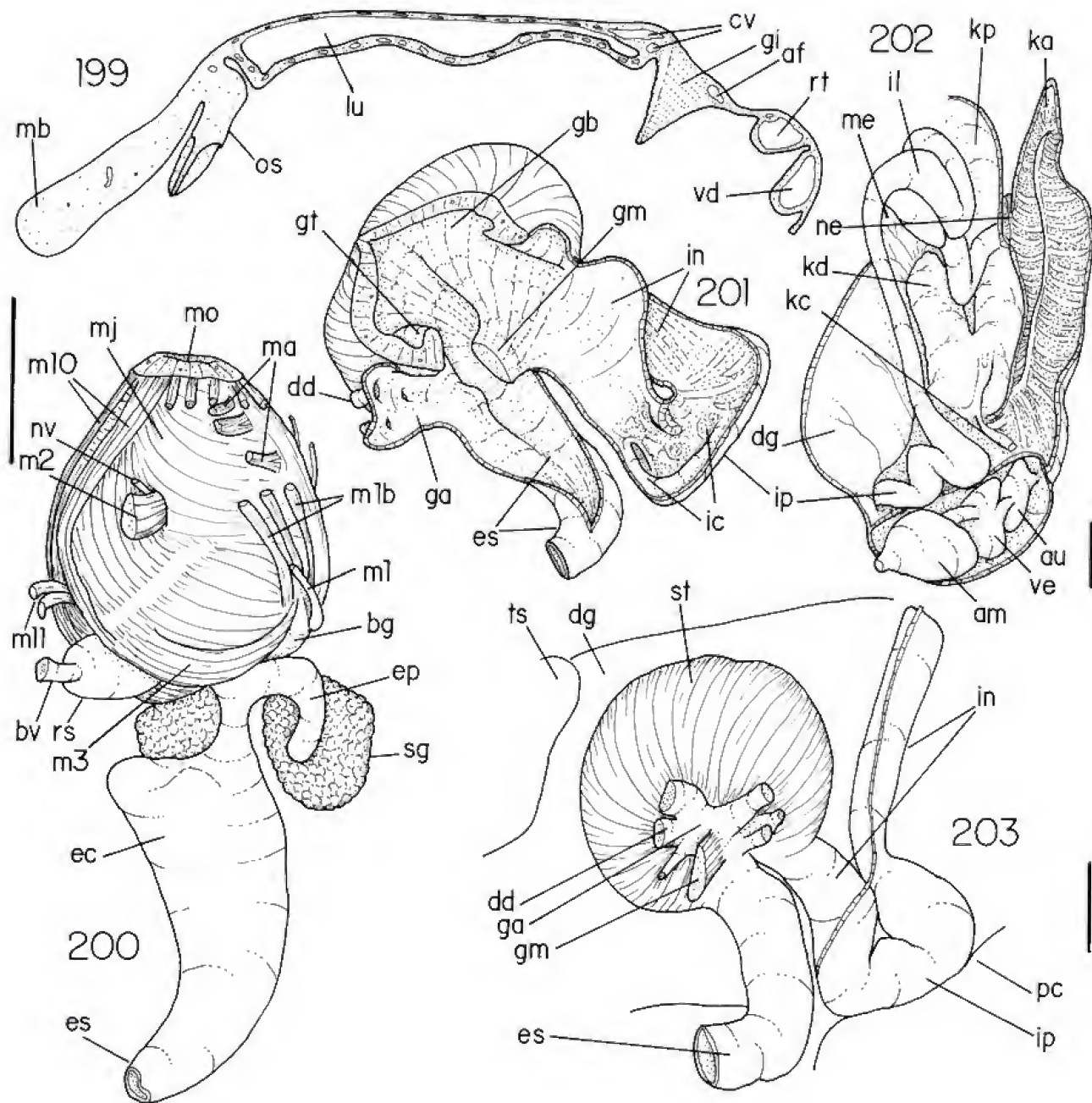
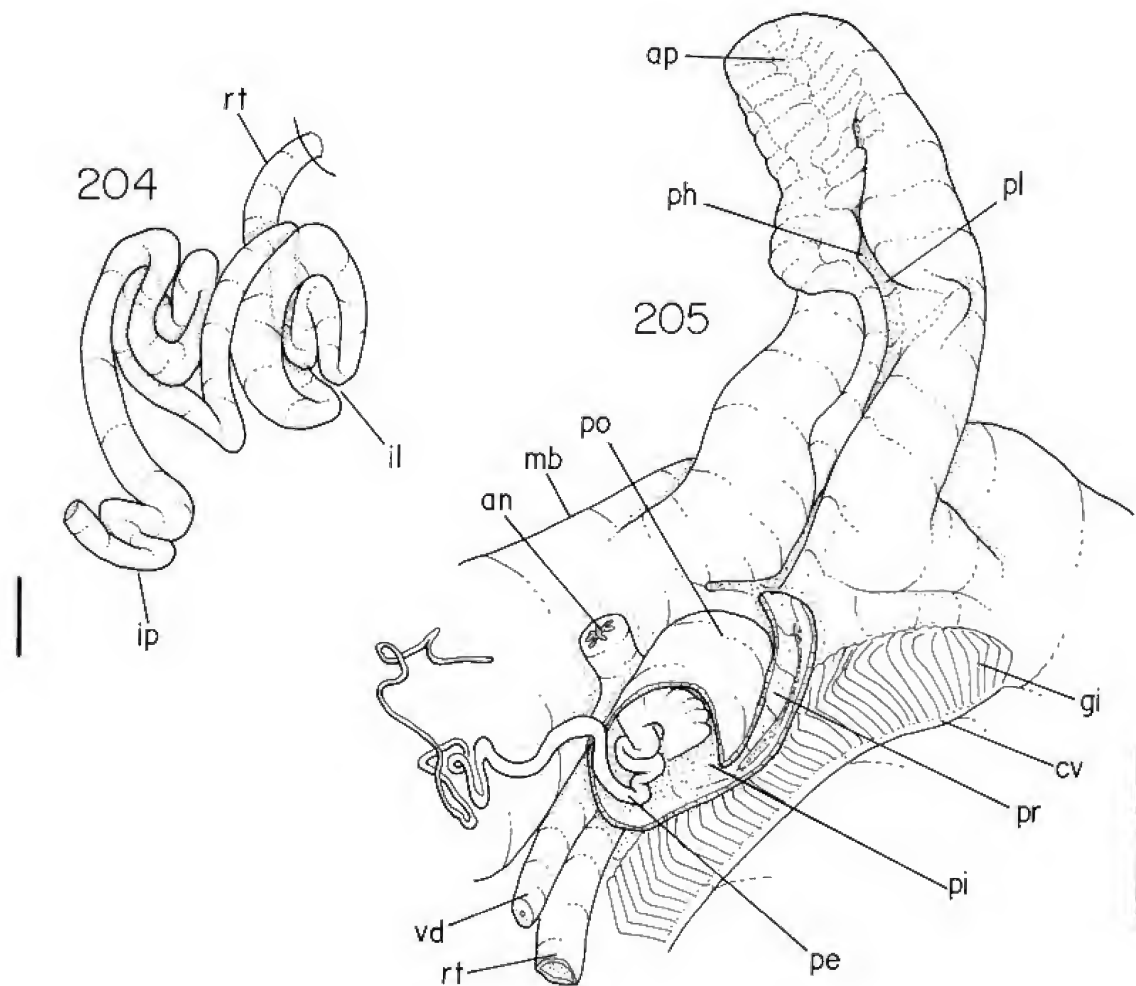


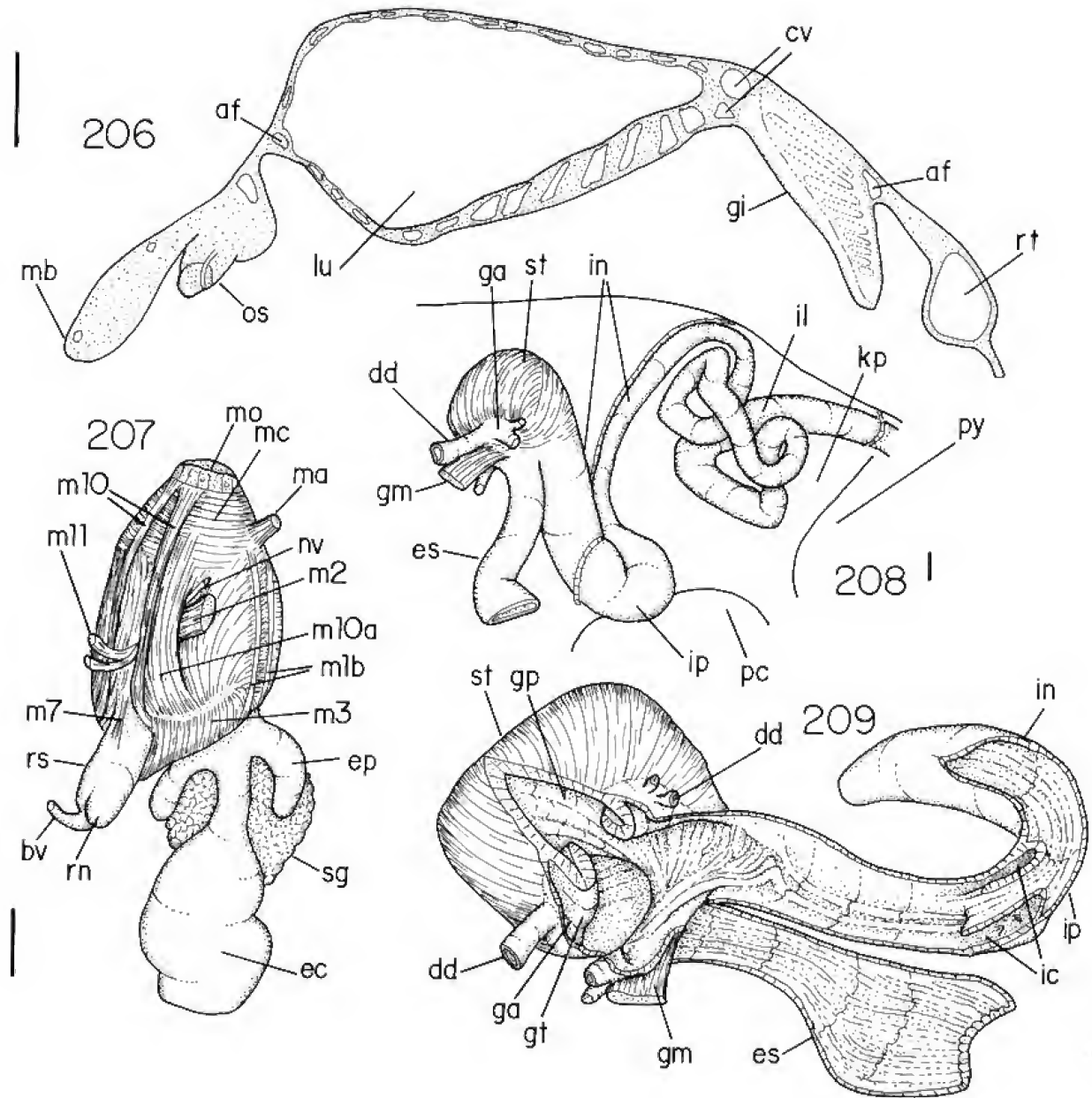
Fig.198- *Pomacea scalaris* anterior region of male reproductive system, penis shield deflected outside, penis sac opened, penis stretched. Scale bar = 2mm.



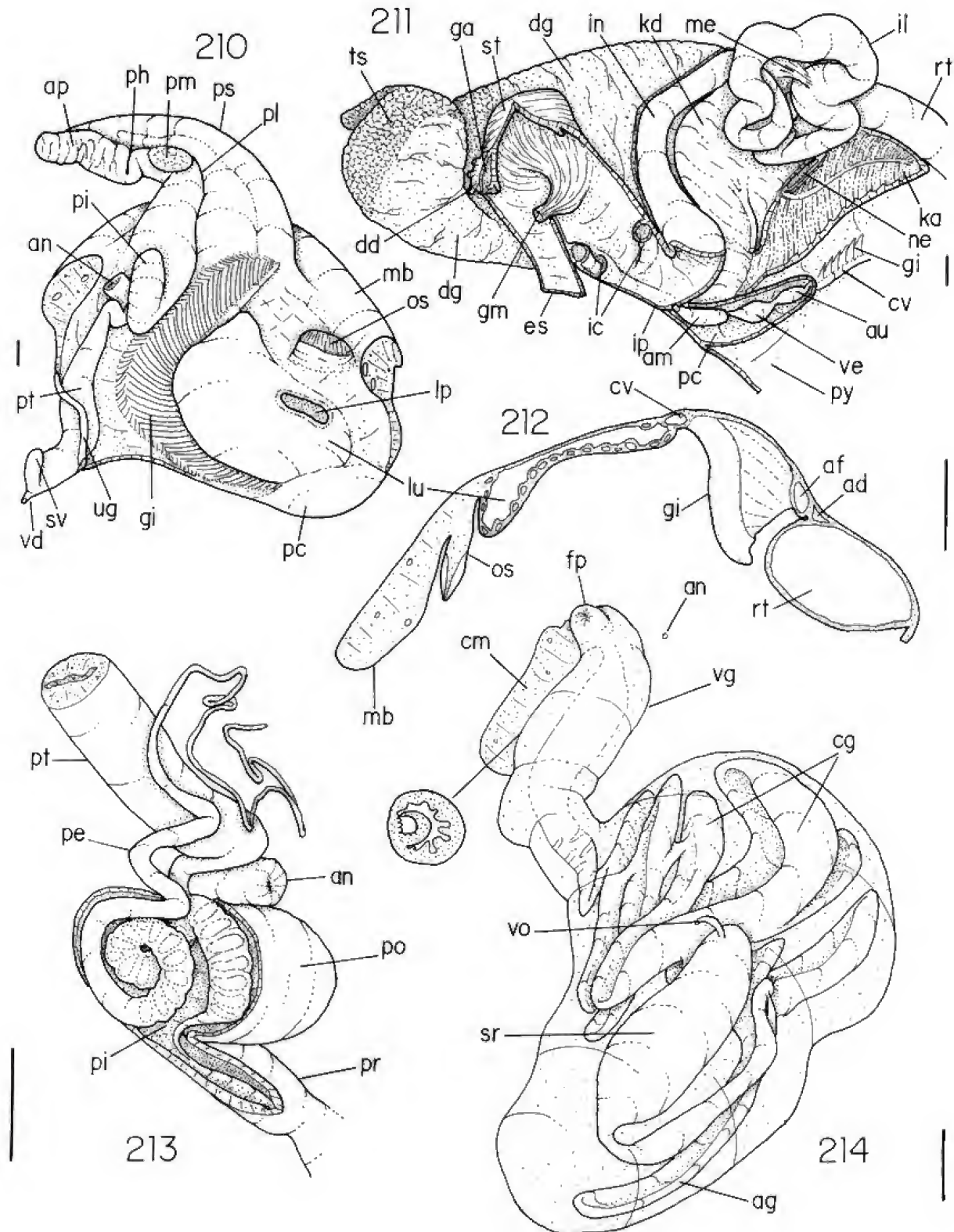
Pomacea canaliculata anatomy: fig.199- pallial cavity roof, transversal section in middle region of osphradium; fig.200- foregut, buccal mass in lateral-left view, remainder structures in ventral view; fig.201- midgut, ventral view, most opened longitudinally, ventral gastric wall greatly deflected; fig.202- kidney and pericardium, ventral view, ventral walls removed, intestinal loops deflected, anterior lobe (ka) opened longitudinally; fig.203- midgut, ventral view as in situ. Scale bars = 5mm.



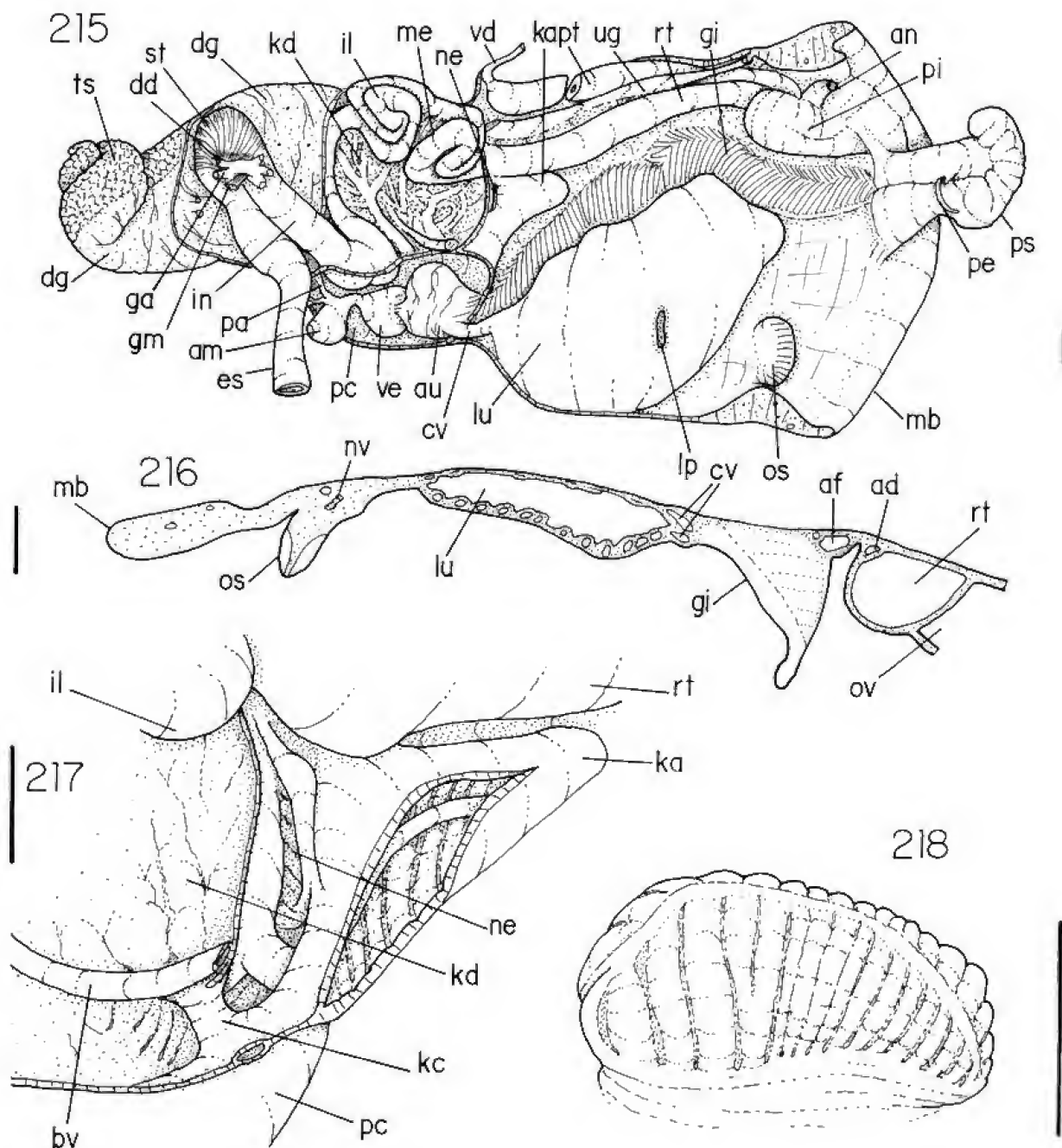
Pomacea canaliculata anatomy: fig.204- renal intestinal loops seen as in situ, ventral view; fig.205- anterior region of male reproductive system and adjacent pallial structures, penis shield deflected outside, penis sac opened, penis almost stretched. Scale bars = 5mm.



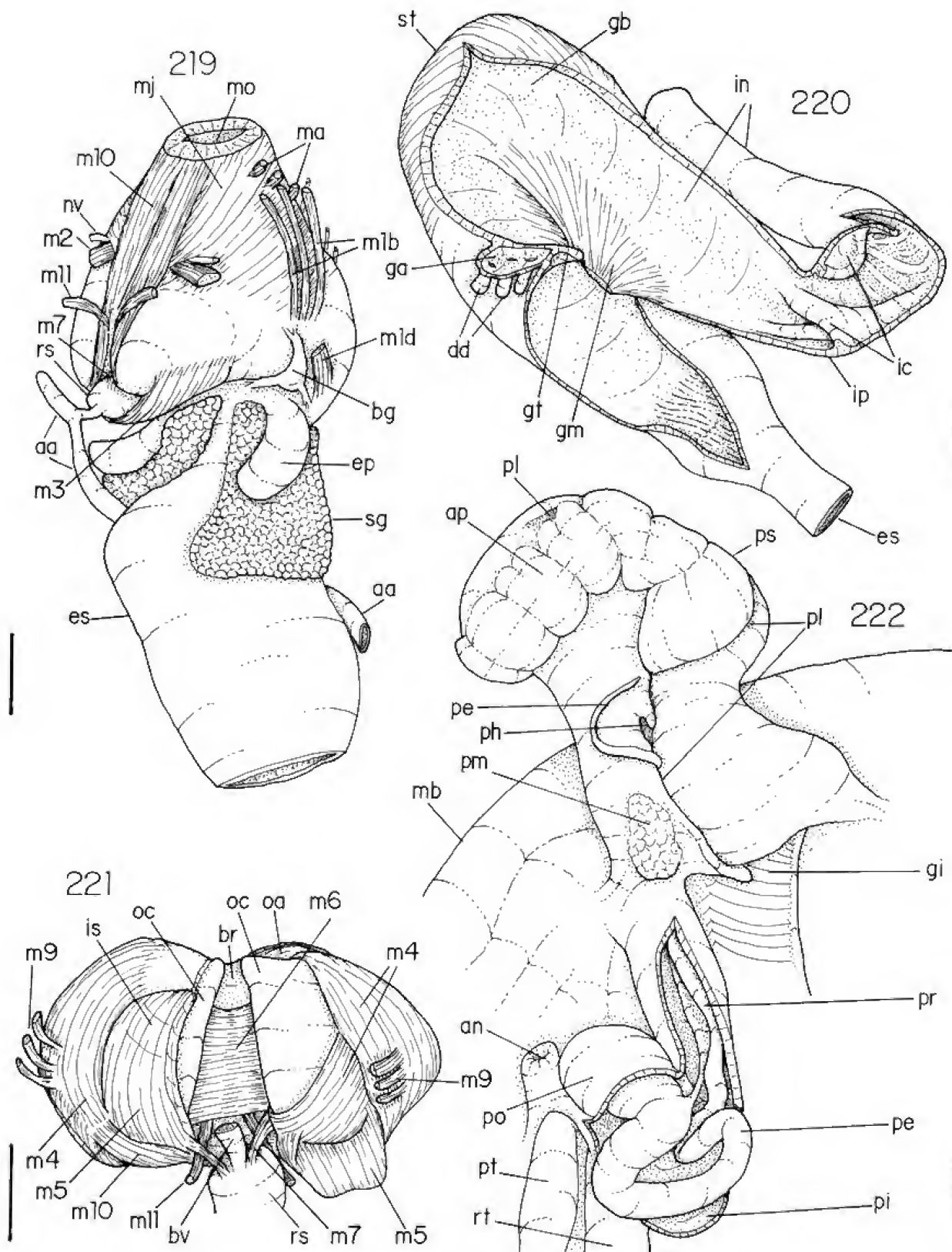
Pomacea lineata anatomy, mainland samples: fig.206- pallial cavity roof, transversal section in middle region of osphradium; fig.207- foregut, ventral-slightly left view; fig.208- middle and hindgut, ventral view as in situ; fig.209- midgut most opened longitudinally, ventral view. Scale bars = 2mm.



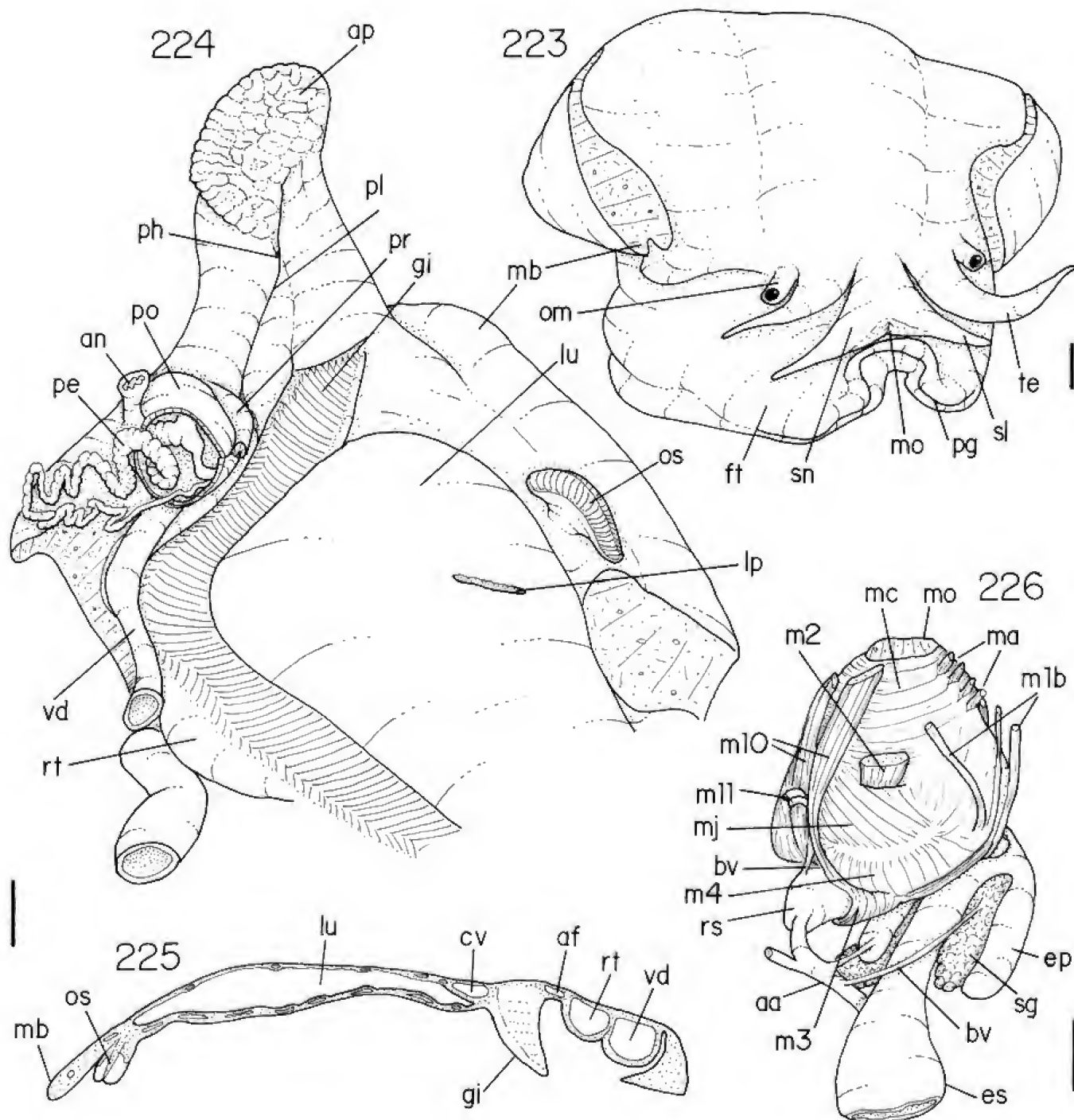
Pomacea lineata anatomy, Fernando de Noronha sample: fig.210- pallial roof, ♂, ventral-inner view, penis shield deflected outside, rectum extracted; fig.211- visceral mass partially uncoiled and posterior region of pallial cavity, ventral view, midgut opened longitudinally, ventral walls of kidney and pericardium removed, renal intestinal loops deflected, anterior lobe (ka) opened longitudinally; fig.212- pallial cavity roof, transversal section in middle region of osphradium; fig.213- penis sac and adjacent structures, ventral view, penis sac opened, penis partially stretched; fig.214- pallial oviduct, ventral view, seen as a transparent structure, a transversal section of indicated level of vaginal tube also shown. Scale bars = 2mm.



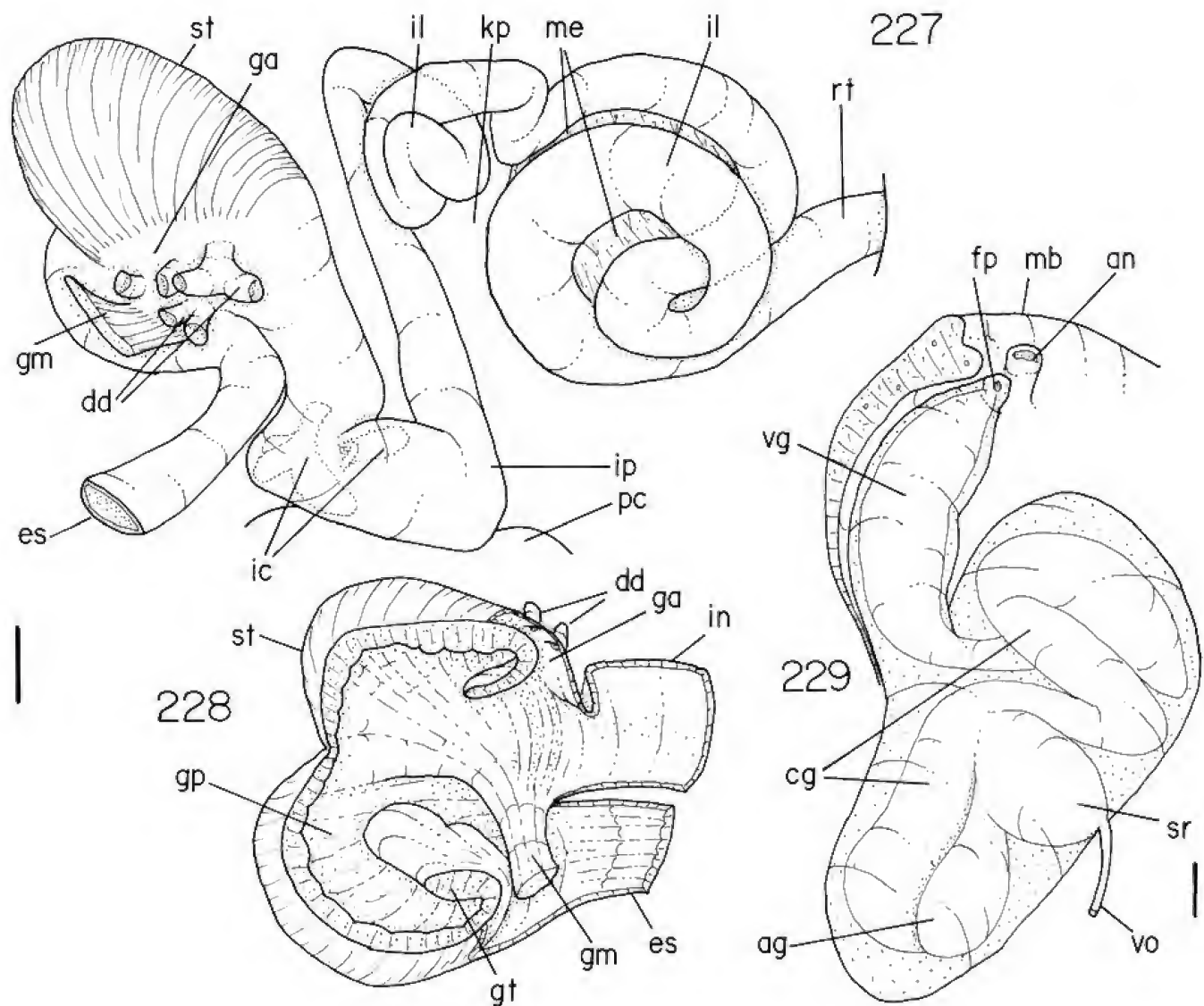
Pomacea sordida anatomy: fig.215- pallial cavity and visceral mass partially uncoiled, ♂, ventral view, penis shield deflected outside, prostate artificially sectioned transversally, ventral walls of kidney and pericardium removed, renal intestinal loops slightly deflected outside, portion of digestive gland ventral to midgut removed; fig.216- pallial cavity roof, transversal section in middle region of osphradium; fig.217- detail of anterior region of kidney, ventral view, ventral renal wall removed, nephrostome opened, anterior renal chamber (ka) partially opened longitudinally; fig.218- osphradium, ventral-slightly posterior view. Scale bars = 2mm.



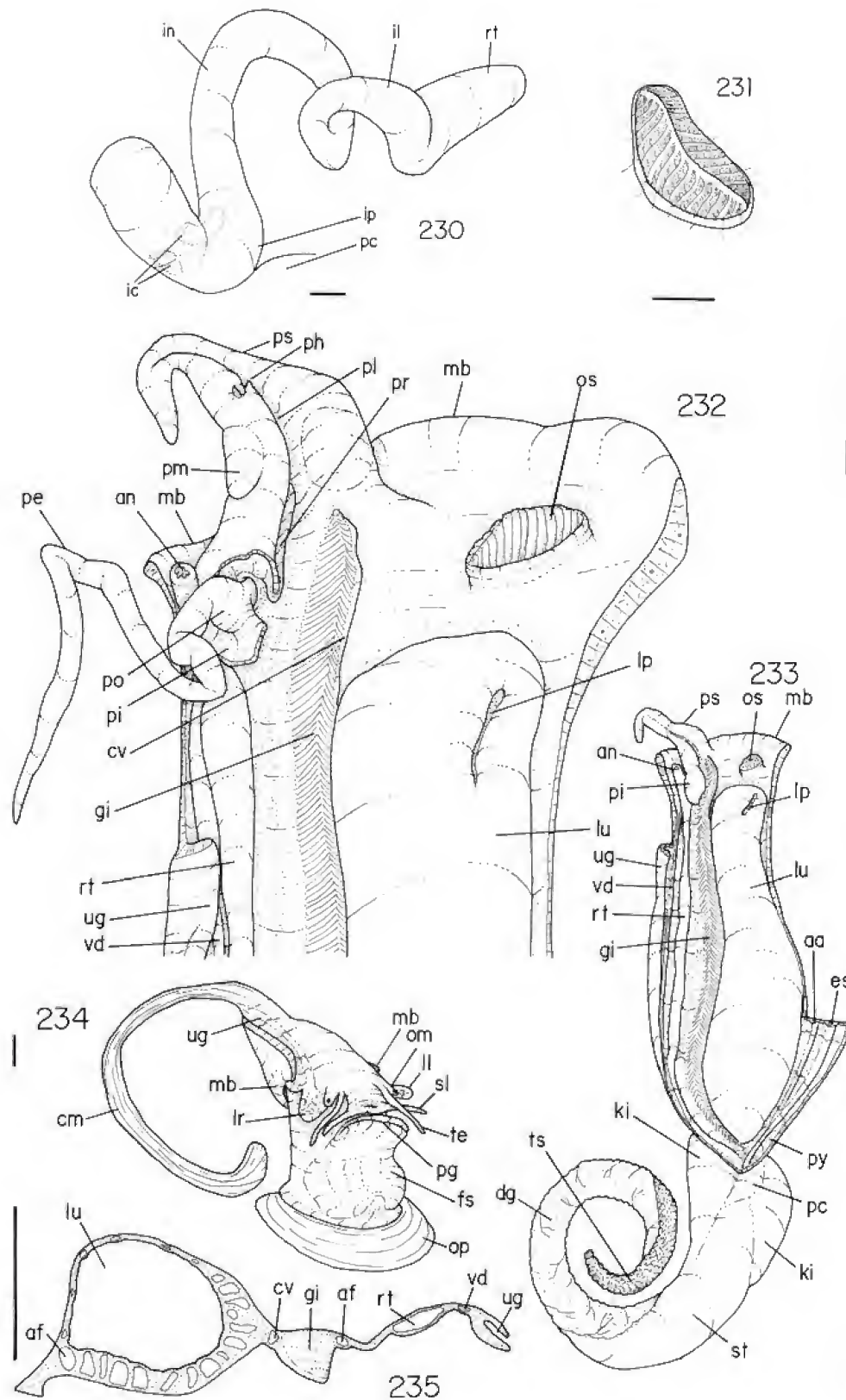
Pomacea sordida anatomy: fig.219- foregut, lateral-right view; fig.220- midgut, ventral view, most opened longitudinally; fig.221- odontophore, dorsal view, radula removed, deflected (only radular nucleus shown), both cartilages and left m5 deflected; fig.222- anterior region of male genital system and adjacent pallial structures, ventral view, penis shield deflected outside, penis sac opened, penis partially uncoiled, but with its apical portion still passing through its groove in penis shield. Scale bars = 2mm.



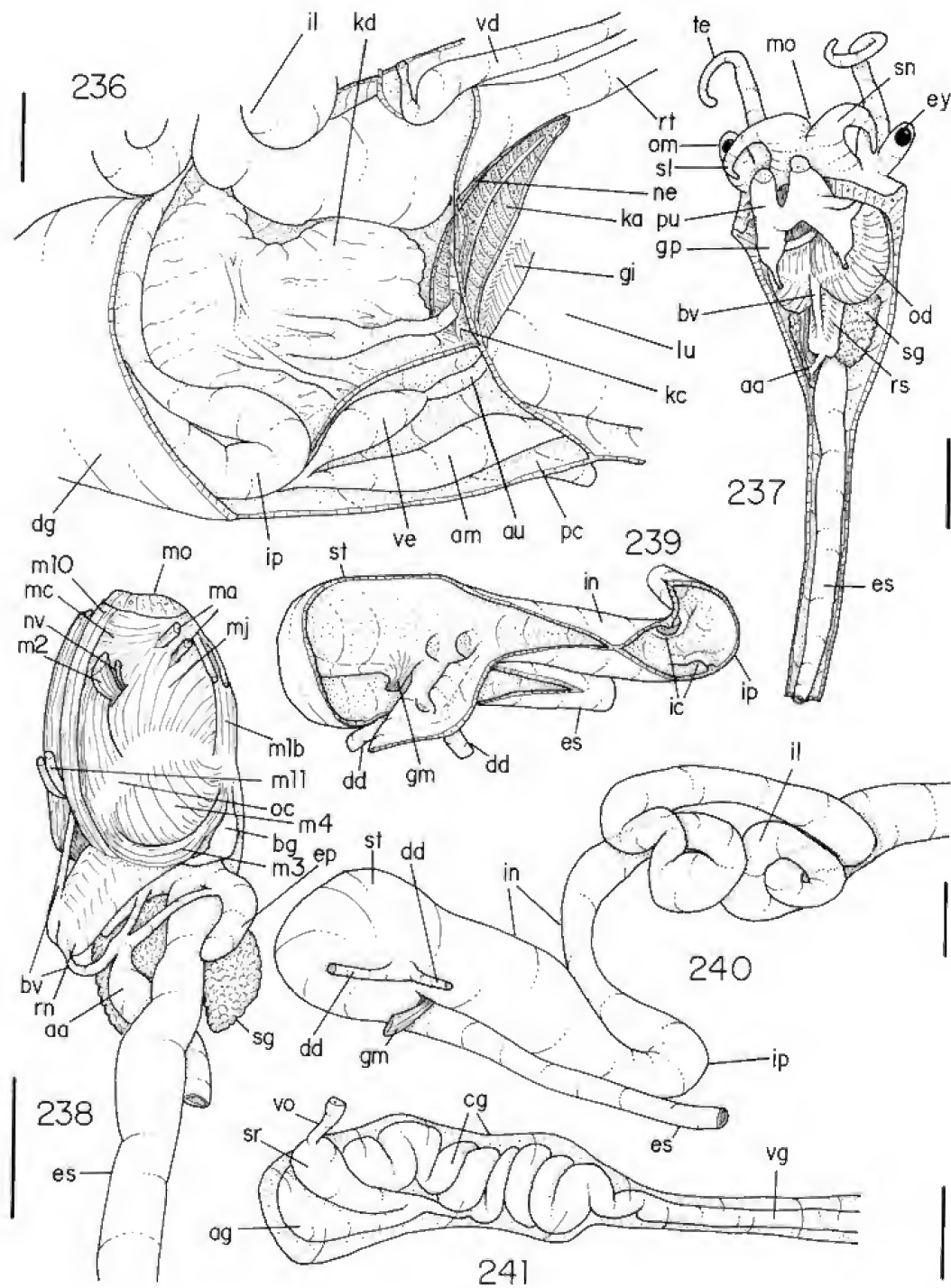
Asolene megastoma anatomy: fig.223- head-foot, ♂, frontal view; fig.224- pallial cavity, ♂, ventral-inner view, penis shield deflected outside, penis sac opened, penis partially stretched, prostate posterior region sectioned; fig.225- pallial cavity roof, transversal section in middle region of osphradium; fig.226- foregut, lateral-left view. Scale bars = 5mm.



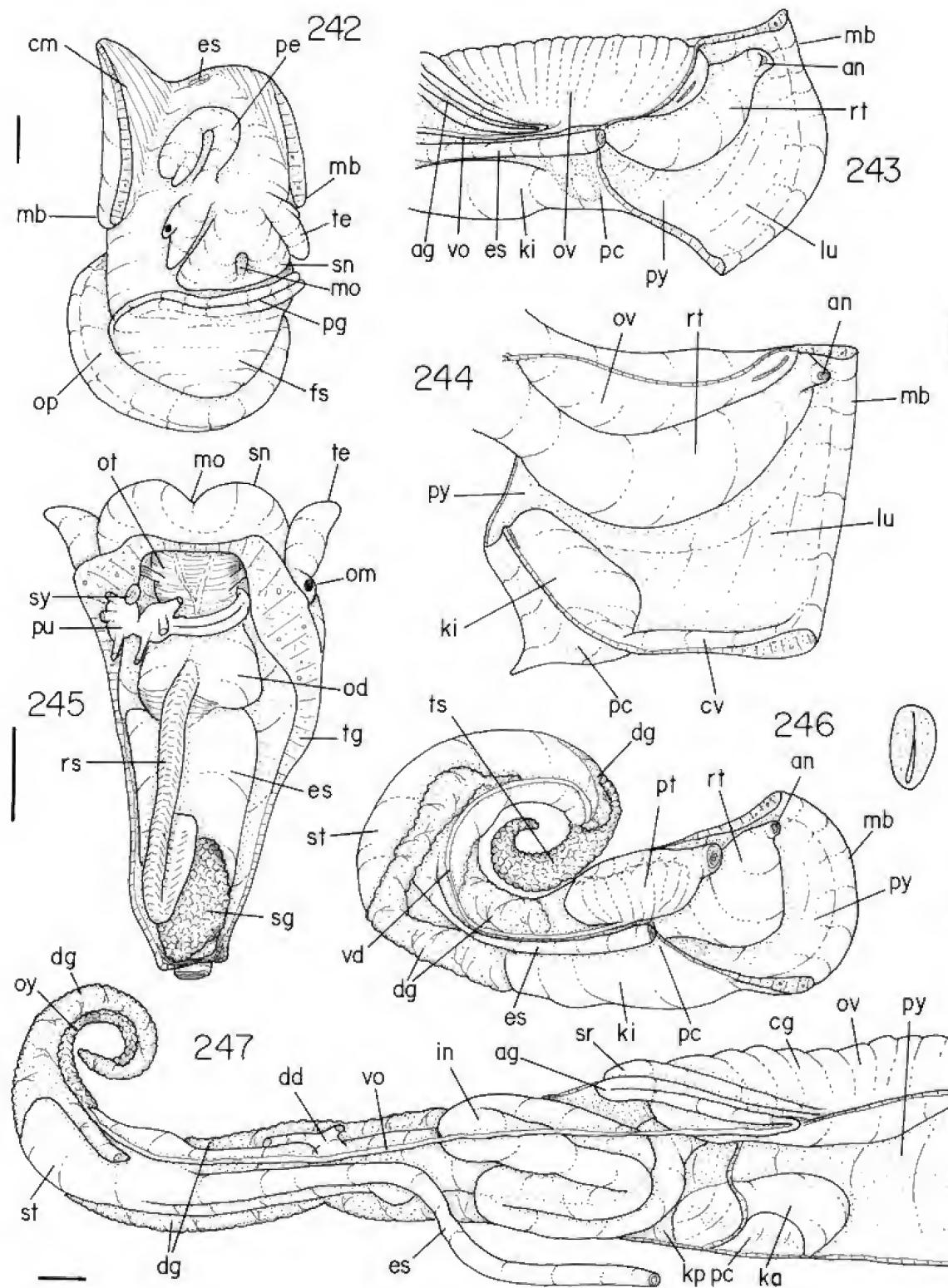
Asolene megastoma anatomy: fig.227- midgut, ventral view as in situ, chambers of intestine (ic) seen as if intestine was a transparent structure; fig.228- stomach and adjacent portions of stomach and intestine, ventral view, entirely opened longitudinally; fig.229- pallial oviduct and adjacent region of pallial cavity, ventral view, oviduct seen as a transparent structure. Scale bars = 5mm.



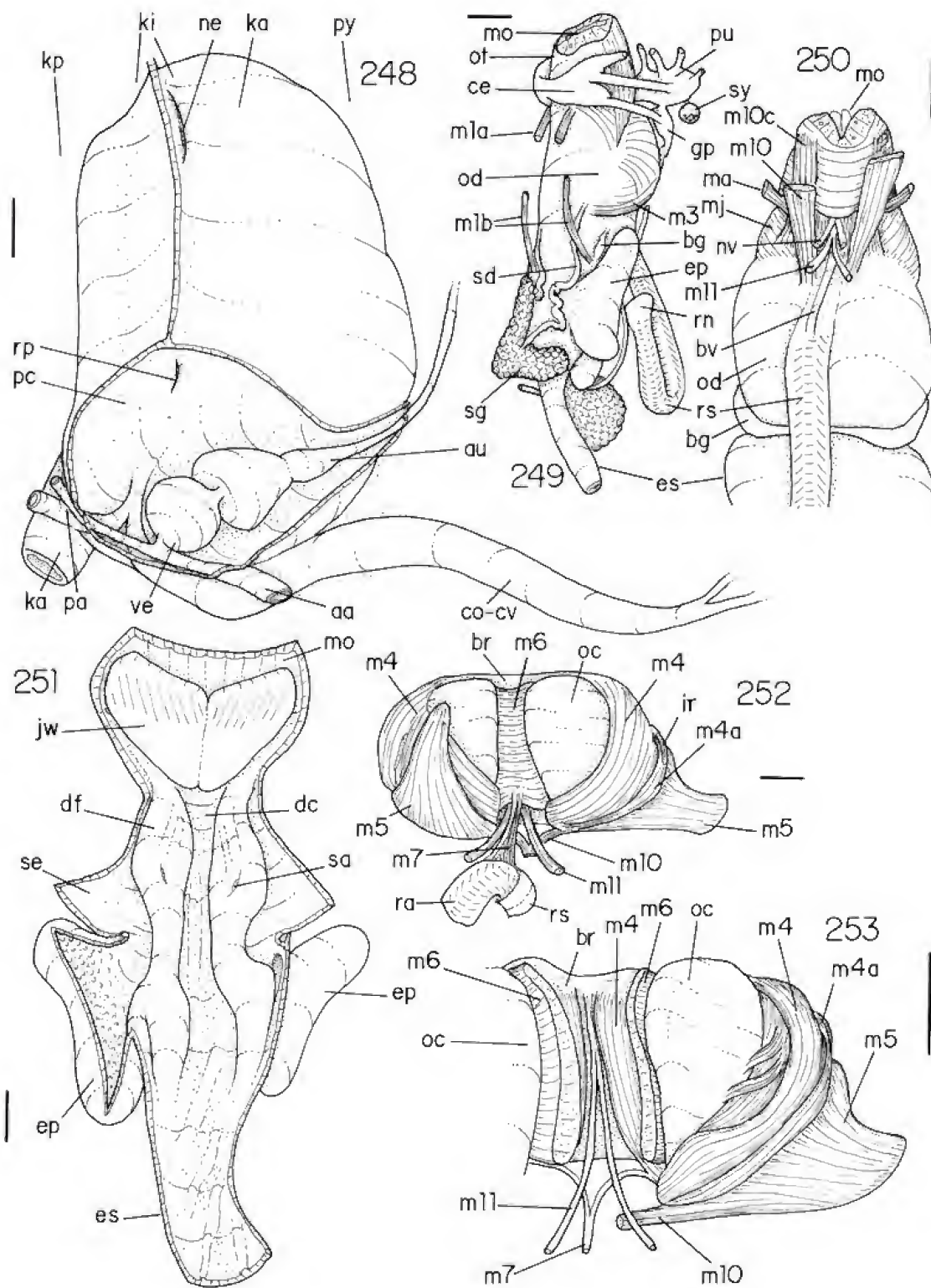
Felipponea neritiformis anatomy: fig.230- midgut, ventral view as in situ, chambers of intestine (ic) seen as if intestine was a transparent structure; fig.231- osphradium, ventral view. Scale bars = 1mm. *Marisa planogyra* anatomy: fig.232- anterior portion of pallial cavity, ♂, ventral-inner view, penis shield deflected outside, penis sac opened, penis partially stretched; fig.233- pallial cavity and visceral mass partially uncoiled, male, ventral view, penis shield deflected outside; fig.234- head-foot, ♂, frontal view; fig.235- pallial cavity roof, transversal section in middle region of lung. Scale bars = 2mm.



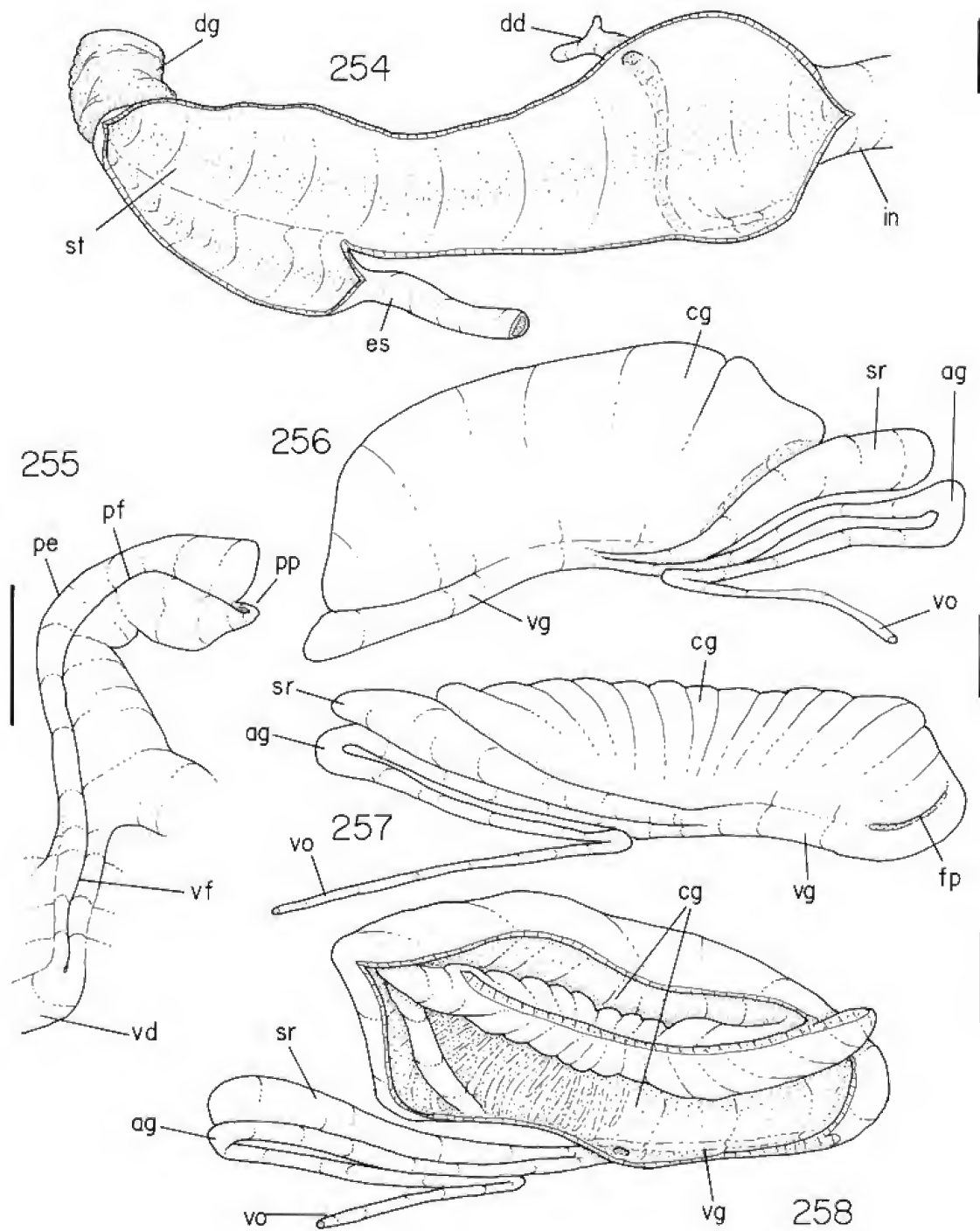
Marisa planogyra anatomy: fig.236- kidney and adjacent structures, ventral view, ventral walls of kidney and pericardium removed, renal intestinal loops deflected outside and only partially shown, anterior renal chamber opened longitudinally; fig.237- head and haemocoel, ventral view, foot removed; fig.238- foregut, lateral-left view; fig.239- midgut, ventral view, most opened longitudinally, ventral gastric wall deflected; fig.240- midgut, ventral view as in situ; fig.241- pallial oviduct posterior region, not fully mature, ventral view, seen as a transparent structure. Scale bars = 2mm.



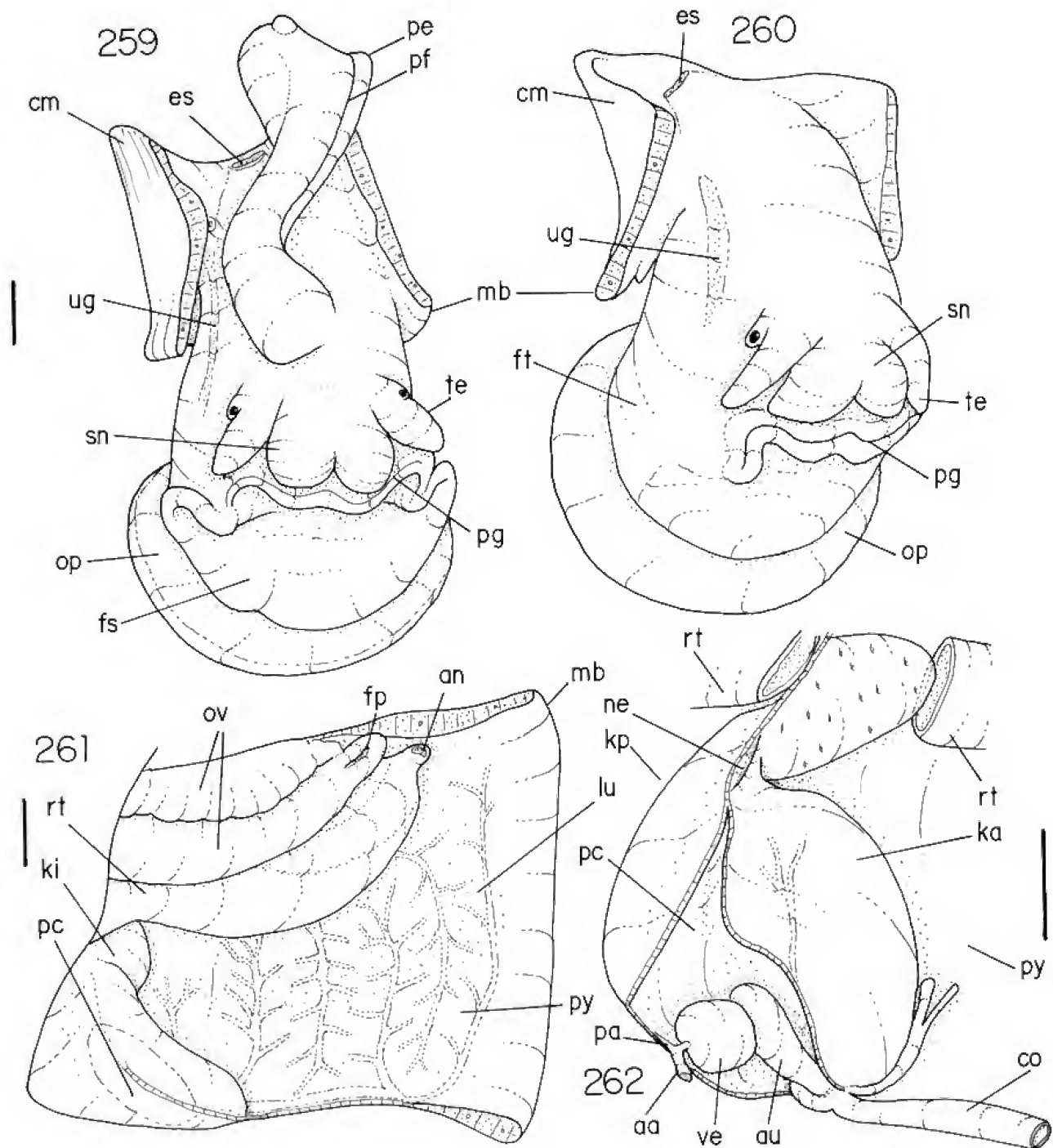
Neocyclotus prominulus anatomy: fig.242- head-foot, ♂, frontal view; fig.243- pallial cavity and anterior region of visceral mass, ♀, ventral view; fig.244- same, mantle posterior region deflected; fig.245- head and haemocoel, ventral view, foot removed; fig.246- pallial cavity and visceral mass partially uncoiled, ♂, ventral view, a detail of a transversal section of prostate shown at right; fig.247- partially uncoiled visceral mass and posterior region of pallial cavity, ventral view, esophagus deflected, digestive gland portion ventral to stomach partially removed. Scale bars = 1mm.



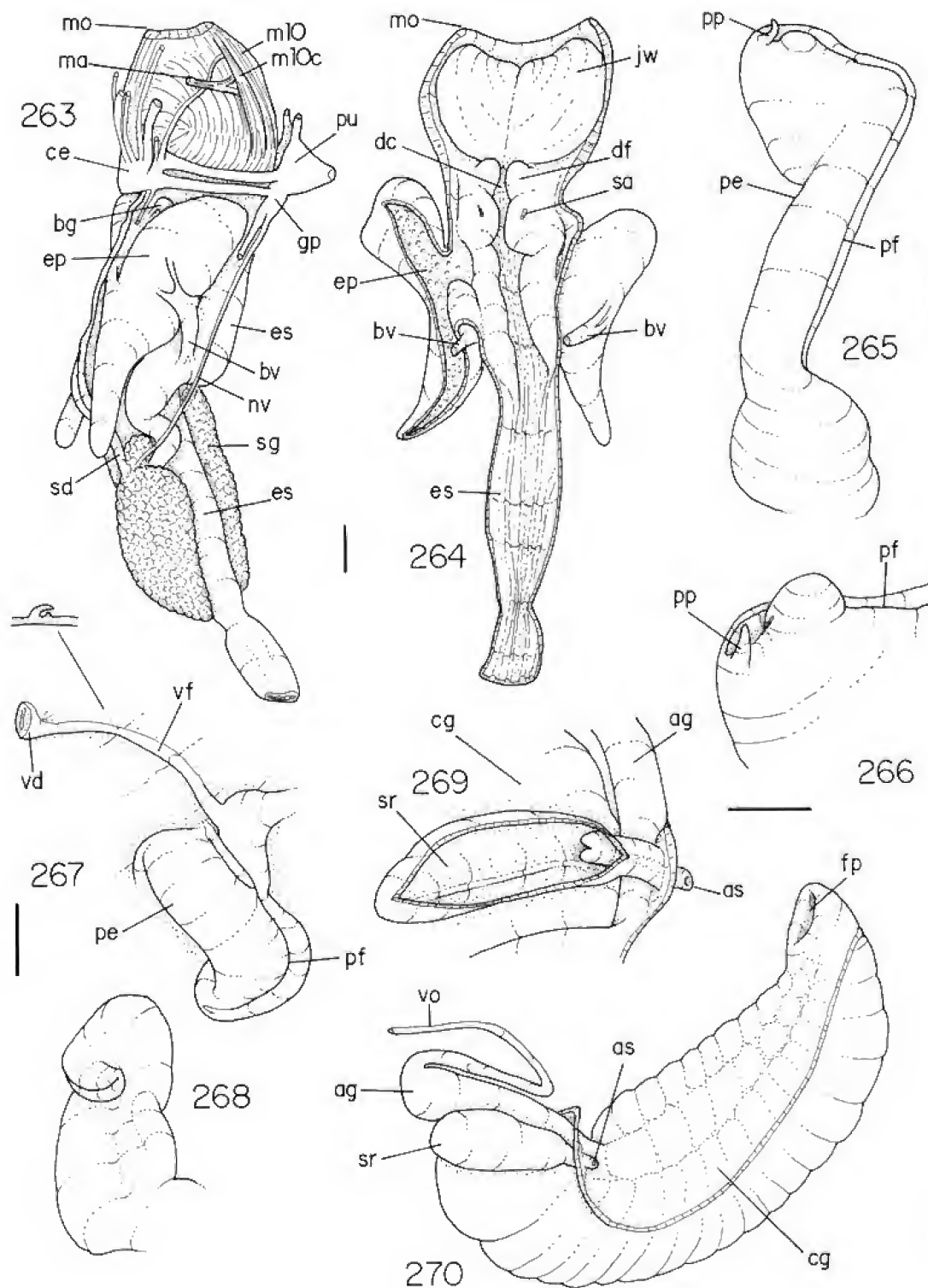
Neocyclotus prominulus anatomy: fig.248- kidney and adjacent structures, ventral view, ventral wall of pericardium removed; fig.249- foregut, lateral-right view; fig.250- buccal mass and anterior region of esophagus, ventral view; fig.251- foregut, ventral view, odontophore removed, esophagus and right esophageal pouch (left in fig.) opened longitudinally; fig.252- odontophore, dorsal view, radula removed, deflected and only partially shown, both cartilages and left m5 deflected; fig.253- same, m6 sectioned longitudinally, only middle and right structures shown, m4 partially separated from cartilage. Scale bars = 0.5mm.



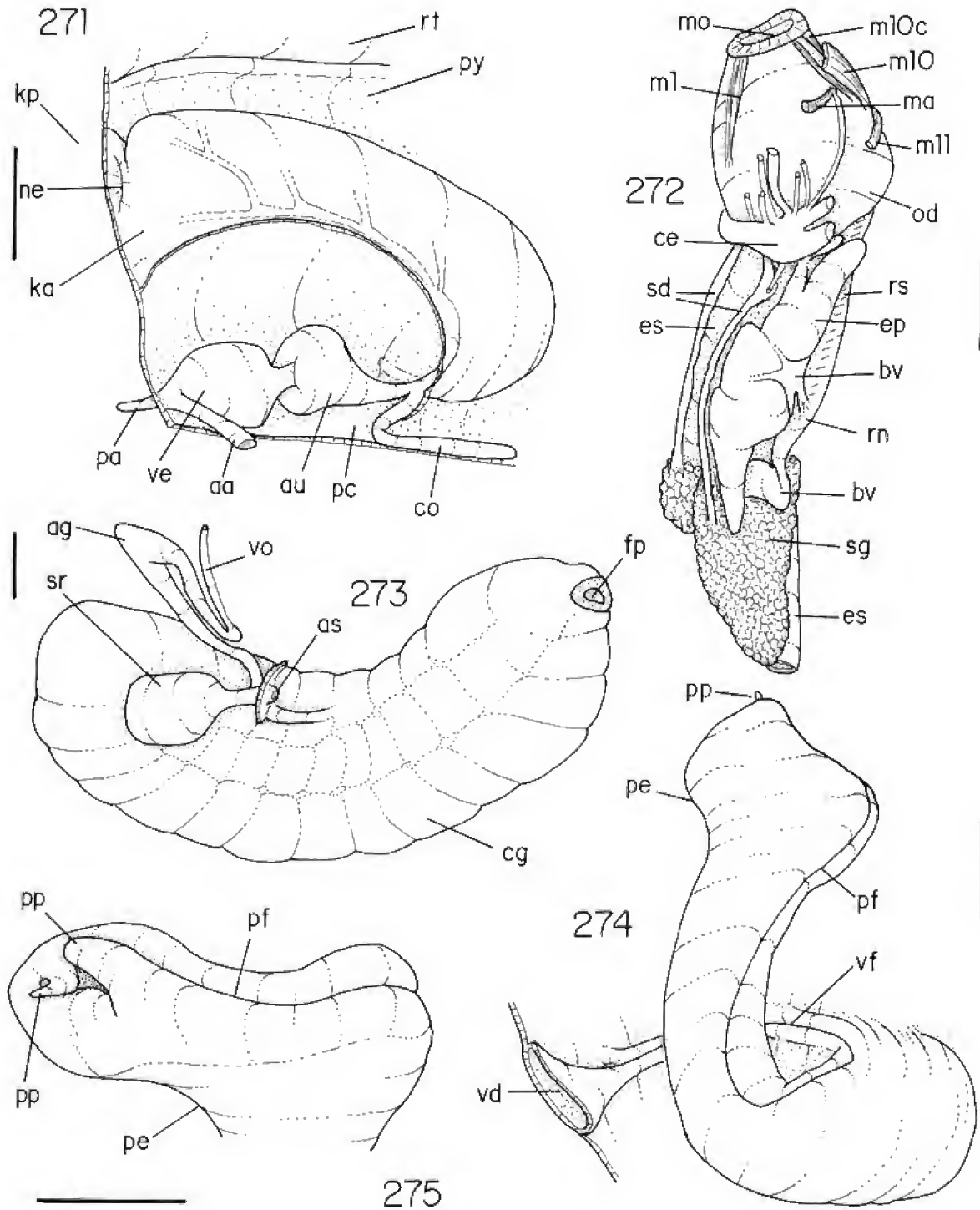
Neocyclotus prominulus anatomy: fig.254- stomach and adjacent portions of esophagus and intestine, ventral view, most opened longitudinally; fig.255- penis and adjacent region of pallial floor, dorsal view; fig.256- pallial oviduct, dorsal view as in situ; fig.257- same, ventral view; fig.258- same, capsule gland (cg) opened longitudinally. Scale bars = 1mm.



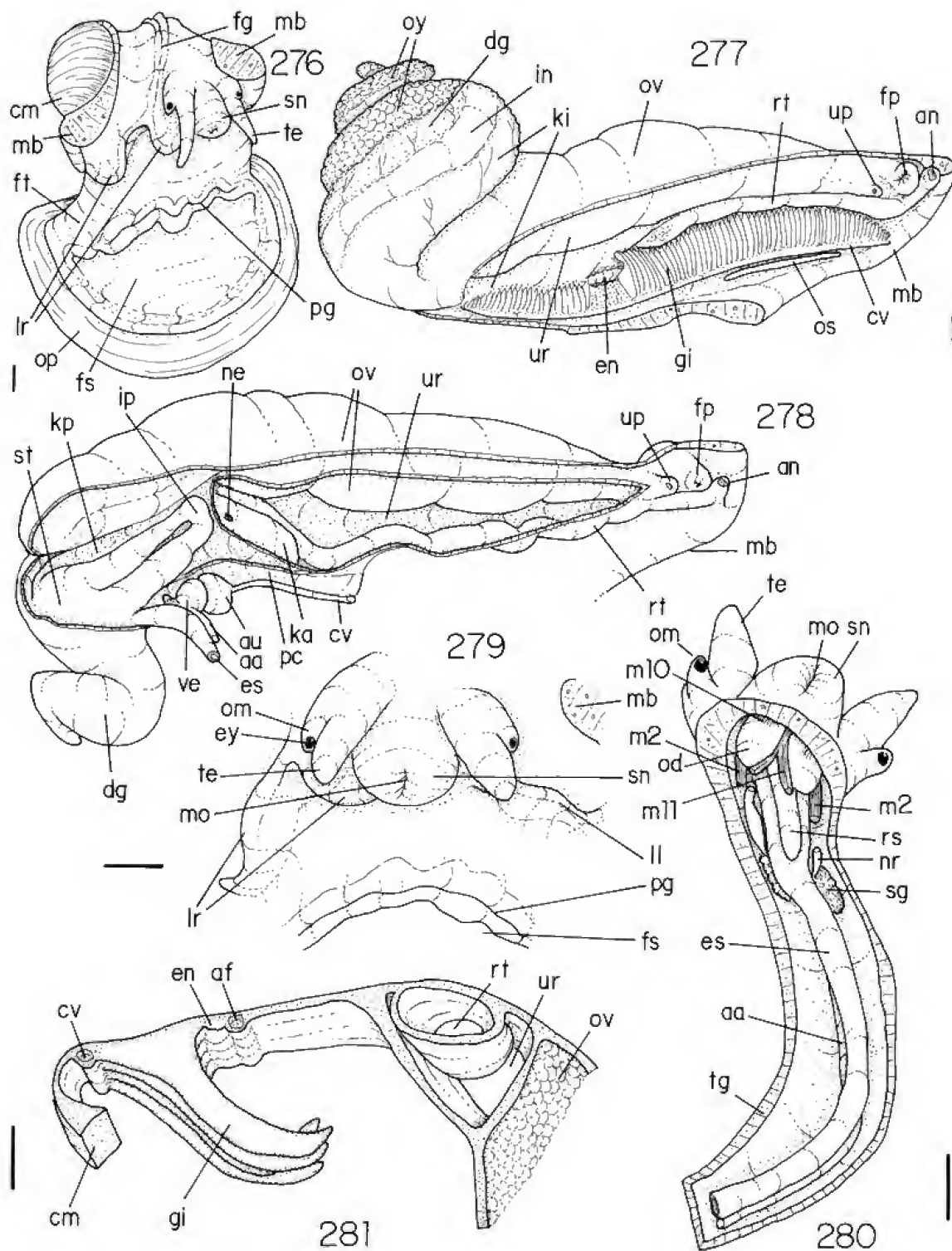
Incidostoma tupy anatomy: fig.259- head-foot, ♂, frontal view; fig.260- head-foot, ♀, frontal-slightly left view; fig.261- pallial cavity (lung), ♀, ventral-inner view; fig.262- region between visceral mass and pallial cavity, ventral view, ventral wall of pericardium and portion of rectum ventral to kidney removed. Scale bars = 2mm.



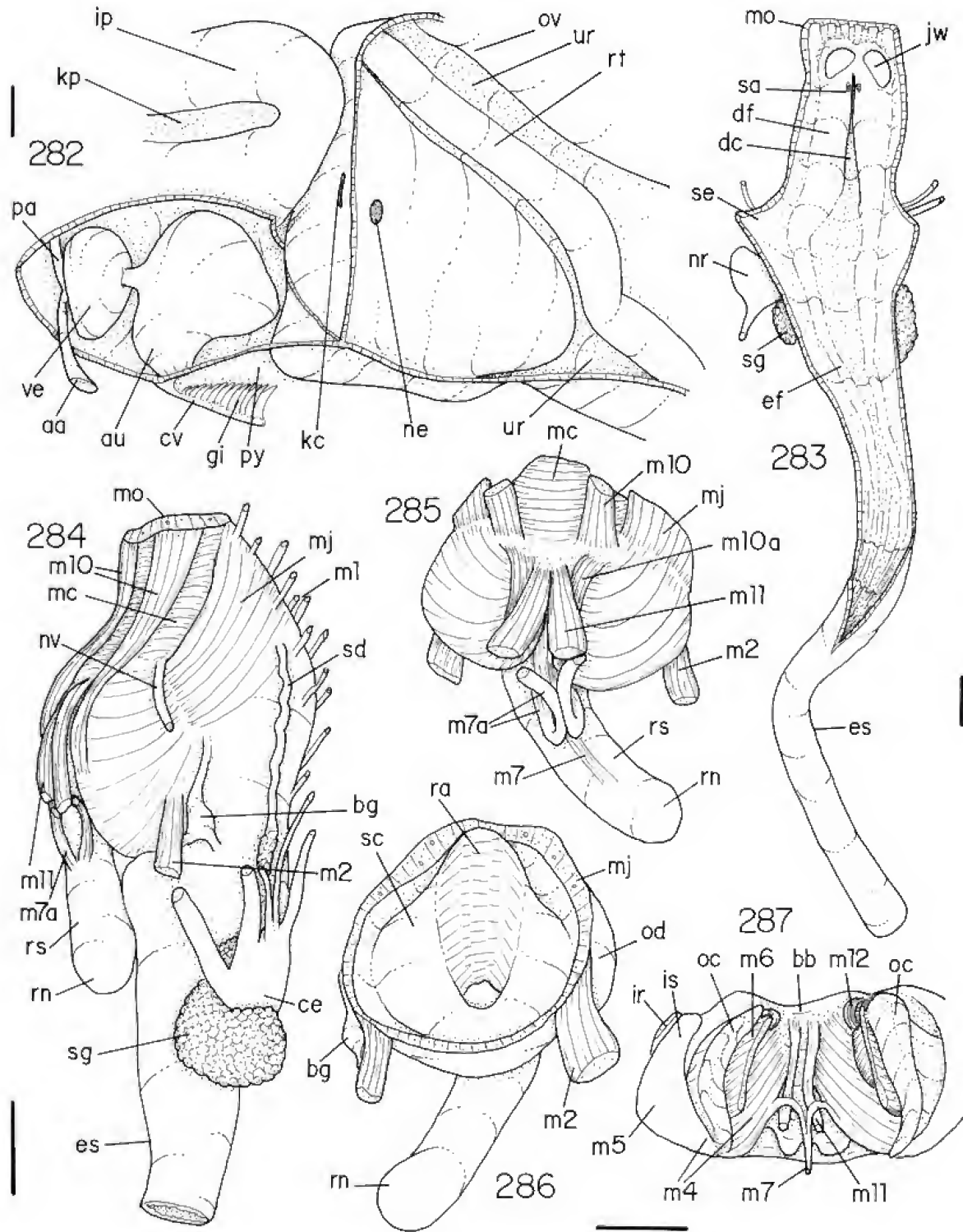
Incidostoma tupy anatomy: fig.263- foregut, lateral-left view; fig.264- same, ventral view, odontophore removed, esophagus and right esophageal pouch (left in fig.) opened longitudinally; fig.265- penis, dorsal view; fig.266- same, detail of its apical region; fig.267- penis and adjacent region of pallial cavity floor of immature male, dorsal view, detail of a transversal section in indicated region of sperm groove also shown; fig.268- same, ventral view; fig.269- detail of posterior region of pallial oviduct, ventral view, seminal receptacle (sr) opened longitudinally; fig.270- pallial oviduct, ventral view as in situ. Scale bars = 1mm.



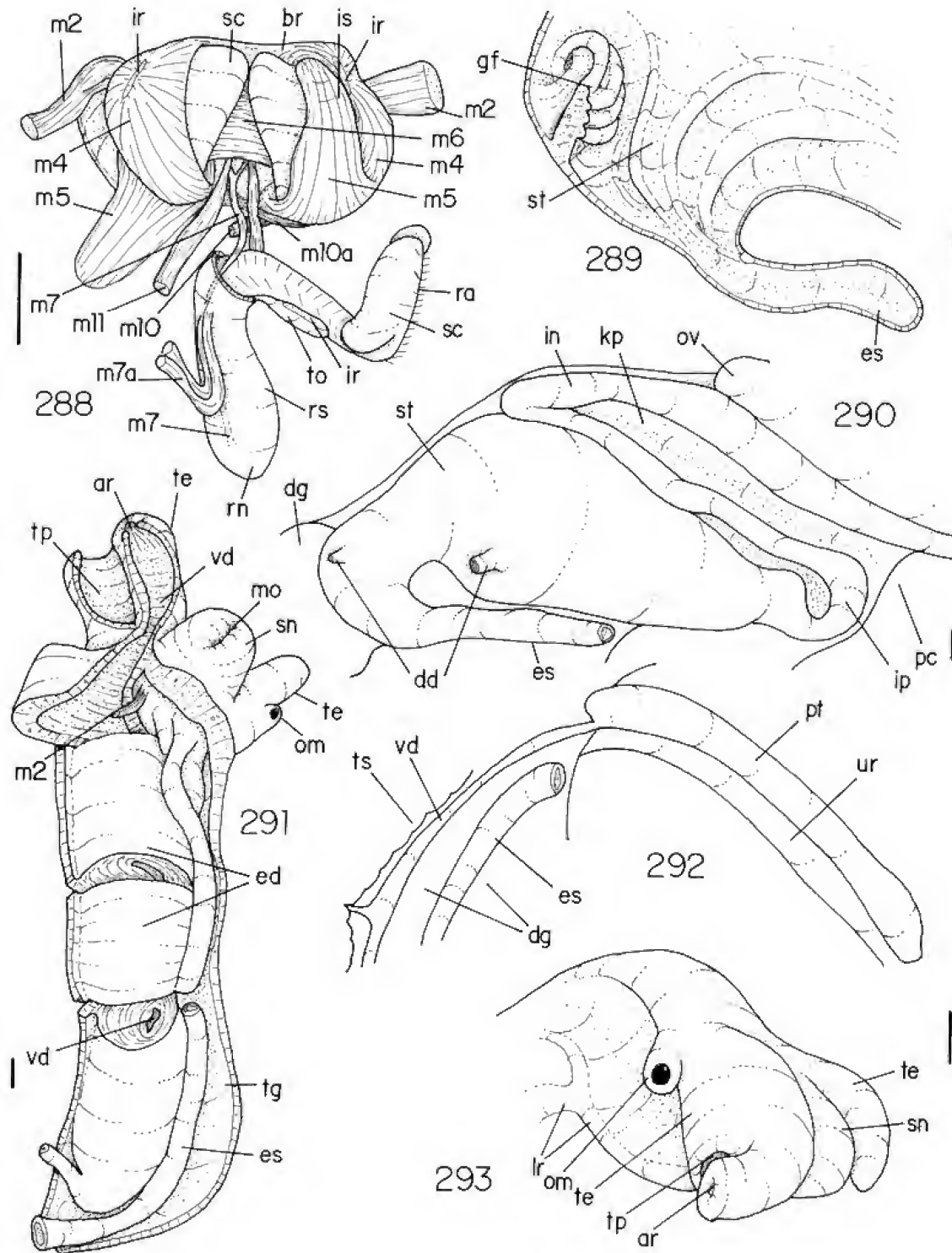
Aperostoma blanchetiana anatomy: fig.271- kidney and adjacent structures, ventral view, ventral wall of pericardium removed; fig.272- foregut, lateral-left view; fig.273- pallial oviduct, ventral view, posterior structures shown as in situ; fig.274- penis and adjacent region of pallial floor, dorsal view; fig.275- same, detail of its apical region. Scale bars = 1mm.



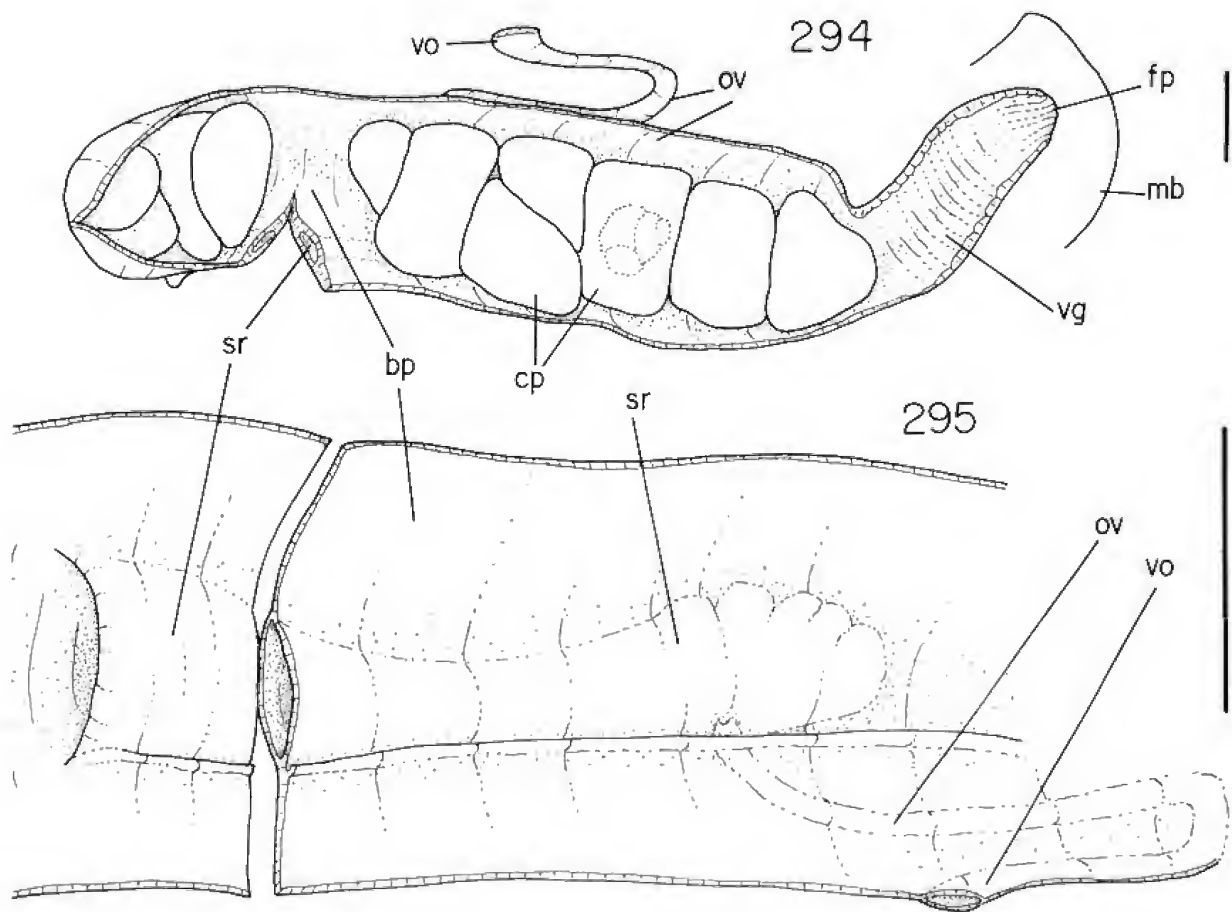
Viviparus acerosus anatomy: fig.276- head-foot, ♀, frontal view; fig.277- pallial cavity in ventral-inner view, and visceral mass, ♀, a portion of gill filaments removed to show the endostyle (en); fig.278- same, visceral mass part uncoiled, digestive gland and mantle ventral to stomach removed, ventral pericardial wall removed, esophagus and anterior aorta deflected, ureter (ur) most opened longitudinally (left pallial structures not shown); fig.279- head and adjacent structures (including anterior edge of foot), frontal view; fig.280- head and haemocoel, ♀, ventral view, foot removed; fig.281- pallial roof, ♀, transversal section in its middle portion. Scale bars = 2mm.



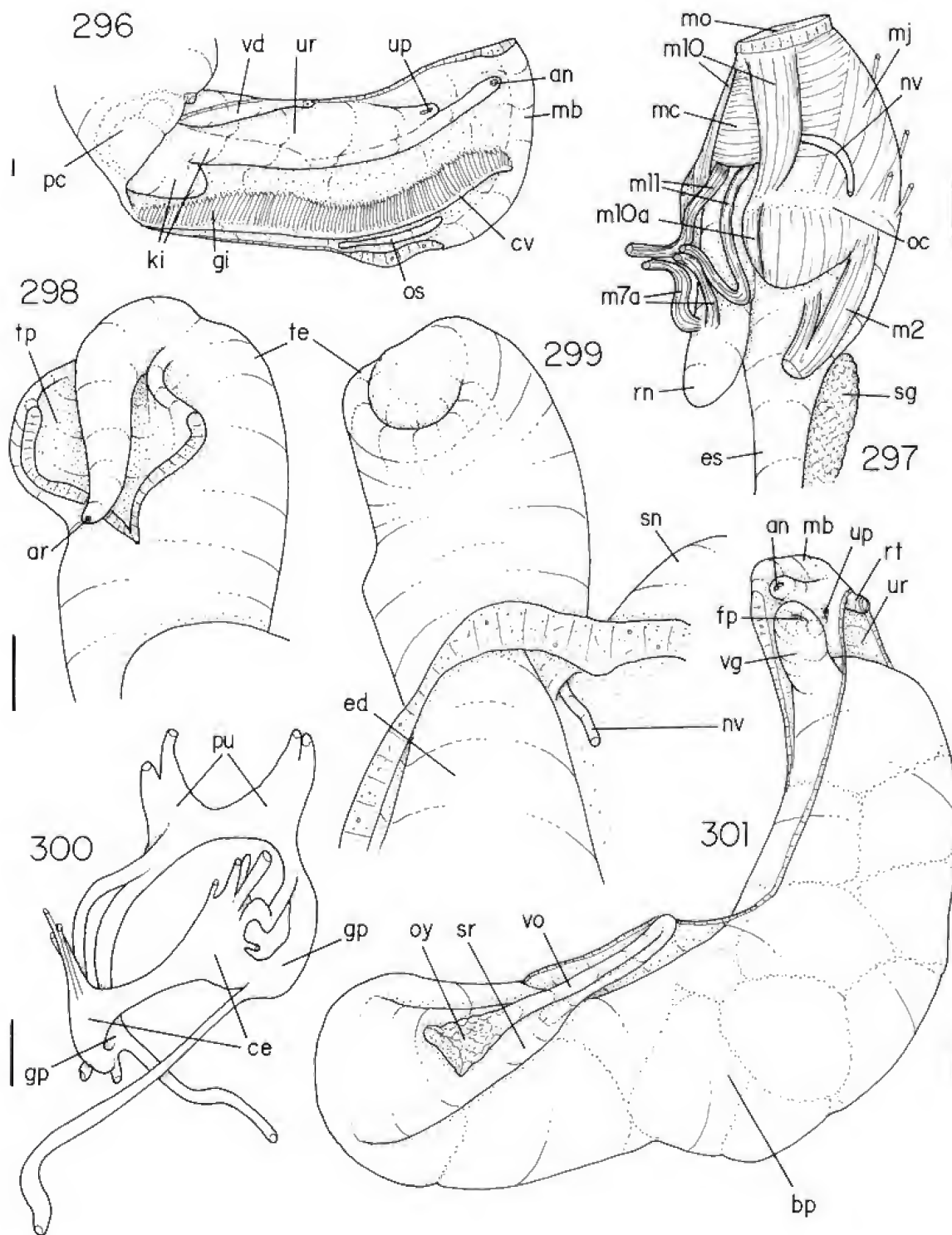
Viviparus acerosus anatomy: fig.282- kidney and adjacent structures, ventral view, ventral wall of pericardium removed, ureter opened longitudinally; fig.283- foregut, ventral view, odontophore removed, esophagus partially opened longitudinally; fig.284- foregut, lateral-left view; fig.285- odontophore, ventral view; fig.286- same, dorsal view; fig.287- same, dorsal view, radular ribbon extracted, both cartilages deflected, m6 sectioned longitudinally, lateral structures weakly shown. Scale bars = 1mm.



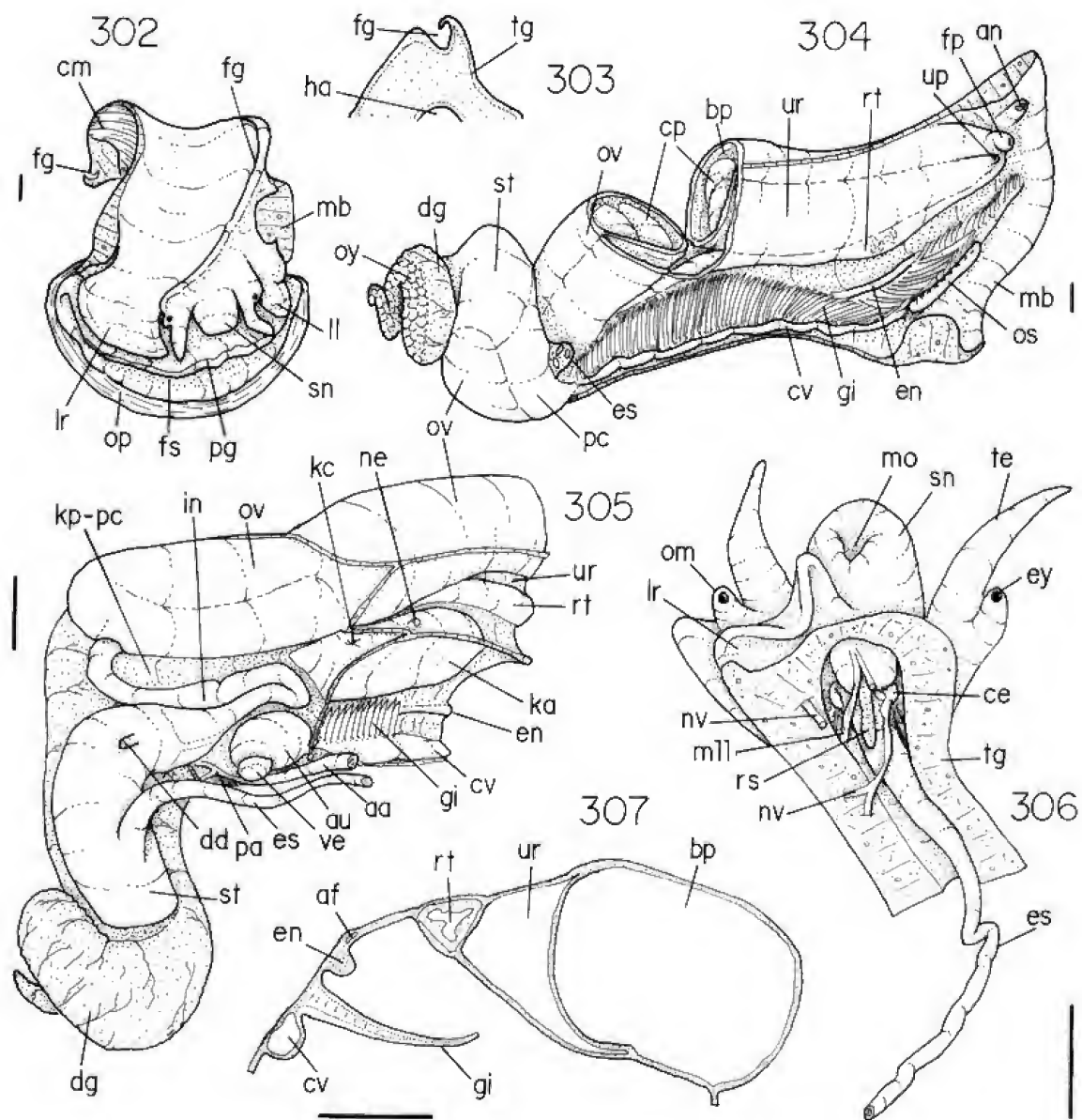
Viviparus acerosus anatomy: fig.288- odontophore, dorsal view, radular ribbon removed and deflected downwards, both cartilages and left m5 deflected; fig.289- stomach opened longitudinally, ventral view, distal region not shown; fig.290- midgut, ventral view, seen as in situ; fig.291- head and haemocoel, ♂, ventral view, foot removed, some transversal sections along vas deferens artificially done, right tentacle (left in fig.) opened longitudinally; fig.292- middle region of male genital system, dorsal view, seen as in situ; fig.293- head, ♂, lateral-right view. Scale bars = 1mm.



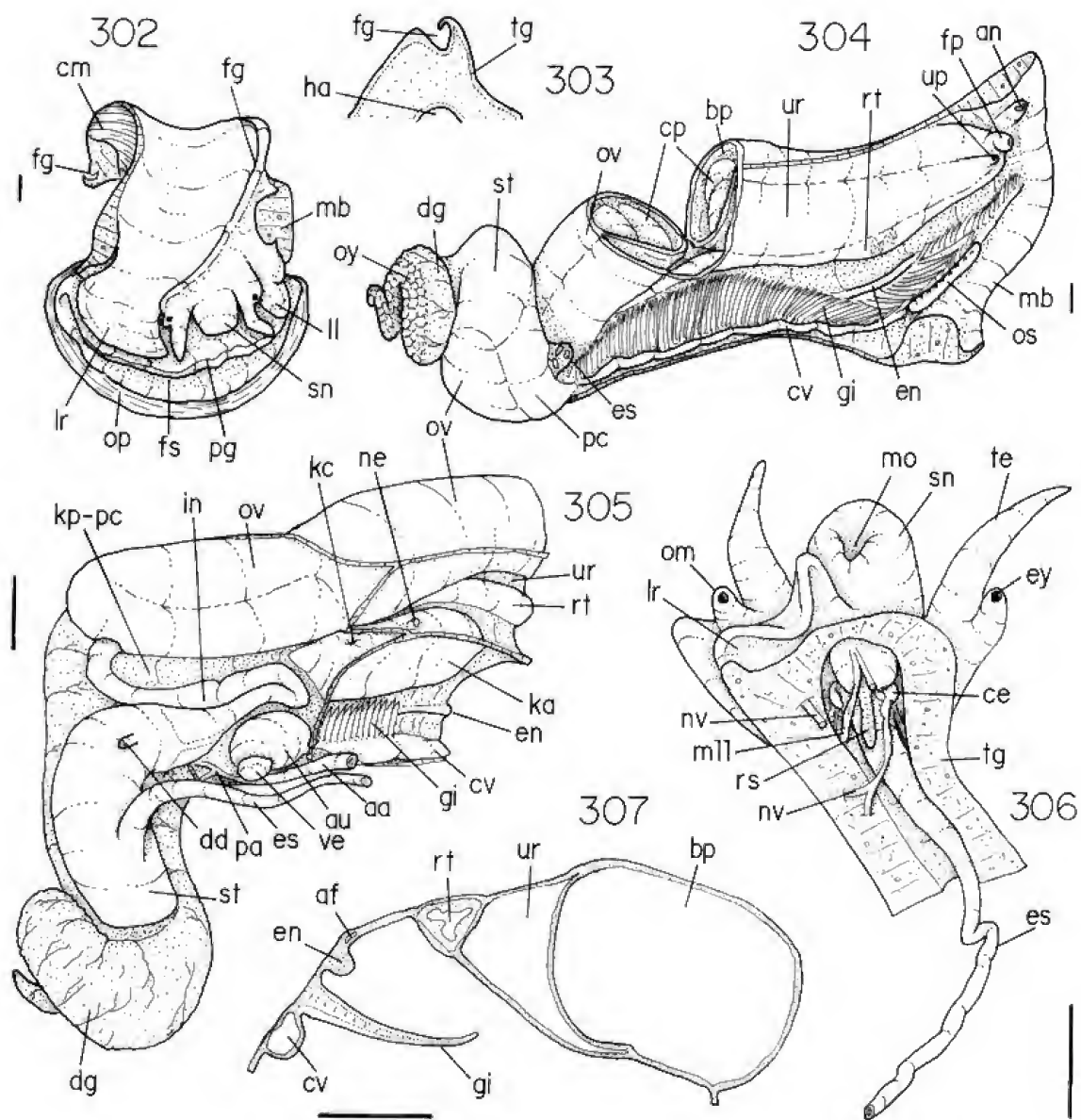
Viviparus acerosus pallial oviduct, ventral view: fig.294- whole view, uterus most opened longitudinally, some capsules still inside, an incomplete transversal section in its posterior region artificially done; fig.295- detail of uterus posterior region, showing middle portion of oviduct by transparency. Scale bars = 5mm.



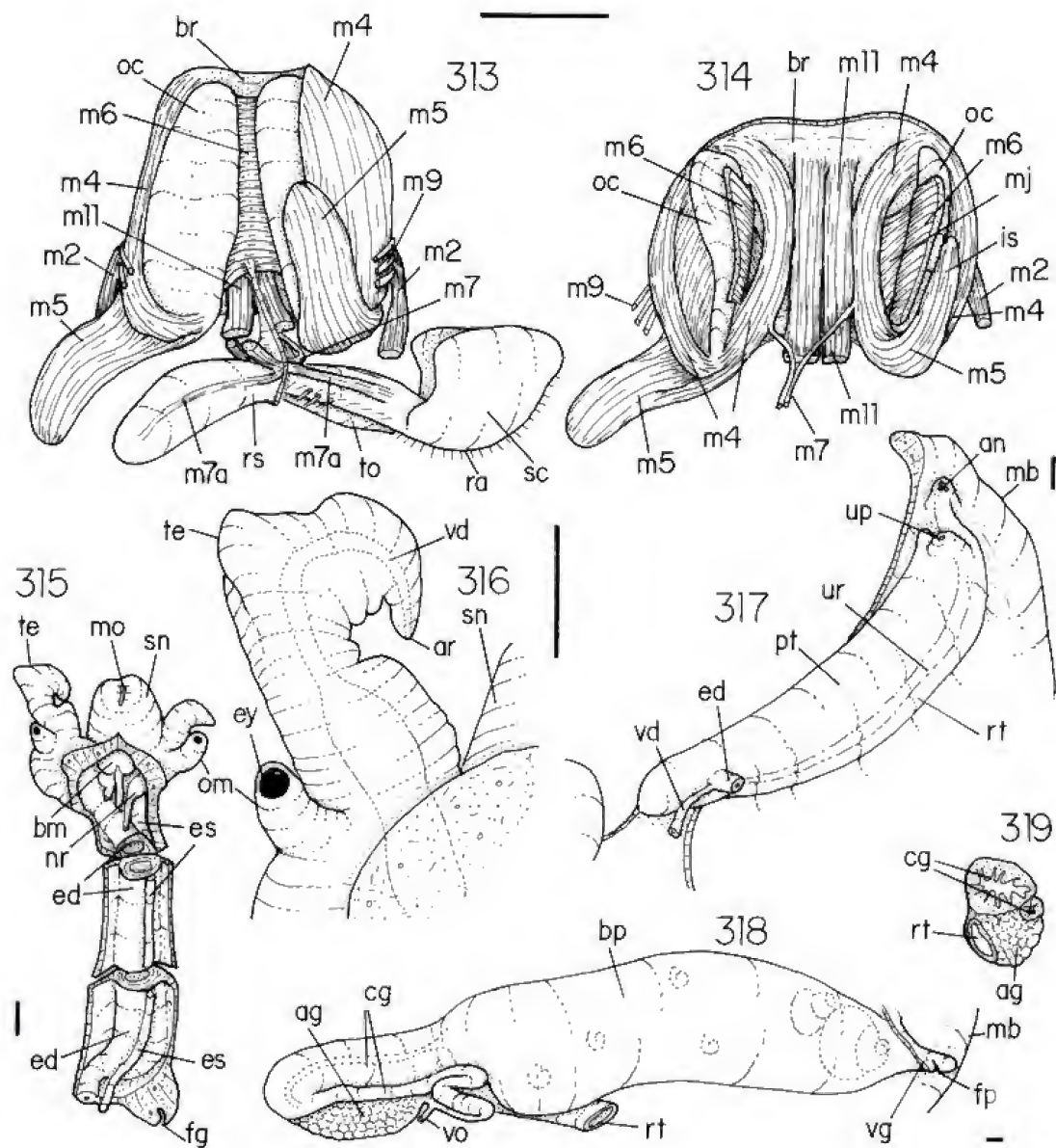
Viviparus contectus anatomy: fig.296- pallial cavity, ♂, ventral-inner view, a portion of visceral mass also shown; fig.297- buccal mass, lateral-left view; fig.298- right copulatory cephalic tentacle, ♂, ventral view, its distal chamber opened longitudinally; fig.299- same, intact, a portion of adjacent region of haemocoel also shown; fig.300- central nervous system, posterior view; fig.301- pallial oviduct and part of adjacent region of pallial cavity. Scale bars = 1mm.



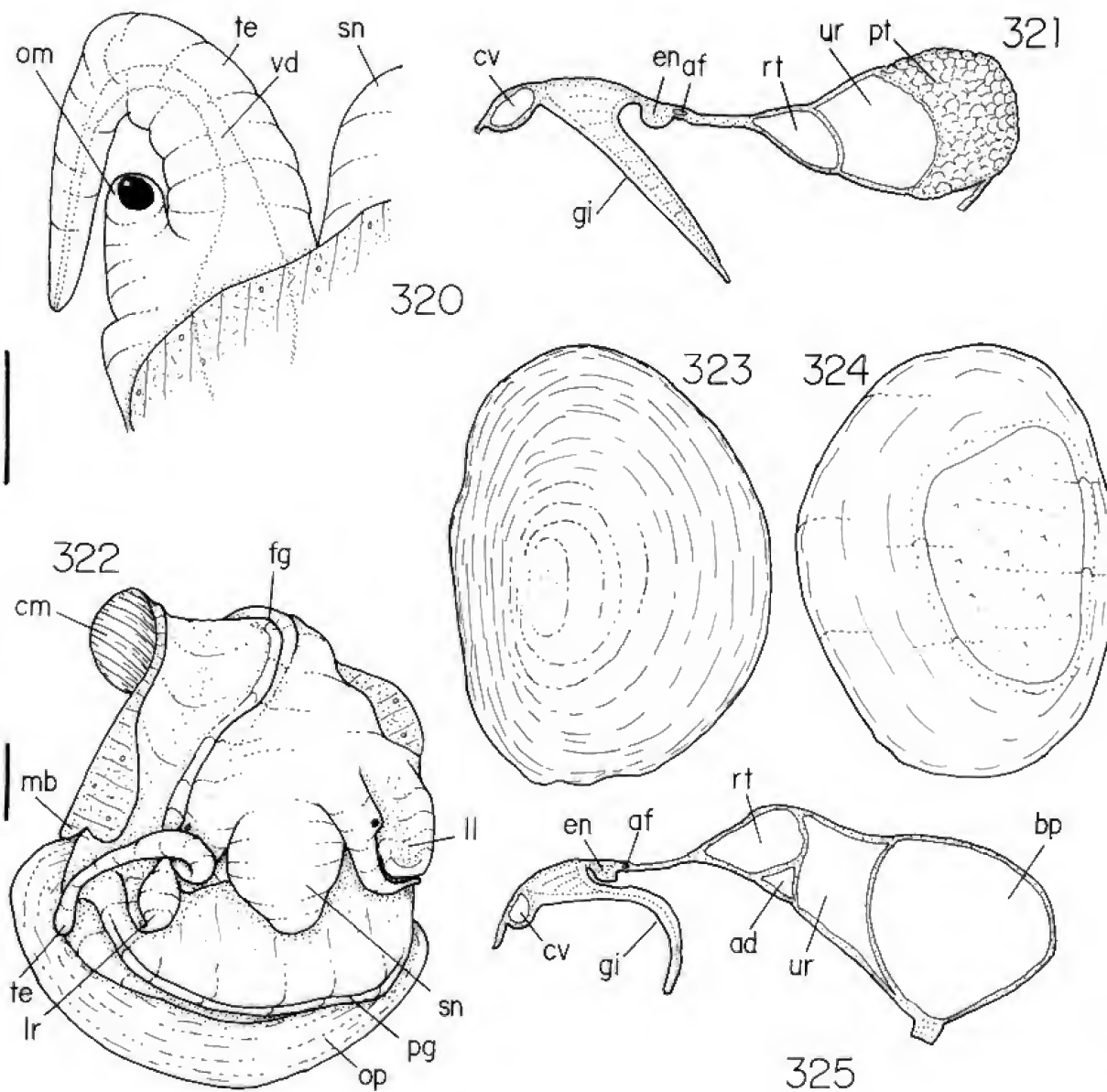
Notopala ampullaroides anatomy: fig.302- head-foot, ♀, frontal view; fig.303- transversal section ♀ on the middle region of pallial floor; fig.304- pallial cavity, ventral-inner view, and visceral mass, female, a transversal section in uterus artificially done; fig.305- visceral mass partially uncoiled, and posterior region of pallial cavity, ventral view, digestive gland and mantle portions ventral to stomach removed, ureter opened longitudinally; fig.306- head and part of haemocoel, ♀, ventral view, foot removed; fig.307- pallial cavity roof, transversal section in its middle region. Scale bars = 2mm.



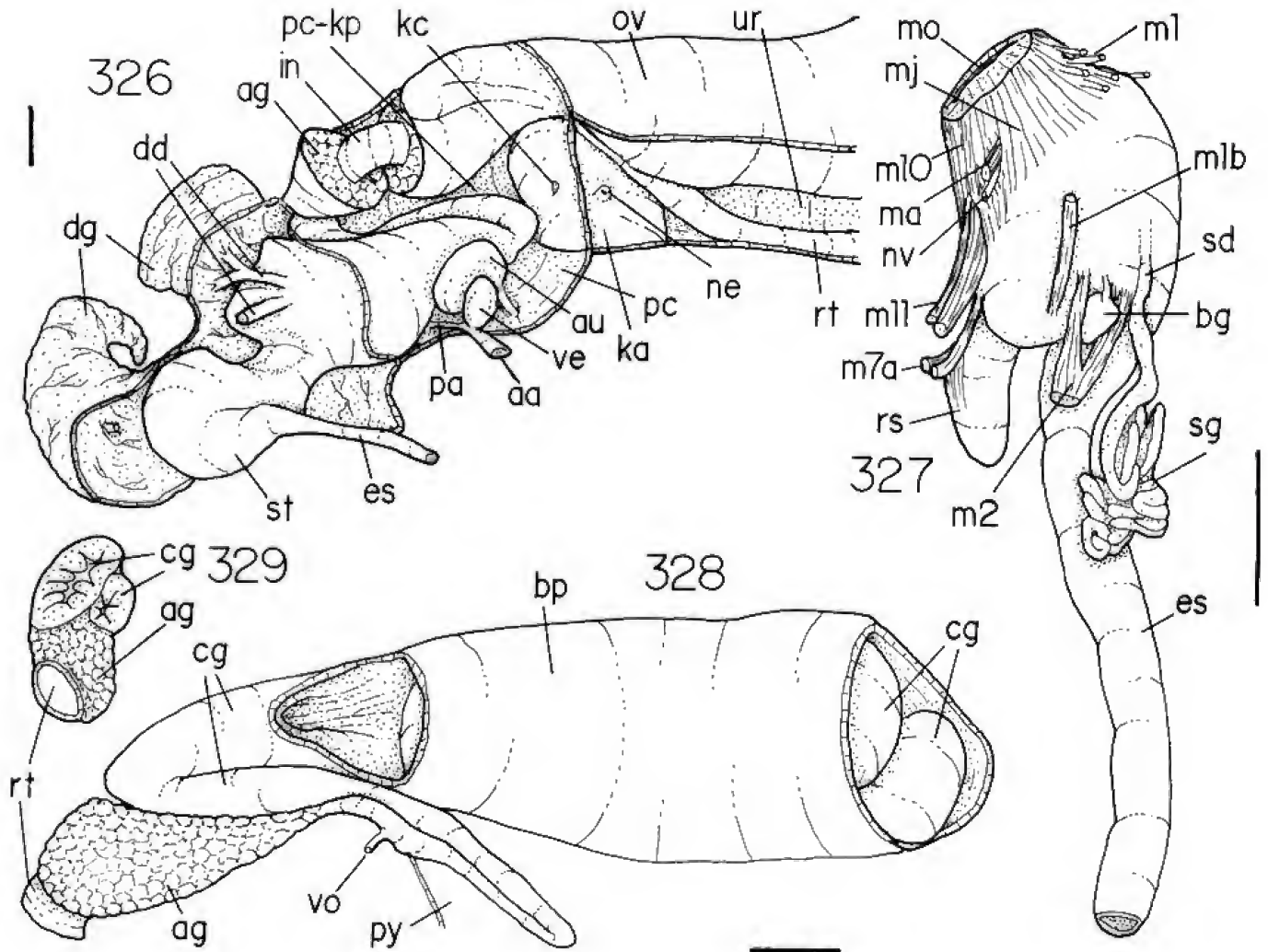
Notopala ampullaroides anatomy: fig.308- foregut, dorsal view; fig.309- same, ventral view; fig.310- same, odontophore removed, esophagus opened longitudinally; fig.311- odontophore, ventral view; fig.312- same, dorsal view. Scale bars = 1mm.



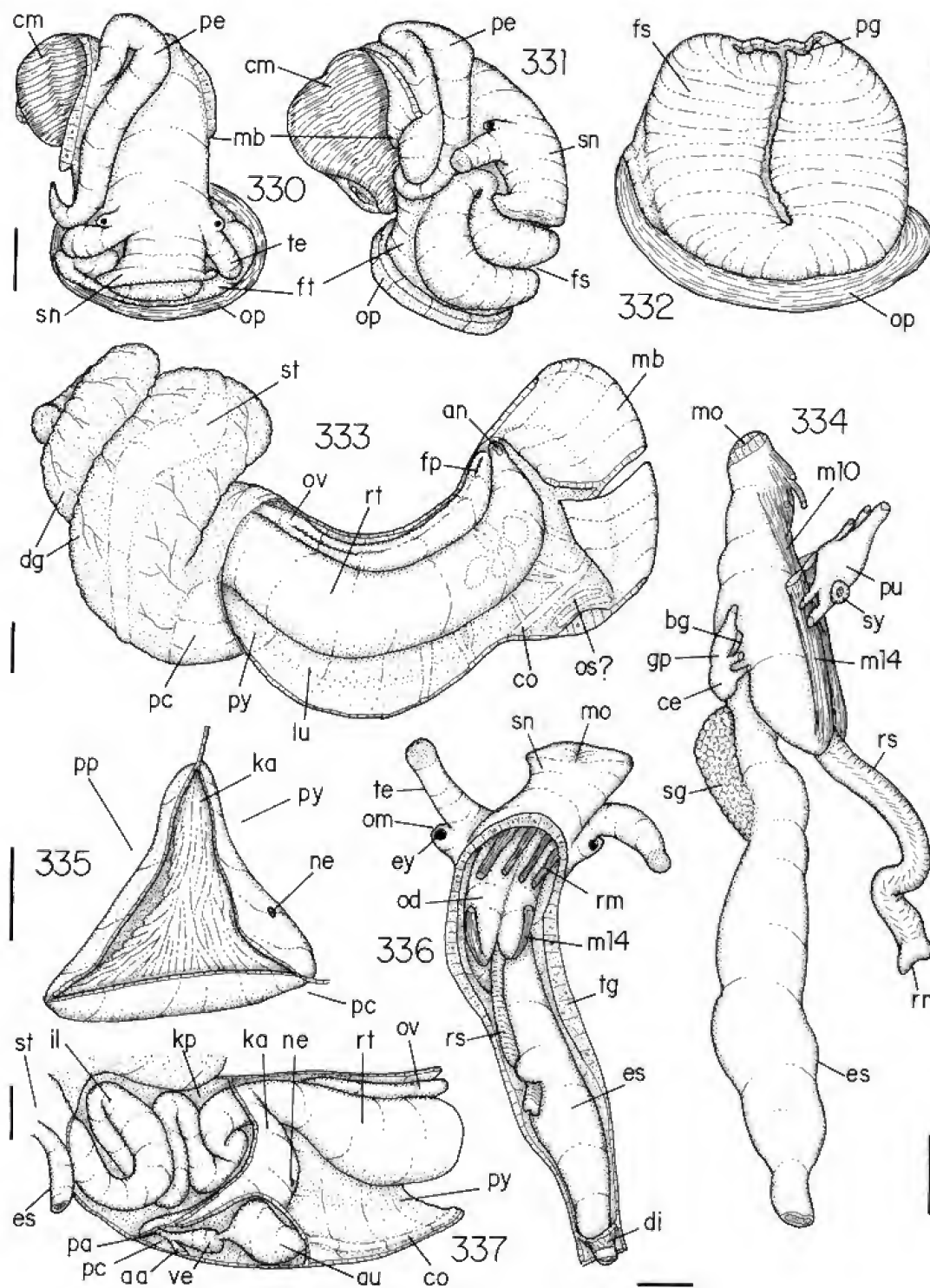
Notopala ampullaroides anatomy: fig.313- odontophore, dorsal view, radular ribbon removed and deflected, both cartilages and left m5 deflected; fig.314- same, m6 sectioned longitudinally and both cartilages still more deflected; fig.315- head and part of haemocoel, ♂, ventral view, foot removed, some transversal sections along vas deferens done; fig.316- right copulatory cephalic tentacle, ♂, ventral view, some adjacent head structures also shown; fig.317- pallial portion of male genital system, and some adjacent structures, ventral view; fig.318- pallial oviduct, ventral view as in situ; fig.319- same, transversal section in its posterior region. Scale bars = 1mm.



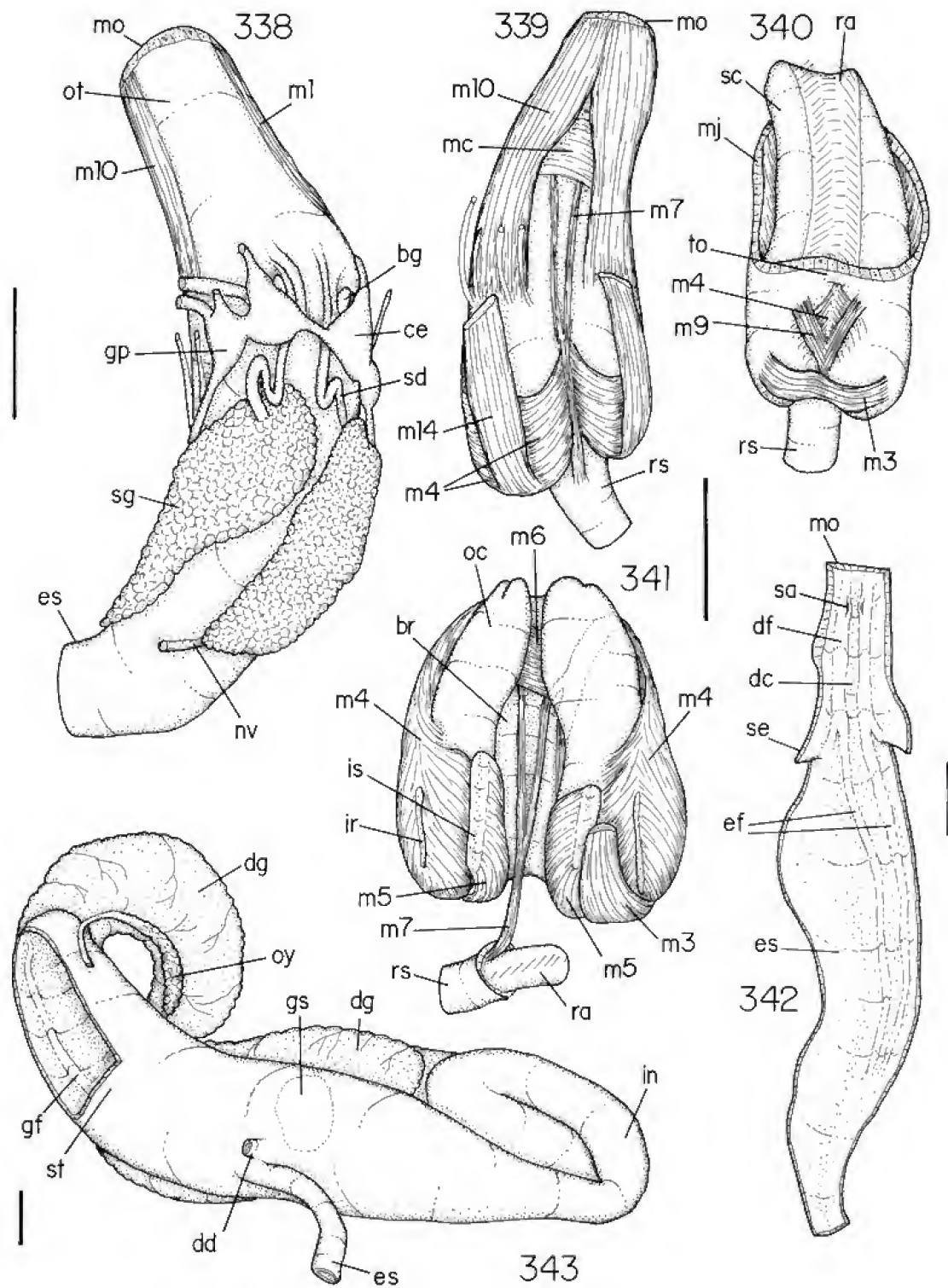
Anatomy of some Australian viviparids - *Notopala essingtonensis*: fig.320- right copulatory cephalic tentacle, ♂, ventral view, some adjacent head structures also shown; fig.321- pallial cavity roof, ♂, transversal section in its middle region; *Larina cf. strangei*: fig.322- head-foot, ♂, frontal view; fig.323- operculum, outer view; fig.324- same, inner view; fig.325- pallial cavity roof, ♀, transversal section in its middle region. Scale bars = 1mm.



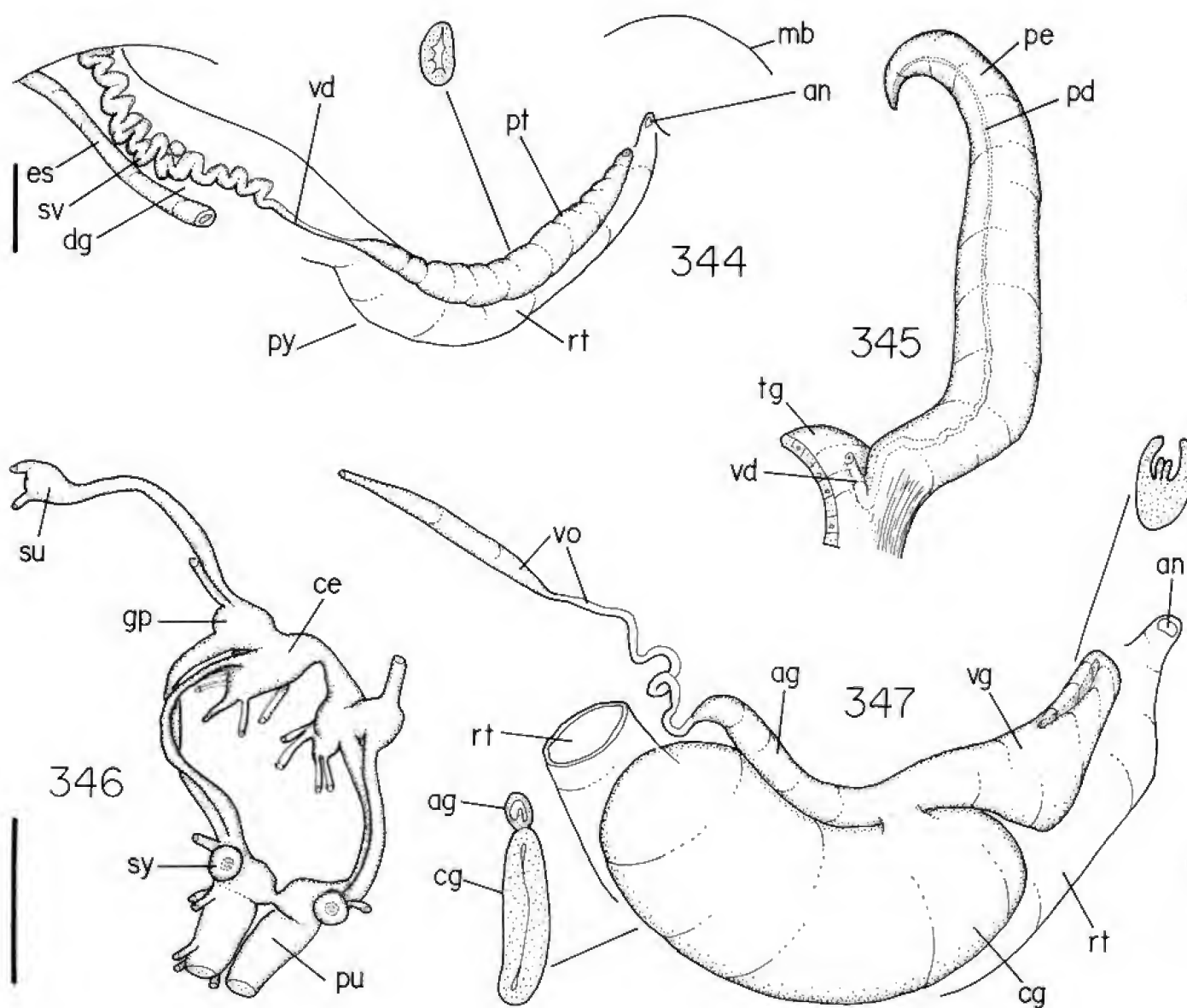
Larina cf. strangei anatomy: fig.326- visceral mass partially uncoiled and posterior region of pallial cavity, ventral view, structures ventral to stomach removed or deflected, albumen gland transversal sectioned, ureter opened longitudinally; fig.327- foregut, lateral-left view; fig.328- posterior 2/3 portion of pallial oviduct, ventral view as in situ; fig.329- same, transversal section in its posterior region. Scale bars = 1mm.



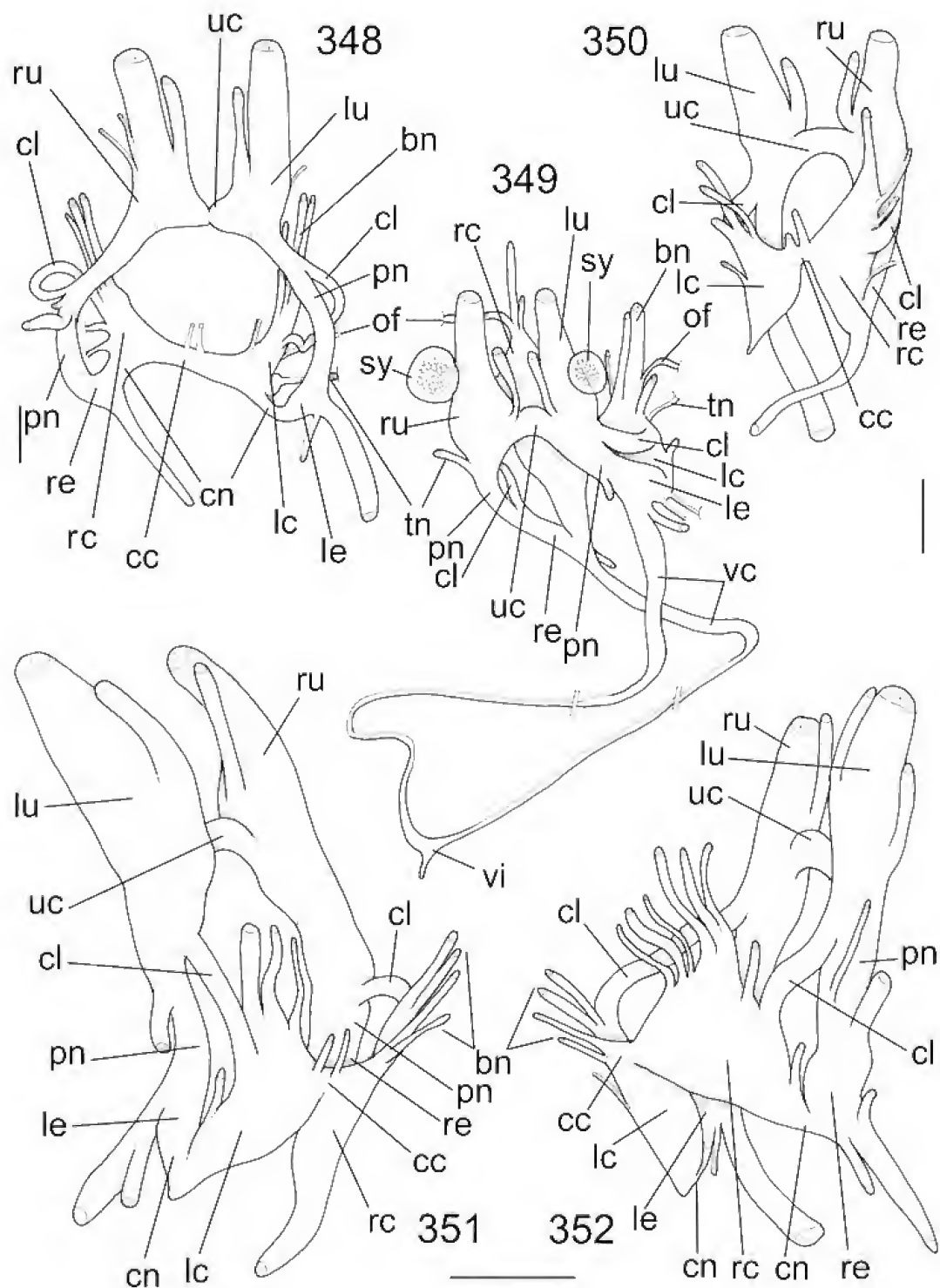
Annularia sp. anatomy: fig.330- head-foot, ♂, frontal view; fig.331- same, lateral-right view; fig.332- foot sole, ventral view; fig.333- pallial cavity, ventral-inner view, and visceral mass, ♀; fig.334- foregut, lateral-right view; fig.335- kidney anterior chamber, ventral view, its ventral wall opened and deflected; fig.336- head and haemocoel, ventral view, foot removed; fig.337- kidney and adjacent structures, ventral view, ventral walls of kidney posterior chamber and pericardium removed. Scale bars = 1mm.



Annularia sp. anatomy: fig.338- foregut, dorsal view; fig.339- buccal mass, ventral view; fig.340- same, dorsal view; fig.341- odontophore, dorsal view, radular ribbon removed, deflected and only partially shown, both cartilages deflected (right more than left one), insertion of m7 shown as if cartilage was transparent, left m3 removed; fig.342- foregut, ventral view, odontophore removed, esophagus opened longitudinally; fig.343- stomach and adjacent visceral structures, ventral view, digestive gland portion ventral to stomach removed, a region of posterior gastric wall extracted, gastric shield (gs) seen by transparency. Scale bars = 1mm.



Annularia sp. anatomy: fig.344- middle region of male genital system and adjacent structures, ventral view as in situ, a transversal section in indicated portion of prostate also shown; fig.345- penis and a small portion of adjacent pallial floor, dorsal view; fig.346- central nervous system, ventral view; fig.347- anterior portion of visceral and whole pallial oviduct, ventral view as in situ, transversal sections of 2 indicated portions also shown. Scale bars = 1mm.



Central nervous system of viviparids: fig.348- *Viviparus contectus*, ventral view; *Notopala ampullaroides*; fig.349- ventral view as in situ, including visceral ganglion, its connectives not shown in total length; fig.350- dorsal view; fig.351- lateral-left view; fig.352- lateral-right view. (bn) nerves to buccal mass; (cc) cerebral commissure; (cl) cerebro-pedal connective; (cn) rebebro-pleural connective; (lc) left cerebral ganglion; (le) left pleural ganglion; (lu) left pedal ganglion; (of) ophthalmic nerve; (pn) pleuro-pedal connective; (rc) right cerebral ganglion; (re) right pleural ganglion; (ru) right pedal ganglion; (sy) statocyst; (tn) tentacular nerve; (uc) pedal commissure; (vc) visceral connectives; (vi) visceral ganglion. Scale bars = 0.5mm.

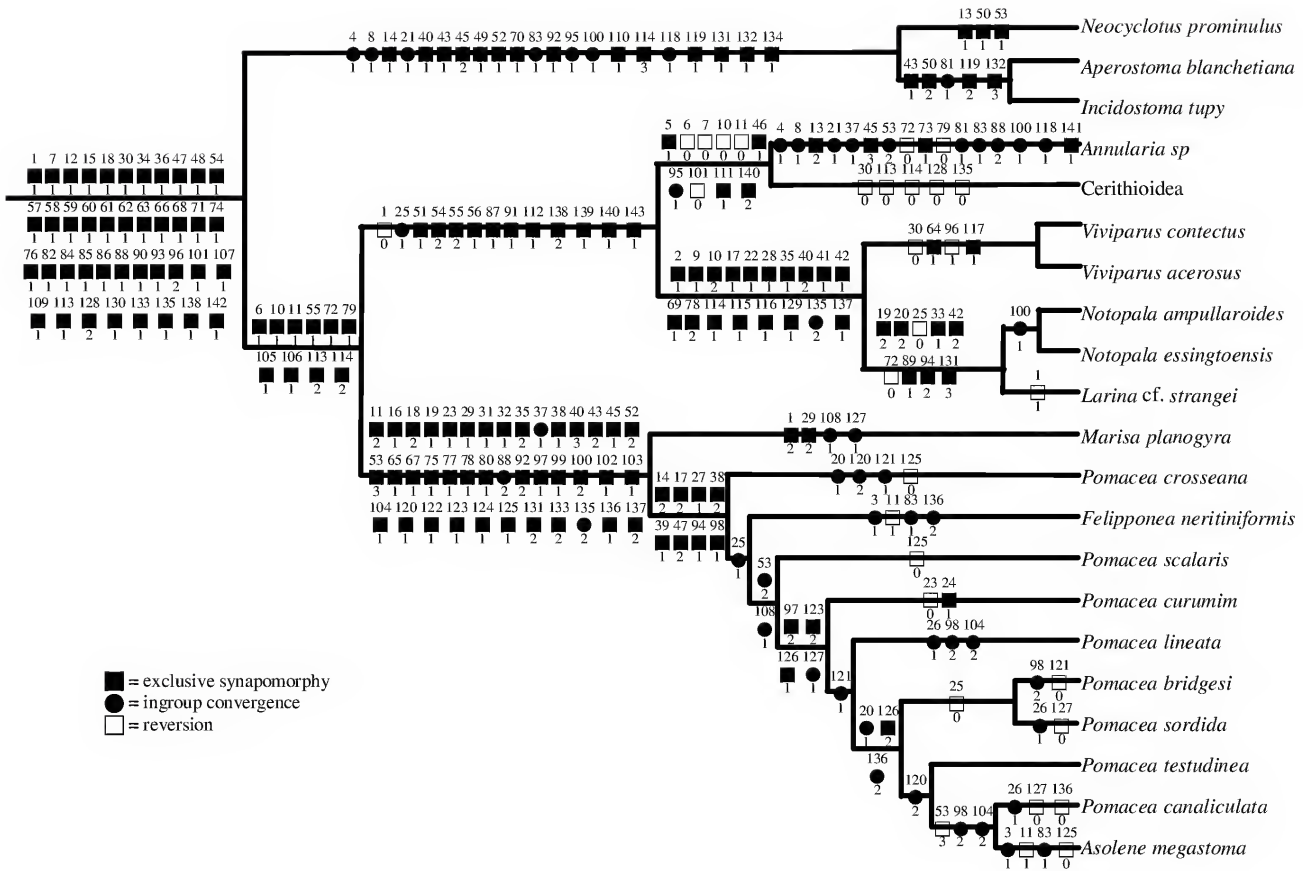


Fig.353- cladogram with synapomorphies of each node shown. Uppermost number indicates the character, the lower the state. Note that two outgroups (*Annularia sp* and *Cerithioidea* ground plan) resulted inside the ingroup. Length: 252; CI= 76; RI= 91.

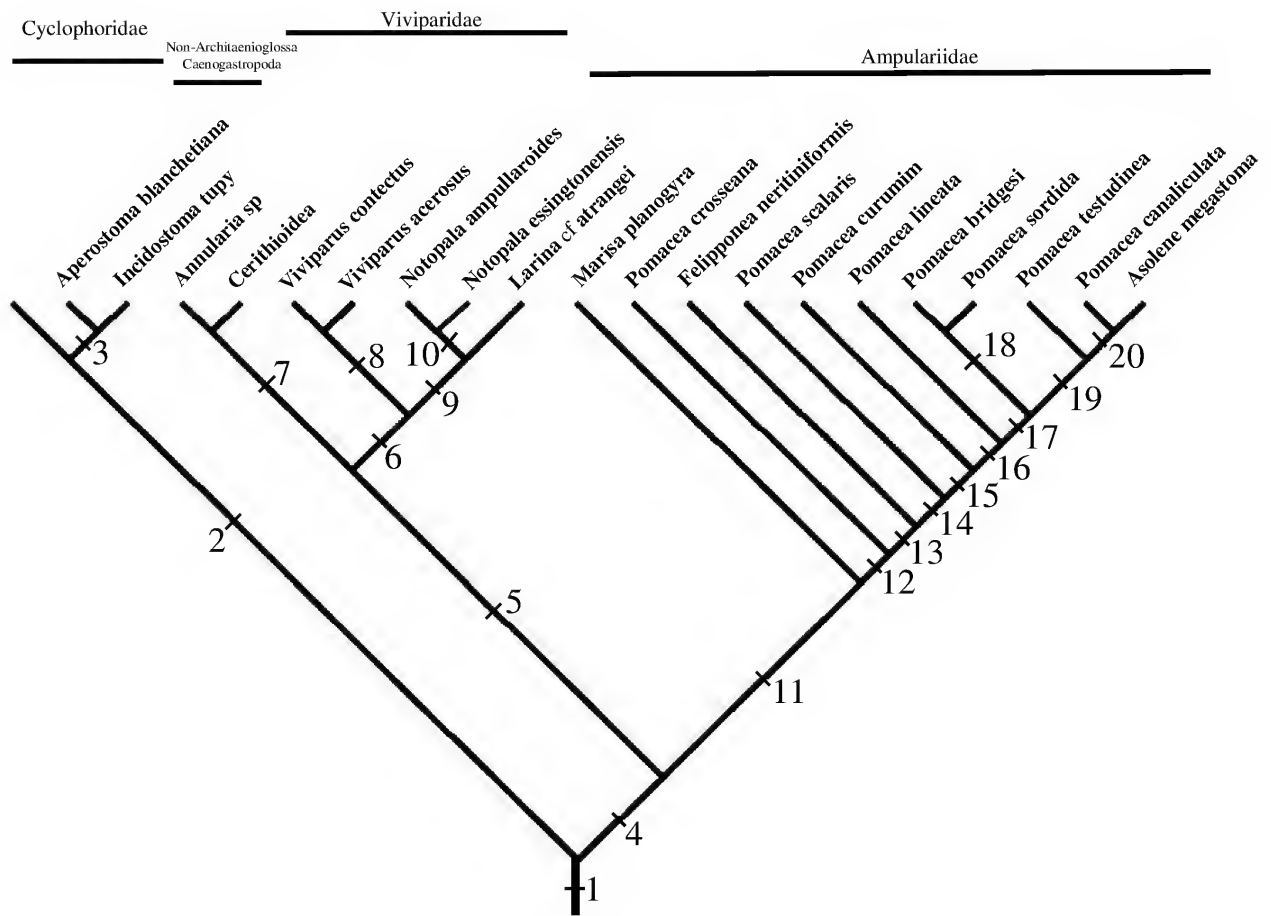


Fig.354- the single cladogram obtained cladogram; each node is numbered and the family of the ingroup taxa also indicated in the superior region, the line corresponds to the terminal branch of the cladogram.

DISCUSSION OF THE CLADOGRAM

As referred in the Material and Methods section, each character was polarized one by one, analyzing each case separately, and deciding which outgroups are selected for separating its states, for polarization, and, in the cases of multistate characters, for deciding the optimization is additive or not. Those parameters can be easily changed in the computer programs, and where changes were made, any modification in the results or indices was reported. Taking into consideration that whether all outgroups are analyzed effectively as outgroups, the monophyly of the ingroup is not tested, since it will absolutely result reunited in a branch. For testing the monophyly of any taxon, it is important to insert in the analysis some outgroups belonging to close taxa, which will be analyzed operationally as part of the ingroup. A more distant taxon (in present study a set of archaeogastropod taxa) was used as the effective outgroup. If the Architaenioglossa is actually monophyletic, the caenogastropod taxa should appear outside of the architaenioglossans clade.

This procedure was applied in the present study. The *Annularia* sp., as well as the Cerithioidea ground plan, appeared inside the architaenioglossans taxa. Both these taxa are undoubtedly considered caenogastropods. The present result suggests that the taxon "Architaenioglossa" is non-monophyletic. The two non-architaenioglossans taxa formed a single terminal branch, and the architaenioglossans formed three successive branches, indicating its paraphyly. Most nodes and branches (Figs.353-354) are analyzed in the following text. The more important synapomorphies that support them are also reported, but are discussed in the previous section. The node number 1 (Fig.354) is supported by 41 synapomorphies (Fig.353). From those, the outstanding are: ommatophore located on tentacles (character 12); osphradium elongated and more complex (18); decrease of the hypobranchial gland (30); duplication of the lobe of the single kidney (34, 36); appearance of a pair of inner dorsal folds in buccal mass (47); jaw muscles separated in a pair of bundles (48); formation of the m4 pair of odontophore muscles from several pairs (54); reduction of ventral tensor muscle of the radula (57); enlargement of dorsal tensor muscle of the radula (58); m5 pair of odontophore muscles becoming longer and inserted on m4 (instead of on the cartilage) (59, 60); horizontal muscle becoming shorter and broader (61, 62); arising the pair m7 (63); loss of approximator muscles of

cartilages (or incorporation to m4) (66); loss of the posterior pair of odontophore cartilages (74); enlargement of subradular cartilage (76); reduction of the radular teeth to 7 per row (82, 85); esophagus origin in posterior region of buccal mass (90); loss of gastric caecum (96); absence of visceral structures in haemocoel (107); fecal pellets (109); pallial vas deferens at least partially closed (113); large and complex pallial oviduct located at right from rectum (128, 130); capsule gland (133); developed female pore (135); nerve ring positioned more posterior from mouth (138); and buccal ganglia positioned far removed from the nerve ring (142). Being the node 1 followed by the 3 architaenioglossan branches plus the remainder caenogastropods (represented by *Annularia* and Cerithioidea ground plan), it is a quite possible that it represents the order Caenogastropoda as a whole. This affirmation is considered still premature, since another study concerned to the phylogeny of the entire order is in progress. The present study is part of it. For a secure affirmation on the caenogastropod synapomorphies and monophyly depends on a deeper analysis of remainder superfamilies of the group and of the sister-group taxon, the Heterobranchia. Those studies are still being performed.

HASZPRUNAR (1988) regarded Architaenioglossa as non-caenogastropod prosobranchs (archaeogastropods). He considered it as the sister taxon of the Caenogastropoda plus Heterobranchia branch. PONDER & LINDBERG (1996, 1997), on the other hand, considered the architaenioglossans as basal caenogastropods. However, as also pointed out by HASZPRUNAR (1988), those authors suggested that there is a possibility that the architaenioglossans are paraphyletic (1997:225) as corroborated with the present result. Harasewych *et al.* (1997) performed a molecular analysis (18S rDNA and cytochrome c oxidase I), included the viviparid *Cipangopaludina japonica* (von Martens, 1860), with this architaenioglossan in the first branch of the Caenogastropoda.

The node 2, supported by 21 synapomorphies, represents the family Cyclophoridae, the single one reunited in the superfamily Cyclophoroidea. From the synapomorphies, those more remarkable are: calcareous operculum (character 8); loss of pallial structures for becoming a lung (21); posterior located nephrostome (40); urinary gutter (43); fusion of jaw plates (45); odontophore muscle pair m1a and m10c (49, 70); esophageal pouches covered internally by papillae (92); the exophalic penis (114, 118, 119); albumen gland as a loop

(131); and special conformation of pallial oviduct (132, 134). Despite the very well supported node, the cyclophorids are a very diverse and widespread group. They have some endemic supra-specific taxa that were not analyzed in present study. It is possible that the family synapomorphies would be diluted when a larger number of representatives will be analyzed. However, a set of synapomorphies of the taxon is here presented by the first time, and is considered important for defining the taxon and for analyzing its relationship with the remainder gastropods.

The node 3 separates *Aperostoma* and *Incidostoma* from *Neocyclotus*. It is supported by 5 synapomorphies, being the more important the different organization of the lung vessels (44), the modification of the odontophore pair of muscles m1a (50); the duplication of the penis papilla (119); and the bursa copulatrix opening directly to the pallial cavity instead of opening to the pallial oviduct (132).

The node 4 encompasses the remainder ingroup except the cyclophoroideans. It is supported by 10 synapomorphies, being the more remarkable the following: the head-foot siphons (10, 11, which reverted in the node 7); the connection of the m4 with tissue on the radula (55); the odontophore muscle pair m12 (72); the closure of the pallial vas deferens (113, 114). The arrangement of the taxa on the cladogram shows that the cyclophorids are the more basal taxon of the caenogastropods, and that the remainder taxa represent another branch, uniting the ampullariids and remainder caenogastropods.

For operational reasons, we will analyze the node 11 to 18, and after them we return to numerical order.

The node 11 represents the Ampullariidae, the single family of the superfamily Ampullarioidea. The node is supported by 40 synapomorphies, being the more remarkable: snout tentacles (character 16); osphradium with bipectinated and pedunculated fashion (18, 19); lung sac (29); ampulla in anterior aorta (32); intestinal loops inside kidney (37); anterior septate renal chamber (38); multiple jaw ditator muscles (ma) (52); odontophore muscle pairs m7b and m9 (65, 67); pair of accessory odontophore cartilages (75); muscular stomach walls (97); gastric muscle (99); multiplication of ducts to digestive gland (100); special arrangement of intestinal chambers in its portion close to pericardium (103, 104); penis and penis shield structures (120-127); enormous capsule gland surrounding most of remainder pallial oviduct structures (131, 133); special brooding strategy (137). The ampullariids

have been the goal of some important papers on their anatomy (*e.g.*, Scott, 1957), and even including phylogenetic approach (BERTHOLD, 1989, 1991; BIELER, 1993). However, several of here presented synapomorphies are apparently introduced by the first time. They are the cases, for example, of the gastric muscle (that connect the stomach with shell columella), the intestinal chambers close to pericardium, and the renal intestinal loops. BIELER (1993), based on the data searched by BERTHOLD (1991), selected 70 ampullariid characters, and obtained 3 equally parsimonious trees. The author showed 3 cladograms (that paper figs. 1-3), the first based on the BERTHOLD's preferences, and the other 2 based on the data matrix. All cladograms are so different from each other and from that obtained herein that it is impracticable to compare. Bieler searched 23 synapomorphies for the family, most of them taken into consideration in the present study and presented in preceding discussion.

The remaining nodes, 12-20, refer to the internal organization of the family Ampullariidae. The first branch is *Marisa*, separated from the remaining branches by 8 synapomorphies. The lasting taxa are, in a broad sense, representatives of the genus *Pomacea*. However, species belonging to the genera *Asolene* and *Felipponea*, considered by some authors as subgenera of *Pomacea*, were mixed. The scattered organization of the ampullariids in the cladogram is considered provisional, since some organs and structures have been under-analyzed (*e.g.*, the kidney, pallial oviduct). This happened because of the insufficient or poorly-preserved material available. For this reason no taxonomical change is proposed. However, on the basis of this result, it appears that a reanalysis of ampullariid taxonomy may necessary.

The node 5 is supported by 13 synapomorphies, including: the appearance of the pair of retractor muscle of buccal mass (m2) (character 51); the simplification and enlargement of the odontophore muscle pair m4 (54-56); the loss of the esophageal pouches (91); the prostate gland located in pallial cavity (112); the nerve ring positioned posterior to buccal mass (138); the approach of the pleural ganglia to the cerebral ganglia (epiathroid organization) (139, 140); and the lateral position of buccal ganglia in buccal mass (143). This branch represents the caenogastropods except the Cyclophoroidea and the Ampullarioidea, encompassing the Viviparioidea and the Sorbeoconcha. PONDER & LINDBERG (1997:225) introduced this taxon, comprising the Cerithioidea

and the rest of the caenogastropods. The current literature usually considers the Viviparidae as Ampullarioidea (*e.g.*, BOSS, 1982; VAUGHT, 1989). The viviparids actually share some characters with the ampullariids, such as the head-foot left and right siphons, the type of operculum, and the freshwater environment. Those characters were here considered homologous between the representatives of both groups. However, despite this, the two groups are paraphyletic. This result indicates that the viviparids should be included in a monotypic superfamily Viviparioidea. The node 6 is supported by 18 synapomorphies, and represents the viviparids. The more important synapomorphies are: adaptations to filter feeding (characters 9, 10, 17, 22, 28); ureter (40, 41); male pallial ducts running by integument and opening in the right cephalic tentacle (114-117); brood pouch in pallial oviduct (129, 137). An internal organization of the viviparids was obtained, represented by the nodes 8 and 9, separating respectively the *Viviparus* sample from the Australian sample. As this organization is considered provisional, then no deeper analysis or taxonomic implications is here proposed. The Australian viviparids studied here belong to the subfamily Bellamyinae (ANNANDALE & SEWELL, 1921; ROHRBACH, 1937; VAIL, 1977; SMITH, 2000), characterized mainly by the testis positioned in the pallial cavity, by side of the rectum (Fig.317:pt); this character is not explored here because the studied material is not well-preserved enough for observing this character in all samples. The Australian sample of *Notopala* and *Larina* are separated from each other (node 10) by a single synapomorphy (single gastric duct to digestive gland, character 100, state 1, convergent with other branches).

The node 7 encompasses supposedly outgroups, representing the "true" caenogastropods, or the Sorbeoconcha, in this study. The node is supported by 10 synapomorphies, being half of them reversions. The more remarkable are: the determinate shell growth (character 5); the reversion of the left and right head-foot siphons (10-11); the reduction of the dorsal chamber of buccal mass (46); the gastric style sac (101); the male seminal vesicle (111); and the approach of the pairs of connectives pedal-cerebral to pedal-pleural ganglia in the nerve ring (140).

As reported above, a more un-depth study on the caenogastropod phylogeny is still been performed, which this study is part. Apparently, the architaenioglossans can be regarded as true Caenogastropoda, being its basal branches.

However, further analysis on caenogastropod phylogeny is still in progress, and depends on the study of remainder superfamilies, as well as of more outgroups. On the other hand, the present studied sample is considered sufficient for analyzing the monophyly and phylogenetic relationship of the contemplated supra-generic taxa, just the main goals of this study.

CONCLUSIONS

1. The taxon Architaenioglossa is not monophyletic, but so paraphyletic, then it should not be used as a formal taxon.
2. The architaenioglossans can be regarded as the 3 first branches of the order Caenogastropoda, respectively: Cyclophoroidea (Cyclophoridae); Ampullarioidea (Ampullariidae) and Viviparioidea (Viviparidae).
3. The combination among the architaenioglossans and remaining caenogastropods are supported by 41 morphological synapomorphies.
4. The Cyclophoroidea, Ampullarioidea and Viviparioidea are supported respectively by 21, 40 and 18 synapomorphies.
5. The Viviparioidea are a separated taxon from the Ampullarioidea.
6. The three architaenioglossan branches presented internal, well-resolved organizations; however, they are considered provisional and no systematic change was proposed.
7. The analysis of all organs and systems are useful for phylogenetic analysis.

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A NEW *SCINAX* WAGLER, 1830 OF THE *S. ROSTRATUS* GROUP FROM CENTRAL BRAZIL (AMPHIBIA, ANURA, HYLIDAE) ¹

(With 8 figures)

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ABSTRACT: A new species of the genus *Scinax* belonging to the *S. rostratus* species group is described from the State of Goiás, Brazil. *Scinax constrictus* sp.nov. is characterized by small snout-vent length (males ranging 20.8-29.4mm; females 28.2-35.6mm), protuberant nostrils, vocal sac pigmented, superior eyelid, calcar, and jaw tubercles present, dermal constriction on the shoulders in adults, two separate tubercles above the cloaca in females, and a discrete anal flap in males; an open land, non-forest species. A description of the advertisement call is provided.

Key words: Amphibia, Anura, Hylidae, *Scinax constrictus* sp.nov., taxonomy.

RESUMO: Nova espécie de *Scinax* Wagler, 1830 do grupo de *S. rostratus* do Brasil Central (Amphibia, Anura, Hylidae).

Uma nova espécie do gênero *Scinax* pertencente ao grupo de *S. rostratus* é descrita do Estado de Goiás, Brasil. *Scinax constrictus* sp.nov. caracteriza-se por apresentar pequeno comprimento rostro-anal (machos 20,8-29,4mm; fêmeas 28,2-35,6mm), narinas protuberantes, saco vocal pigmentado, presença de tubérculos na pálpebra superior, calcâneo e na mandíbula, constricção dérmica sobre os ombros dos adultos, dois tubérculos separados acima da cloaca nas fêmeas e um discreto *flap* anal nos machos; espécie de área aberta. O canto de anúncio é descrito.

Palavras-chave: Amphibia, Anura, Hylidae, *Scinax constrictus* sp.nov., taxonomia.

INTRODUCTION

Scinax Wagler, 1830 is one of the most diversified genus among the neotropical hylid frogs, including 85 species (CARAMASCHI, 2004; FROST, 2002). POMBAL & GORDO (1991) recognized the priority of *Scinax* in relation to *Ololygon* Fitzinger, 1843, and DUELLMAN & WIENS (1992) diagnosed the genus based on external morphology, osteology, and larval/reproductive features, defining several species groups. Among them, the *S. rostratus* group is defined by characteristics as the presence of an acuminate snout, pointed tubercle on heel, and head-down calling position (DUELLMAN, 1972; FAIVOVICH, 2002). Currently, nine species are recognized in this group (FROST, 2002): *S. boulengeri* (Cope, 1887), *S. garbei* (Miranda-Ribeiro, 1926), *S. jolyi* Lescure & Martin, 2001, *S. kennedyi* (Pyburn, 1973), *S. nebulosus* (Spix, 1824), *S. pedromedinae* (Henle, 1991), *S. proboscideus*

(Brongersma, 1933), *S. rostratus* (Peters, 1863), and *S. sugillatus* (Duellman, 1973). Herein, we describe a new species of the *S. rostratus* group from the Brazilian Cerrado biome.

MATERIAL AND METHODS

Specimens used in the description or examined for comparisons are deposited in MNRJ (Museu Nacional, Rio de Janeiro, Brazil), ZUEC (Museu de História Natural, Universidade Estadual de Campinas, Brazil), and ZUFG (Universidade Federal de Goiás, Brazil).

The following measurements were taken to the nearest 0.01mm with calipers: SVL (snout-vent length), HW (head width), HL (head length), THL (thigh length), TBL (tibia length), and FL (foot length). Six others variables, ED (eye diameter), IOD (interorbital distance), IND (internarial distance),

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END (eye-nostril distance), NSD (nostril-snout distance), and TD (tympanum diameter), were measured using an ocular micrometer in a Zeiss stereomicroscope. All measurements are in millimeters and followed DUELLMAN (2001) and CEI (1980). Webbing formula notation was described following SAVAGE & HEYER (1967), as modified by MYERS & DUELLMAN (1982).

Advertisement calls of six males were recorded with a DAT Sony TCD-D100 or DAT Tascam recorder and microphone ECM-MS 907 or Sennheiser ME66, respectively. The vocalizations were edited at a sampling frequency of 12kHz and 16 bits resolution with a PC-Pentium computer, and analyzed with Avisoft-Sonograph Light and Cool Edit 96 softwares. The sonogram was produced with 256 points, overlap of 87.5%, and in flat top.

RESULTS

Scinax constrictus sp.nov. (Figs.1-8)

Holotype – BRAZIL - GOIÁS: Municipality of Palmeiras (16°48'S; 49°55'W), Sítio dos Pinheiros, MNRJ 31205, adult ♂, L.P.Lima col., 26/II/2001.

Paratopotypes – MNRJ 31206-31225, 19 adult ♂ and one adult ♀, L.P.Lima col., 26/II/2000; ZUFG 883-886, four adult ♂, L.P.Lima col., 12/II/2000;

ZUFG 942-943, two adult ♂, L.P.Lima col., 24/III/2002; ZUFG 958, adult ♂, L.P.Lima col., 13/II/2000; ZUFG 961-962, two adult ♂, L.P.Lima col., 04/XI/2000; ZUFG 979, adult ♂, L.P.Lima col., 30/X/2000; ZUFG 980-981, two adult ♂, L.P.Lima col., 13/X/2000; ZUFG 992-995, four adult ♂, L.P.Lima col., 24/III/2001; ZUFG 1008-1012, 1014-1022, 13 adult ♂ and one adult ♀, collected with the holotype; ZUFG 1665 (Fig.1), adult ♂, L.P.Lima, R.C.D.Pinheiro e R.P.Bastos cols., 07/II/2003.

Referred specimens – BRAZIL - GOIÁS: Municipality of Guapó: ZUFG 947-948, two adult ♂, R.F.Juliano col., 24/III/2000. Municipality of Itaberaí: ZUFG 1300-1303, four adult ♂, R.P.Bastos, L.P.Lima e D.Brandão cols., 12/I/2001. Municipality of Jussara: ZUFG 1192, adult ♂, R.P.Bastos, L.P.Lima e D.Brandão cols., 13/I/2001. Municipality of Mossâmedes: ZUFG 821-822, 845, two adult ♂ and one adult ♀, Fazenda Água Fria, R.P.Bastos e R.F.Juliano cols., 23/I/2000. Municipality of Pirenópolis: ZUEC 10273-10276, 10277-10285, 11 adult ♂ and two adult ♀, A.J.Cardoso, A.S.Rand e A.A.Giaretta cols., 04/XII/1992. Municipality of Pontalina: MNRJ 31226-31227, adult ♂ and adult ♀, Fazenda Lagoa Grande, L.D.Guimarães, C.F.B.Haddad, J.P.Pombal Jr. and R.P.Bastos cols., 16/XII/1998; ZUFG 288-289, two adult ♂, L.D.Guimarães e R.P.Bastos cols., 17/III/1997;



Fig.1- *Scinax constrictus* sp.nov., paratopotype (ZUFG 1665), adult male in life.

ZUFG 515- 522, eight adult ♂, L.D.Guimarães e R.P.Bastos cols., 26/X/1998. Municipality of Porangatu: ZUFG 1402, adult ♂, Leôncio P.Lima e Leopoldo P.Lima cols., 21/XII/2000. Municipality of Uirapuru: ZUFG 702, adult ♂, M.B.Alcantara col., 01/IV/1999.

Diagnosis – A small species (Figs.2-3) of the *Scinax rostratus* group; SVL of males 20.8-28.4mm, females 28.2-35.6mm; protuberant nostril; vocal sac pigmented; upper eyelid, calcar, and jaw tubercles present; nostrils not projected from head contour in dorsal view; a dorsolateral dermal constriction on the shoulders in adults; two separate tubercles above the cloaca in females and a discrete anal flap in males; an open area inhabitant species.

Comparisons with others species – *Scinax constrictus* sp.nov. most resembles *S. nebulosus* (characters in parentheses) in general aspect, but it can be distinguished generally by the smaller SVL (\bar{x} =26.1mm, range=24-30mm in males; \bar{x} =38.0mm, range= 35-40mm in females; LUTZ, 1968, DUELLMAN, 1972); presence of discrete anal flap in males (no anal flap; LUTZ, 1968); presence of one row of small tubercles on the edge of lower jaw (absent or indistinct row; LUTZ, 1968, DUELLMAN, 1972); advertisement call with higher or lower dominant frequency (\bar{x} =2867.3Hz, range=2685.6-3129.8Hz according to DE LA RIVA, MÁRQUEZ & BOSCH, 1994; \bar{x} =4500Hz, range=4200-4800Hz according to

HÖDL, 1977), generally lower call duration (\bar{x} = 277ms, range=190-385ms according to HÖDL, 1977, or \bar{x} =240.6ms, range=201.1-305ms according to DE LA RIVA, MÁRQUEZ & BOSCH, 1994), and higher note number (4-7 notes according to DUELLMAN, 1972, or one note by call according to DE LA RIVA, MÁRQUEZ & BOSCH, 1994).

Scinax constrictus sp.nov. differs from *S. boulengeri* (characters in parentheses) by the smaller SVL (\bar{x} =41.1mm, range=35.5-48.7mm in males; SVL maximum=53mm in females; LEÓN, 1969; DUELLMAN, 1972); presence of discrete anal flap in males (no anal flap; DUELLMAN, 1972), posterior surface of legs brown or pale green (greenish yellow or orange; DUELLMAN, 1972); advertisement call with lower dominant frequency (\bar{x} =2840Hz, range=2520-3182Hz; LEÓN, 1969), lower call duration (\bar{x} =350ms, range=240-470ms; LEÓN, 1969), and higher note number (one note; LEÓN, 1969).

From *S. garbei* (characters in parentheses), *S. constrictus* sp.nov. differs by the smaller SVL (range=30-42mm in males, range=38-48mm in females; RODRIGUEZ & DUELLMAN, 1994); posterior surface of legs brown or pale green (yellow or orange; DUELLMAN, 1972); advertisement call with higher note number (one note; DUELLMAN, 1970) and lower duration (\bar{x} =690ms, range=230-1860ms; DUELLMAN, 1970).



Scinax constrictus sp.nov., holotype (MNRJ 31205): fig.2- dorsal view, fig.3- ventral view.

Scinax constrictus sp.nov. can be distinguished from *S. jolyi* (characters in parentheses; LESCURE & MARTY, 2001) by the smaller SVL (\bar{x} = 37.7mm, range = 36.5-39.1 in males; \bar{x} = 41.85mm, range = 40.0-43.7mm in females); presence of one row of small tubercles on the edge of lower jaw (no row); advertisement call with only pulsioned structure (advertisement call with harmonic and pulsioned structure).

Scinax constrictus sp.nov. differs from *S. kennedyi* (characters in parentheses; PYBURN, 1973) by the smaller SVL (\bar{x} = 33.0mm, range = 31.5-35.3 in males; SVL of one female = 37.3mm); presence of one row of small tubercles on the edge of lower jaw (no row); posterior surface of legs brown or pale green (orange); advertisement call with lower duration (\bar{x} = 1770ms, range = 690-2100ms) and higher dominant frequency (\bar{x} = 1200Hz, range = 1050-1600Hz).

From *S. pedromedinae* (characters in parentheses), *S. constrictus* sp.nov. differs by, generally, the smaller SVL (\bar{x} = 26.4mm, range = 22.2-28.9mm in males; \bar{x} = 29.4mm, range = 27.5-31.5mm in females; DUELLMAN & WIENS, 1993); jaw tubercles less evident (line of tubercles evident; DUELLMAN & WIENS, 1993); open land species (primary rainforest species; HENLE, 1991); advertisement call with higher duration (90-100ms; DUELLMAN & WIENS, 1993).

Scinax constrictus sp.nov. differs from *S. proboscideus* (characters in parentheses; DUELLMAN, 2001) by the smaller SVL (\bar{x} = 37.4mm, range = 33.0-39.8mm in males; SVL = 37.0mm in one female); absence of a fleshy proboscis (presence); concealed parts of the legs brown or pale green (yellow); advertisement call with higher note number (\bar{x} = 1.3, range = 1-3) and higher dominant frequency (\bar{x} = 2012Hz).

Scinax constrictus sp.nov. can be distinguished from *S. rostratus* (characters in parentheses; DUELLMAN, 2001) by the smaller SVL (\bar{x} = 45.7mm in males; \bar{x} = 48.0mm in females); presence of a line of tubercles on lower jaw (no line); presence of tubercle on hell (no tubercle); concealed parts of the legs brown or pale green (orange or dark yellow); advertisement call with higher dominant frequency (\bar{x} = 920Hz) and lower duration (\bar{x} = 690, range = 230-860ms).

Scinax constrictus sp.nov. differs from *S. sugillatus* (characters in parentheses; DUELLMAN, 1973) by the smaller SVL (\bar{x} = 39.9mm, range = 38.7-42.0mm in males; SVL of one female = 45.5mm in); jaw tubercles less evident (line more evident); higher

note number (1-2 notes); advertisement call with higher dominant frequency (\bar{x} = 2023Hz, range = 1017-2904Hz), and lower duration (\bar{x} = 390, range = 280-600ms).

Description of the holotype – Head 12.5% longer than wide; snout elongate, pointed in dorsal view (Fig. 4) and acute in lateral view (Fig. 5); nostrils not projected from head contour in dorsal view, projected in lateral view; canthus rostralis distinct; tympanum evident, circular; supratympanic fold evident with enlarged tubercles; lower eyelid bordered by a tinny white stripe; tongue slightly cordiform, free behind; vomerine teeth in two small groups between choanae; single subgular vocal sac; five tubercles along the edge of the lower jaw; upper arm strong, with 2-4 tubercles on outer side; fingers size I < II ~ IV < III (Fig. 6); fingers I and II free, II and III, and III and IV linked at base by web; nuptial pads present but poorly developed; outer metacarpal tubercle cordiform, inner metacarpal tubercle oval; subarticular tubercles rounded; finger disks wider than long; toes size I < II < V ~ III < IV (Fig. 7); foot webbing formula I 2 2/3-2 II 1-2 III 1-2 IV 2-1 V; inner metatarsal tubercle rounded, the outer with half size of the inner; subarticular tubercles rounded; supernumerary tubercles discrete on hands and feet; outer margin of tarsus and foot with a ridge of tubercles; calcar tubercle prominent; a discrete anal flap formed by two enlarged tubercles; a dermal groove from the cloaca to venter of thighs; dorsum and head smooth with many enlarged tubercles; loreal and shoulder regions more tuberculate; body constricted at the level of shoulders; dorsal surfaces of arms and legs with scattered tubercles; venter granular; ventral surfaces of legs and arms smooth.

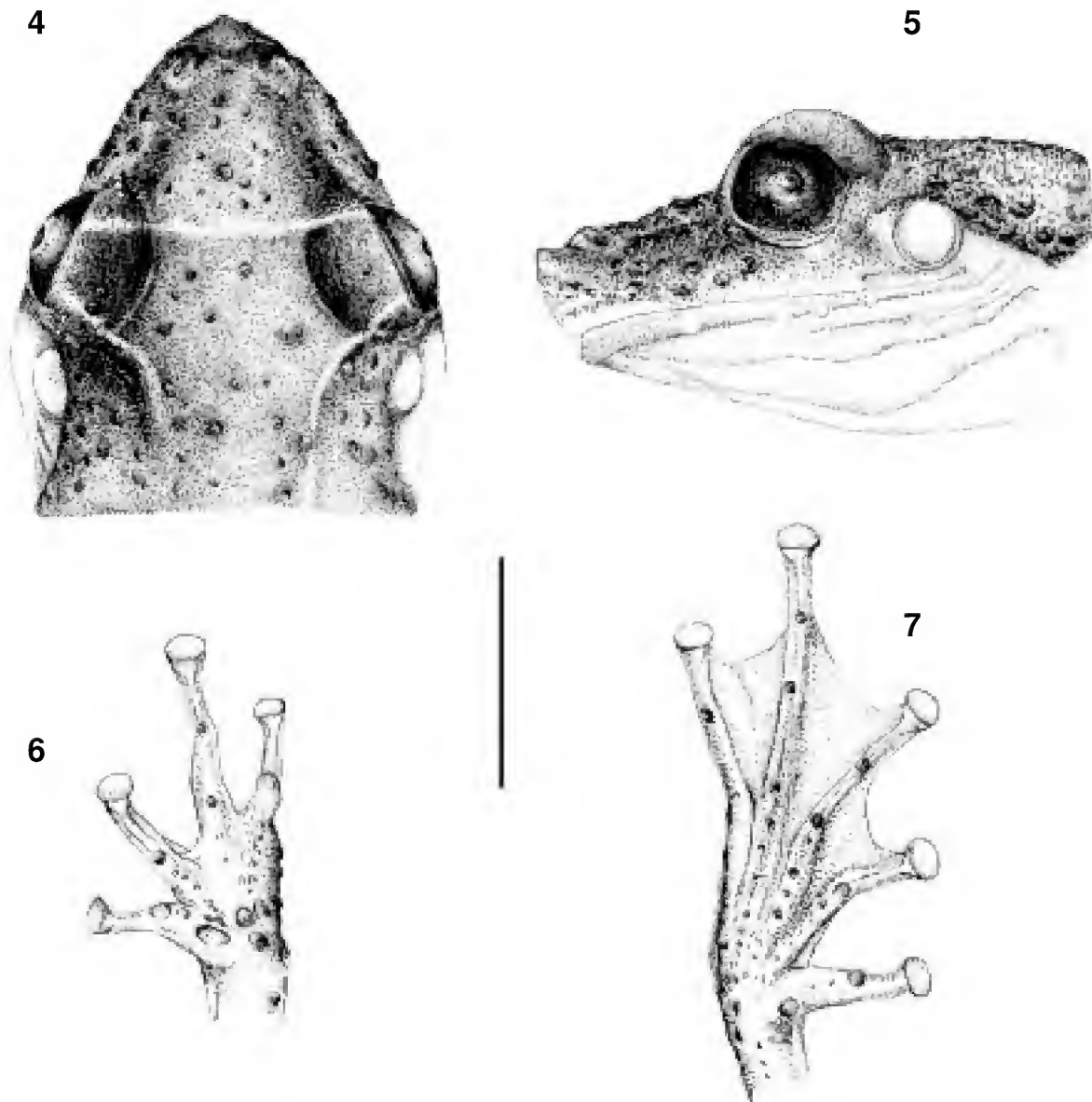
Color in life – Males and females showed dorsum color ranging from beige or pale green to brown or dark brown, with black irregular spots. Granules of dorsum brown, yellow or orange. Tympanum bronze. A triangular spot with apex directed posteriorly, bordered by a yellow line, between the eyes. Upper surfaces of arms and legs brown with irregular stripes dark brown. Concealed parts of the legs brown or pale green. Belly white to light brown. Throat whitish with brown flecks. Iris pale to dull bronze with black median vertical streak.

Color in preservative (70% alcohol) – Color similar to those in life, however more dark. The colors yellow or orange of the dorsal granules, yellow of tympanum, and yellow of line around the spot between the eyes become opaque and brown.

Measurements of holotype – SVL 24.2; HL 8.2; HW 7.2; ED 2.5; TD 1.3; IOD 2.5; END 2.5; NSD 1.0; IND 1.7; THL 12.2; TBL 13.9; FL 10.5.

Variation – About 82% of specimens (males and females) have the triangular spot between eyes. Skin on dorsum varied from slightly tuberculate to tuberculate. The dorsum may be brown or dark brown. Most of the specimens (87%) showed limbs with three dark brown transverse bars. Nuptial pads present in 95% of the adult males. Mean, standard deviation, and range of measurements of 82 males and six females are presented in table 1.

Advertisement call – The call showed pulsioned structure (Fig.8). Average call duration 213.4 ± 24.0 ms (range=180.2-242.2ms; n=30 calls of five males); 9.3 ± 0.9 notes (range=6.0-10.0 notes; n=30 calls), each with average duration of 17.08 ± 2.01 ms (range=14.5-20.4ms; n=150 notes); notes given at intervals of 6.9 ± 0.7 ms (range=6.0-8.0ms; n=30 calls). Each note is constituted, in average, by 7.0 ± 2.0 pulses (range=4.0-9.0 pulses; n=150 notes) with average duration of 2.4 ± 0.4 ms (range=2.0-4.0ms; n=150 pulses). Repetition call rate was 18.0 ± 3.5 calls/min (range=14.0-23.0 calls/min, n=5 males); average dominant frequency



Scinax constrictus sp.nov., holotype (MNRJ 31205): fig.4- dorsal view of head, fig.5- lateral view of head, fig.6- ventral view of hand, fig.7- ventral view of foot. Scale bar = 5mm.

was 3292.1 ± 123.2 Hz (range=3115.2-3487.6Hz; n=30 calls of five males).

Habitat and natural history – The reproductive activity was observed between December and March in permanent ponds localized in open areas. Generally, the males vocalized with head down, on the branches of the marginal arbustive vegetation. The average height of the site of vocalization was 79.2 ± 13.5 cm (range=38.0-112.2cm; n=46). Gravid females were collected in December, January, and February. The spawning had 207 black eggs (n=1 clutch), with a diameter of 1.3 ± 0.13 mm (n=10 eggs). Tadpoles are unknown.

Distribution – The new species is known from the municipalities of Guapó, Itaberaí, Jussara, Mossâmedes, Palmeiras, Pirenópolis, Pontalina, Porangatu, and Uirapuru, in the State of Goiás, Brazil.

Etymology – The specific epithet *constrictus* comes from the Latin word *constrictio*; it is used here in reference to the presence of a dorsolateral dermal constriction on the shoulders of the new species.

Remarks – *Scinax constrictus* sp.nov. has the southernmost distribution of the species of the *S. rostratus* group, being the first species cited for the Cerrado biome. As mentioned in the comparison with other species, in spite of the resemblance of *S. constrictus* sp.nov. with *S. nebulosus*, its possible to separate these two species by morphology and advertisement call characteristics. The advertisement call of the new species is quite different in relation to the

dominant frequency and note number, despite the great variation of the call characteristics of *S. nebulosus* (DUELLMAN, 1970; HÖDL, 1977; DUELLMAN & PYLES, 1983; DE LA RIVA, MÁRQUEZ & BOSCH, 1994). As example, the dominant frequency in *S. nebulosus* changed from 2867.3 to 4800Hz, in spite of male SVL of different populations which is similar. So, this discrepancy could be indicative that different taxa are being considered as *S. nebulosus*. A carefull evaluation of the taxonomics status of *S. nebulosus* along its geographical distribution would be necessary.

SPECIMENS EXAMINED

Scinax garbei – BRAZIL - ACRE: Municipality of Cruzeiro do Sul: (ZUEC 4396, 5389-5390, 10640), Humaitá do Moa (ZUEC 5433), Miritizal (ZUEC 9505), Vila Militar (ZUEC 4603, 4654-4655, 4667-4671, 4710-4715). Municipality of Mâncio Lima: Colônia São Francisco (ZUEC 4370-4371, 4636-4639). Municipality of Rio Branco: Parque Zoobotânico da UFAC (ZUEC 5577-5578, ZUEC 7125). Municipality of Xapuri: Caminho da Boa Vista (ZUEC 5706-5707).

Scinax nebulosus – BRAZIL - PARÁ: Municipality of Altamira: camping Juruá da CNEC Km 10 (ZUEC 7240), camping Juruá da CNEC Km 26 (ZUEC 7253-7254); camping Kararaho da CNEC (ZUEC 7331), Mr. Oswaldo's small farm, surroundings of the camping Meu Sossego (ZUEC 7395).

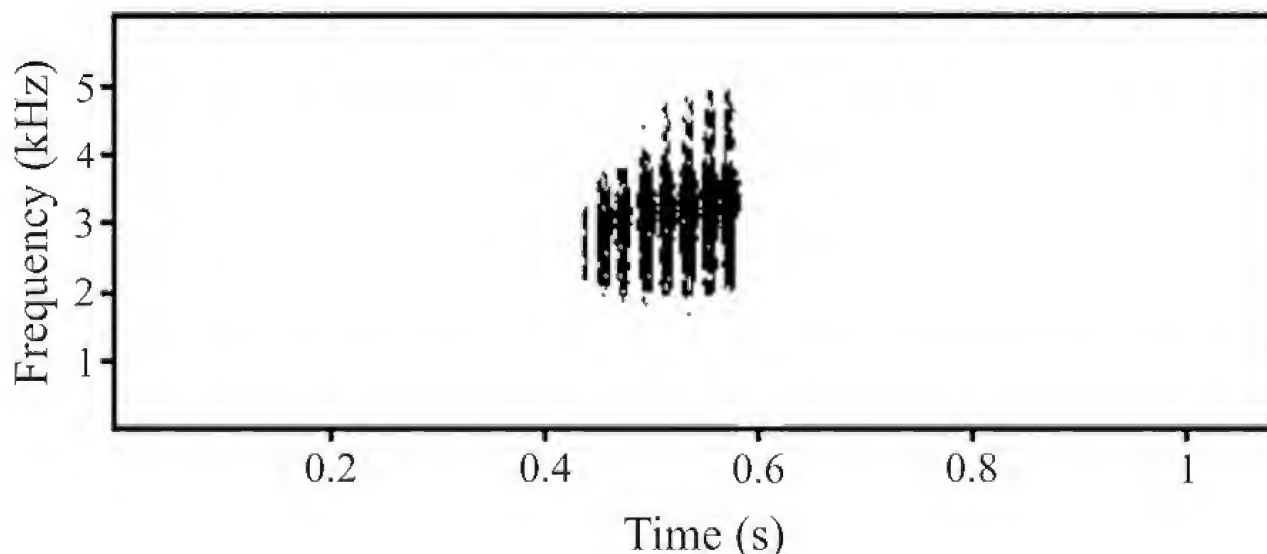


Fig.8- *Scinax constrictus* sp.nov., sonogram of advertisement call (MNRJ 31205; air temperature 24.1°C).

TABLE 1. Mean (\bar{x}), standard deviation (s), and range of the measurements (mm) of males and females of *Scinax constrictus* sp.nov.

	♂ (n = 82)			♀ (n = 6)		
	\bar{x}	s	Range	\bar{x}	s	Range
SVL	26.09	1.83	20.8-28.4	31.93	2.53	28.2-35.6
HL	8.97	0.81	7.2-10.7	12.09	1.36	10.3-13.7
HW	7.97	0.59	6.6-9.1	10.67	0.81	9.4-11.7
ED	3.56	0.52	2.4-4.4	4.1	0.34	3.7-4.3
TD	1.31	0.52	2.4-4.4	1.9	0.39	1.3-2.2
IOD	3.03	0.29	2.4-3.7	3.67	0.24	3.3-3.8
IND	2.41	0.19	1.5-2.7	2.67	0.38	2.2-3.1
END	3.13	0.32	2.4-3.8	3.65	0.33	3.3-4.1
NSD	1.78	0.21	1.0-2.1	2.39	0.47	1.8-2.3
THL	12.56	0.87	10.4-14.4	18.96	1.08	15-17.3
TBL	14.14	1.11	11.2-17.0	17.64	1.23	1.66-19.6
FL	11.33	0.96	7.9-13.0	14.71	0.99	13.7-15.7

(n) number of specimens.

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REGISTRO DA ATIVIDADE DE ORGANISMOS EM UM CAULE DO PERMIANO DO RIO GRANDE DO SUL, BRASIL ¹

(Com 6 figuras)

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RESUMO: Neste trabalho são analisadas perfurações e galerias identificadas em um fragmento de lenho proveniente da Formação Serra Alta, Permiano Superior da Bacia do Paraná. No exemplar ocorrem áreas com uma preservação anatômica excelente refletindo em células bem preservadas. A destruição do tecido lenhoso produzida por insetos foi acompanhada pela degradação dos tecidos por ação de fungos e bactérias. Nas regiões onde a atividade de organismos se manifesta, a sílica precipitou a partir das bordas formando estruturas com anéis concêntricos indicando que estas estavam vazias antes da mineralização, o que sugere um processo diagenético posterior.

Palavras-chave: Icnofósseis, caules fósseis, Permiano, Bacia do Paraná.

ABSTRACT: Activity of Organisms in a Stem of the Rio Grande do Sul State, Brazil.

Borings and galleries were analysed in one fossil wood fragment from Serra Alta Formation, Upper Permian, Paraná Basin. Some regions were well preserved allowing for the observation of well preserved wall cells. The wood destruction by insects was accompanied by the degradation of wood cell by fungi and bacteria. In these regions the silica precipitated from the borders to the center forming concentric rings that were empty before mineralization, suggesting a subsequent diagenetic process.

Key words: Ichnofossils, fossil wood, Permian, Paraná Basin.

INTRODUÇÃO

O registro geológico demonstra que, a partir do Devoniano, ficaram mais evidentes as interações entre as plantas vasculares e os animais (LABANDEIRA, 1997, 1998). Em vegetais fósseis, as atividades biológicas incluem diferentes processos, que resultam em galerias, perfurações, degradação por ação de fungos e bactérias e coprólitos. Perfurações resultantes da atividade de insetos são encontradas em folhas, pecíolos e caules fósseis. Em folhas fósseis, manifestam-se principalmente como fitofagia e galerias. É comum, além disso, a presença de coprólitos no interior de caules fósseis.

No Brasil, poucos são os registros de atividades biológicas em vegetais fósseis. GUERRA-SOMMER (1995) registrou a ocorrência de fitofagia em folhas de *Glossopteridales* do

Eopermiano da Bacia do Paraná, no sul do Brasil, atribuindo aos Ortopterídeos (Protorthoptera). ADAMI-RODRIGUES *et al.* (2003) analisaram folhas fósseis de *Glossopteris* Brongniart, 1828 e *Cordaites* Unger, 1850, das formações Rio Bonito e Irati/Serra Alta, do Estado do Rio Grande do Sul, atacadas por insetos herbívoros.

O presente estudo teve como objetivo identificar os tipos de atividades biológicas encontradas em um fragmento de lenho mineralizado do Permiano Inferior da Bacia do Paraná, relacionando-as ao possível agente causador e a parâmetros de natureza tafonômica.

MATERIAL E MÉTODOS

O material corresponde a um fragmento de lenho com xilema secundário (*Gymnospermae*),

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coletado em um afloramento da rodovia São Gabriel – Batovi (km 18), Formação Serra Alta (ALVES, 1999; MERLOTTI, 2000), do Permiano da Bacia do Paraná, Estado do Rio Grande do Sul. O afloramento é constituído por siltitos oliva a verde-oliva ou cinzentos, com laminação plano-paralela irregular, argilitos maciços, raros arenitos intercalados e concreções silicosas freqüentemente acompanhadas por veios de sílica (GUERRA, 1976; GUERRA-SOMMER, 1978; MERLOTTI, 2000). De acordo com SCHNEIDER *et al.* (1974), esta seqüência está incluída litoestratigraficamente na Formação Serra Alta, de idade Neopermiano, Kazaniano (DAEMON & QUADROS, 1970). A deposição dos sedimentos provavelmente ocorreu abaixo do nível de ação de ondas, em ambiente marinho de águas calmas (SCHNEIDER *et al.*, 1974).

O lenho composto por medula e xilema secundário possui 90mm de comprimento, com diâmetro maior de 80mm e diâmetro menor de 50mm, sendo a diferença no diâmetro ocasionada provavelmente pela perda de tecido (Fig.1). O exemplar foi cortado nos três planos anatômicos (transversal, longitudinal e radial) e as secções analisadas em microscópio estereoscópico e ótico. O material está depositado na Coleção de Paleobotânica da Universidade Federal do Rio Grande do Sul (UFRGS, PB965).

CARACTERÍSTICAS DO LENHO

Os cortes transversais indicam um lenho eustélico com medula cêntrica, xilema primário endarco e lenho secundário picnoxílico. A medula pequena (4mm) está mal preservada e rompida. Na periferia da medula observa-se a provável presença de canais secretores. As células do parênquima possuem parede fina. O xilema secundário é homogêneo e constituído de traqueóides e raios; as pontoações intertraqueoidais são unisseriadas e, às vezes, bisseriadas opostas.

O tecido radial está mal preservado e mostra-se homogêneo, com os raios unisseriados e muito baixos com poucas células de altura (2-4-9) e as pontoações do campo de cruzamento pequenas e em número de 4 ou mais. Os anéis de crescimento, em número de 10, são marcados pela redução gradual do diâmetro dos lumens das células axiais do lenho inicial para o tardio, que é estreito (1 a 7 células de largura). A identificação taxonômica mais específica ficou prejudicada, devido a não

visualização de características diagnósticas do exemplar, em especial, da medula. O lenho eustélico e a presença de canais secretores periféricos na medula sugerem a inclusão no Grupo Solenóide (MUSSA, 1986).

CARACTERÍSTICAS DAS ATIVIDADES BIOLÓGICAS

O xilema secundário do exemplar foi destruído pela atividade orgânica em várias regiões. As perfurações aparecem normalmente preenchidas por sílica e são facilmente visíveis pela coloração esbranquiçada em plano transversal (Fig.1) e longitudinal (Fig.2). No plano transversal aparecem em número e forma variável, desde circulares a ovais, até alongadas e irregulares. As alongadas sugerem a presença de duas ou mais perfurações sobrepostas. No plano anatômico transversal, as regiões com perfurações e conseqüentemente com o tecido lenhoso destruído ocorrem em número superior a 200. Em todo o xilema secundário, o número médio de perfurações corresponde a 12 por cm², com mínimo de 8 e máximo de 18 por cm². O diâmetro das perfurações varia de 0,85 a 2,3mm. Fraturas radiais e tangenciais são encontradas no tecido lenhoso originadas, possivelmente antes da silicificação. Estes padrões de fraturas podem ser comumente observados em situações *post-mortem* nos caules atuais.

A observação microscópica dos espaços vazios remanescentes após as perfurações no xilema secundário evidencia que essas estão preenchidas principalmente por bandas de sílica (Figs.3-4). A precipitação ocorreu da periferia para o centro, determinando a formação de anéis concêntricos. Os limites destas áreas possuem células com parede parcialmente preservada (Fig.5).

Nas secções longitudinais, as perfurações no xilema secundário são tubiformes, com diâmetro constante e extremidades arredondadas, e uma altura média de 6,15mm. Normalmente as perfurações mostram fundo cego, mas algumas possuem intercomunicações diagonais ao eixo anatômico longitudinal formando galerias (Fig.2). Na periferia de algumas galerias foram observadas estruturas com morfologia análoga a hifas de fungos, similar as já descritas para lenhos fósseis (BUURMAN, 1972). Também são observados traqueóides com paredes incompletas (Fig. 6) e concentrações de material amarelo escuro a marrom, correspondendo possivelmente a fragmentos de tecido lenhoso.

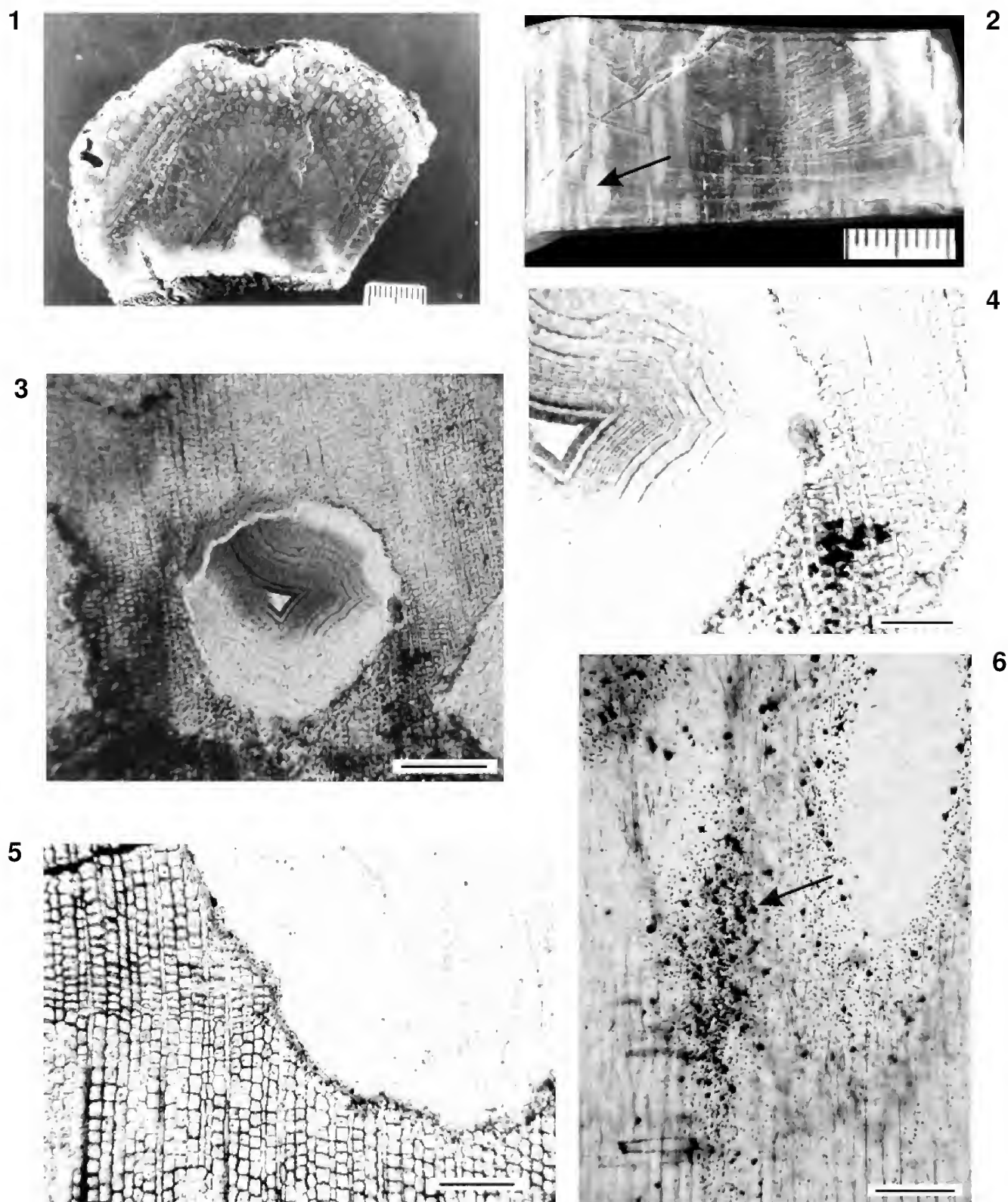


Fig.1- Secção transversal do lenho; fig.2- secção longitudinal mostrando as intercomunicações entre as galerias; fig.3- secção transversal em microscopia ótica de galeria preenchida por sílica bandeada; fig.4- detalhe da figura anterior. Células junto à borda da galeria com paredes incompletas; fig.5- detalhe da galeria com células do lenho tardio e células de raio bem preservadas; fig.6- secção longitudinal com células traqueóides bem preservadas adjacentes à galeria. Concentração de substância marrom escura junto à borda, correspondendo provavelmente a fragmentos de tecido lenhoso. Escalas: 1-2 = mm; 3 = 500 μ m; 4-6 = 200 μ m.

DISCUSSÃO

A atividade biológica identificada no lenho estudado inclui perfurações, galerias e outras manifestações, realizadas por insetos, fungos e provavelmente bactérias, embora seja difícil precisar, entre estes, os grupos responsáveis.

Poucos dados sobre atividades biológicas em lenhos fósseis são conhecidos no Brasil, até o momento. As galerias e as perfurações observadas podem ser classificadas como icnitos de alimentação (*Fodinichnia*) do tipo *Xylichnia*, que reúnem perfurações de insetos produzidas em madeiras. FERNANDES *et al.* (2002) fizeram referência ao material em estudo e classificaram as perfurações como estruturas de bioerosão.

No final do Paleozóico, os artrópodes dos grupos Diplopoda, Arthropleura, Collembola e Coleoptera foram considerados como possíveis habitantes das madeiras em decomposição e os Orthoptera (Blattodea), Diplopoda, Arthropleura, Collembola, Acarida e Coleoptera, seriam xilófagos (SCOTT & TAYLOR, 1983; TAYLOR & TAYLOR, 1993).

LABANDEIRA (1998) apresentou alguns critérios para identificar no registro fóssil, a herbivoria, ou seja, as atividades ocorridas durante a vida do vegetal e diferenciá-las das ocorridas após a morte do vegetal, detritivoria. Considerou como mais importante no reconhecimento da herbivoria, a detecção da resposta do vegetal, incluindo a reação dos tecidos que implicam na multiplicação e no aumento anormal das células. De acordo com os critérios indicados pelo autor, o material estudado apresenta evidências de detritivoria.

Segundo STUBBLEFIELD & TAYLOR (1986), as galerias originadas por insetos em tecidos lenhosos, em geral, variam pouco em tamanho, não são vazias e formam uma rede anastomosada de espaços sugerindo escavações.

CICHAN & TAYLOR (1982) registraram evidências de atividade biológica, na forma de pelotas fecais de coleópteros e túneis conectando galerias verticais em lenhos mineralizados de *Premnoxylon* Pierce & Hall 1953, do Carbonífero dos Estados Unidos. ZHOU & ZHANG (1989) também apontam coprólitos deste mesmo grupo de insetos, em lenhos de *Protocupressinoxylon* Eckhold, 1922, do Jurássico da China. Os ácaros perfuradores de madeira seriam muitas vezes responsáveis por túneis, preservados em madeiras permineralizadas ou petrificadas, contendo muitas vezes, coprólitos em seu interior (DEREK & TAYLOR, 2002). O registro fóssil indica que este grupo de ácaros ocorre

desde o Neocarbonífero (ASH, 2000; DEREK & TAYLOR, 2002). ASH (2000) descreveu um caule de Filicales do Triássico do Arizona contendo cavidades irregulares de várias formas e tamanhos, além de coprólitos pequenos (40-50µm de diâmetro e 80 a 100µm de comprimento) preenchidos por minerais, atribuídos a ácaros Oribatida.

A ocorrência de fósseis de insetos das ordens Mecopteroidea (Família Permochoristidae); Neuropteris (Família Permithonidae); Coleoptera (Família Permocupididae) e Homoptera (Famílias Pereboridae, Prosboleccididae, Prosbolidae e Fulguringuidae) é registrada para o Permiano do Rio Grande do Sul (Formação Irati/Serra Alta, localidade de Mina do Leão, km 90 BR290), conforme PINTO (2000).

As comparações entre caules atuais atacados por larvas de coleópteros e o lenho fóssil analisado mostram semelhanças no padrão de destruição, principalmente com relação ao diâmetro das perfurações circulares e as intercomunicações entre elas. Essas semelhanças e os dados do registro fóssil permitem sugerir que as perfurações e as galerias foram realizadas por larvas de coleópteros, provavelmente após a morte do vegetal. Além disso, em madeiras atuais, as galerias ocasionadas pela atividade de invertebrados (larvas de insetos e moluscos) são rapidamente colonizadas por fungos e bactérias que intensificam a destruição do lenho. Segundo KIM & SINGH (2000), em ambientes úmidos, as bactérias são mais tolerantes às condições anóxicas ou com pouco oxigênio. O padrão de decomposição da madeira por bactérias é diferente do padrão ocasionado por fungos. As bactérias atacam principalmente os elementos não lignificados da madeira e podem ser reconhecidas três diferentes formas de decomposição das paredes celulares: túneis tortuosos, erosão produzindo valas e cavidades que ocorrem na direção perpendicular ao eixo longitudinal da célula. Para os autores, a degradação por fungos é o resultado da ação de alguns ascomicetos, deuteromicetos e basidiomicetos. Os ascomicetos e deuteromicetos causam a podridão branda, mais comum em solos e, às vezes, associada com a degradação por bactérias. Já sob condições de oxigênio reduzido, a madeira pode ser atacada e degradada por fungos basidiomicetos e bactérias, causadores da podridão branca e da podridão parda. Na podridão branca ocorre a degradação e a corrosão dos componentes das paredes celulares. No segundo tipo, a celulose é rapidamente despolimerizada e, embora a parede fique muito porosa, a forma original da célula é mantida.

STUBBLEFIELD & TAYLOR (1986), ao estudarem amostras de caules de *Araucarioxylon* Kraus, 1870 e *Vertebraria* (Royle) Schopf, 1965 do Permiano da Antártica, sugeriram seu ataque por fungos. As regiões atacadas do lenho ficaram mais claras em comparação com as células adjacentes, refletindo uma redução da quantidade de matéria orgânica na parede de algumas células. Os autores observaram que nas margens das escavações, as células estavam parcialmente degradadas e as paredes das células do tecido lenhoso de regiões próximas foram modificadas.

A colonização por fungos e provavelmente bactérias ocorreu no lenho fóssil estudado, pois algumas regiões com tecido lenhoso destruído indicam um padrão semelhante ao encontrado em lenhos com áreas de podridão. As hifas de fungos foram observadas na periferia das galerias e teriam penetrado no tecido lenhoso após a sua formação. A decomposição por fungos e a degradação por bactérias dos constituintes das paredes celulares do lenho alteraram a morfologia original de muitas perfurações e as dimensões de algumas galerias.

Os processos relacionados com a diagênese de um lenho resultam na preservação ou destruição do tecido lenhoso. As células ao redor das perfurações no caule estudado estão preservadas e indicam que não ocorreram mudanças morfológicas significativas durante os processos diagenéticos. As fraturas radiais, tangenciais e oblíquas sugerem o ressecamento do tecido lenhoso após a formação das galerias. Estas fraturas estão preenchidas por minerais similares aos que ocorrem nas galerias.

A preservação do tecido lenhoso, muitas vezes, ocorre da superfície da parede, onde a sílica precipita, para o interior da célula (LEO & BARGHOORN, 1976). Assim, em grandes espaços (SCURFIELD & SEGNET, 1984) ou em estruturas celulares grandes, como um elemento de vaso (BOLZON & OLIVEIRA, 2000), os minerais precipitam em bandas.

No material estudado, a atividade biológica ocorreu antes do sepultamento final. A análise da mineralogia permitiu inferir que as perfurações e as galerias estavam vazias no início do processo de silicificação do lenho, pois durante a fossildiagênese, a precipitação da sílica, que iniciou provavelmente após o sepultamento, ocorreu da borda para o centro formando anéis concêntricos.

CONCLUSÃO

Um grande número de indícios de atividade de perfuração foi identificado em regiões do tecido lenhoso de um fragmento de caule proveniente de níveis do Permiano, provavelmente produzidas por insetos. No início do processo de silicificação estas perfurações e galerias estavam vazias, e posteriormente, com a precipitação da sílica, formaram-se estruturas com bandas concêntricas. Associada à ação dos insetos, ocorreu a degradação por fungos e bactérias.

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DUAS NOVAS ICNOESPÉCIES DE *BIFUNGITES* DESIO, 1940
NA FORMAÇÃO PIMENTEIRA,
DEVONIANO DA BACIA DO PARNAÍBA, BRASIL ¹

(Com 5 figuras)

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RESUMO: Este trabalho descreve duas novas icnoespécies, *Bifungites munizi* isp.nov. e *Bifungites piauiensis* isp.nov., para os arenitos da Formação Pimenteira (Devoniano, Bacia do Parnaíba), no Estado do Piauí, Brasil. *Bifungites munizi* isp.nov. caracteriza-se por apresentar, em um mesmo exemplar, dois corpos terminais de morfologias diferentes, um maior, reniforme ou em forma de âncora e outro menor de formato globóide, circular, ambos interligados por um eixo central retilíneo de seção semi-cilíndrica. *Bifungites piauiensis* isp.nov. caracteriza-se pela presença de um eixo basal retilíneo, subcilíndrico, prolongando-se em extremidades em forma de setas cujas bases apresentam projeções para trás com ângulos de 10° a 35°. As duas novas icnoespécies apresentam características morfológicas e dimensões que as diferenciam das demais formas conhecidas na literatura, acrescentando dois novos icnotaxa às duas icnoespécies de *Bifungites* já formalizadas para o Devoniano no Brasil.

Palavras-chave: Icnologia, Formação Pimenteira, Devoniano, Bacia do Parnaíba, *Bifungites*.

ABSTRACT: Two new ichnospecies of *Bifungites* Desio, 1940 from the Pimenteira Formation, Devonian of Parnaíba Basin, Brazil.

This paper describes two new ichnospecies, *Bifungites munizi* isp.nov. and *Bifungites piauiensis* isp.nov., that occur in sandstones of the Pimenteira Formation (Devonian, Parnaíba Basin), in the Piauí State, Brazil. *Bifungites munizi* isp.nov. is morphologically characterized by different terminations, one of which is reniform and the other is dumbbell-like. *Bifungites piauiensis* isp.nov. shows a horizontal, straight and subcircular shaft, with double arrow-shaped terminations which bases have projections with angles of 10° to 35°. The morphological characteristics and dimensions of the two new ichnospecies allow their differentiation from other ichnospecies of *Bifungites*, resulting in two new ichnotaxa of this ichnogenus in the Brazilian Devonian.

Key words: Ichnology, Pimenteira Formation, Devonian, Parnaíba Basin, *Bifungites*.

INTRODUÇÃO

A Bacia do Parnaíba localiza-se principalmente na região Nordeste, abrangendo uma área com cerca de 600.000km² e ocupando parte dos estados do Piauí, Maranhão, Tocantins, Pará, Ceará, Bahia e Goiás. Também conhecida como Bacia do Maranhão é, sobretudo, uma bacia paleozóica, embora depósitos mesozóicos e cenozóicos pouco espessos cubram grandes

áreas de sua extensão. A Bacia do Parnaíba desenvolveu-se diretamente sobre um substrato composto principalmente por rochas metamórficas oriundas de processos tectonomagmáticos não mais antigos que o Mesoproterozóico, sobre os quais se superpõem *grabens* (GÓES & FEIJÓ, 1994) preenchidos no Neoproterozóico (Formação Riachão) e no Cambriano-Ordoviciano (Formação Mirador). Segundo GÓES & FEIJÓ (1994), a coluna

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sedimentar foi subdividida em cinco seqüências depositadas do Siluriano ao Cretáceo, com uma sedimentação predominantemente siliciclástica, ocorrendo subordinadamente calcário, anidrita e sílex, além de diabásio e basalto, representativos de eventos magmáticos do Neotriássico ao Eocretáceo. As cinco seqüências deposicionais são: (i) Seqüência Siluriana (Grupo Serra Grande), (ii) Seqüência Devoniana (Grupo Canindé), (iii) Seqüência Carbonífero-triássica (Grupo Balsas), (iv) Seqüência Jurássica (Grupo Mearim) e (v) Seqüência Cretácea (formações Grajaú, Codó, Corda e Itapecuru). Na Seqüência Devoniana, o Grupo Canindé é constituído pelas formações Itaim, Pimenteira, Cabeças e Poti, sendo representativo da maior ingressão marinha na Bacia do Parnaíba, com o término da sedimentação atribuído ao soerguimento provocado pelos reflexos de uma Orogenia Eo-herciniana. Os icnofósseis estudados procedem de um afloramento da Formação Pimenteira, a qual é composta por espessas camadas de folhelhos cinza-escuros a pretos, depositadas em um paleoambiente nerítico dominado por tempestades as quais depositaram camadas de arenito muito fino, durante o Givetiano-Frasniano (*q.v.* DELLA FÁVERA, 1990).

A Formação Pimenteira tem revelado um conteúdo icnofossilífero bastante significativo, auxiliando em seus estudos estratigráficos e de interpretação paleoambiental. Em seus estratos, até o presente, foram identificados os icnogêneros *Arenicolites*, *Asteriacites*, *Asterosoma*, *Bifungites*, *Chondrites*, *Cruziana*, *Cylindrichnus*, *Diplichnites*, *Diplocraterion*, *Helminthopsis*, *Lophochtenium*, *Isopodichnus*, *Macaronichnus*, *Merostomichnites*, *Neoskolithos*, *Nereites*, *Palaeohelminthoidea*, *Palaeophycus*, *Phycosiphon*, *Planolites*, *Rhizocorallium*, *Rosselia*, *Rusophycus*, *Scolicia*, *Skolithos*, *Spirophyton*, *Subphyllocorda*, *Teichichnus* e *Zoophycos*, como resultado dos estudos de AGOSTINHO (2001), AGOSTINHO & VALENÇA (1999), AGOSTINHO, CORRÊA & FERNANDES (2003), AGOSTINHO, VIANA & FERNANDES (2003), AGOSTINHO *et al.* (2001), ASSIS & FERNANDES (1980), BRITO (1977), CAMPANHA (1974), CAMPELO & VIANA (2003), FERNANDES, AGOSTINHO & VIANA (2003), FERREIRA & FERNANDES (1983), FONSECA & MELO (1987), KEGEL (1961, 1966), MUNIZ (1988), NASCIMENTO *et al.* (2003), RODRIGUES

(2001), SILVA (1999), YOUNG & BORGHI (2003) e YOUNG, BORGHI & FERNANDES (2002), em grande parte sintetizados por FERNANDES *et al.* (2002). Destes autores, somente ASSIS & FERNANDES (1980), FERNANDES, AGOSTINHO & VIANA (2003) e SILVA (1999) procederam a estudos mais detalhados das ocorrências do icnogênero *Bifungites*.

Os icnofósseis descritos neste trabalho são procedentes de duas localidades situadas no Estado do Piauí (Figs.1-3) e encontram-se depositados na coleção de macrofósseis do Departamento de Geologia do Centro de Tecnologia e Geociências (DG-CTG) da Universidade Federal de Pernambuco (UFPE).

SISTEMÁTICA

ICNOGÊNERO *Bifungites* Desio, 1940

ICNOESPÉCIE-TIPO – *Bifungites fezzanensis* Desio, 1940 por monotipia.

DIAGNÓSE – Escavações com tubos verticais em forma de π invertido, com as estruturas da base geralmente preservadas em epi-relevo convexo (positivo) em forma de halteres e com dois corpos terminais, globulares a triangulares (em seta), interligados por um eixo central (HÄNTZSCHEL, 1975).

OBSERVAÇÕES: *Bifungites* foi originalmente reconhecido por DESIO (1940) como um novo tipo de icnofóssil em forma de halteres presente em rochas da Líbia, sendo em seguida interpretado como moldes de aberturas de tubos em forma de U de *Rhizocorallium* (DUBOIS & LESSERTISSEUR, 1964) ou de *Corophioides* (OSGOOD, 1970) e, posteriormente, registrado em associação a tubos em U sem *spreiten* (GUTSCHICK, SUTTNER & SWITEK, 1962; RODRIGUEZ & GUTSCHICK, 1970). Sua caracterização como tubos duplos verticais em forma de π invertido, sem *spreiten*, terminando na base em câmaras ou expansões saculiformes ligadas entre si por um tubo horizontal, foi defendida por GUTSCHICK & LAMBORN (1975), classificando etologicamente *Bifungites* como icnito de habitação (*Domichnia*), gerado por organismos sedentários de corpo mole, suspensívoros, como anelídeos ou artrópodes. Posteriormente, FILLION & PICKERILL (1984), ao analisarem exemplares do icnogênero *Arthraria*

procedentes de Newfoundland, Canadá, teceram comentários a respeito da distinção entre este último icnogênero, *Diplocraterion* e *Bifungites*, face às suas semelhanças; ressaltaram ainda o fato de autores como OSGOOD (1970) e SEILACHER (1955) terem interpretado, respectivamente, *Bifungites* como a base de um tubo em U dotado

de *spreiten* ou uma escavação do mesmo tipo truncada, e de outros autores, como os já citados anteriormente, como escavações em forma de π invertido, sem *spreiten*. De acordo com FILLION & PICKERILL (1984), considerando esta última interpretação e o fato da presença ou ausência de *spreiten* ser uma característica significativa na

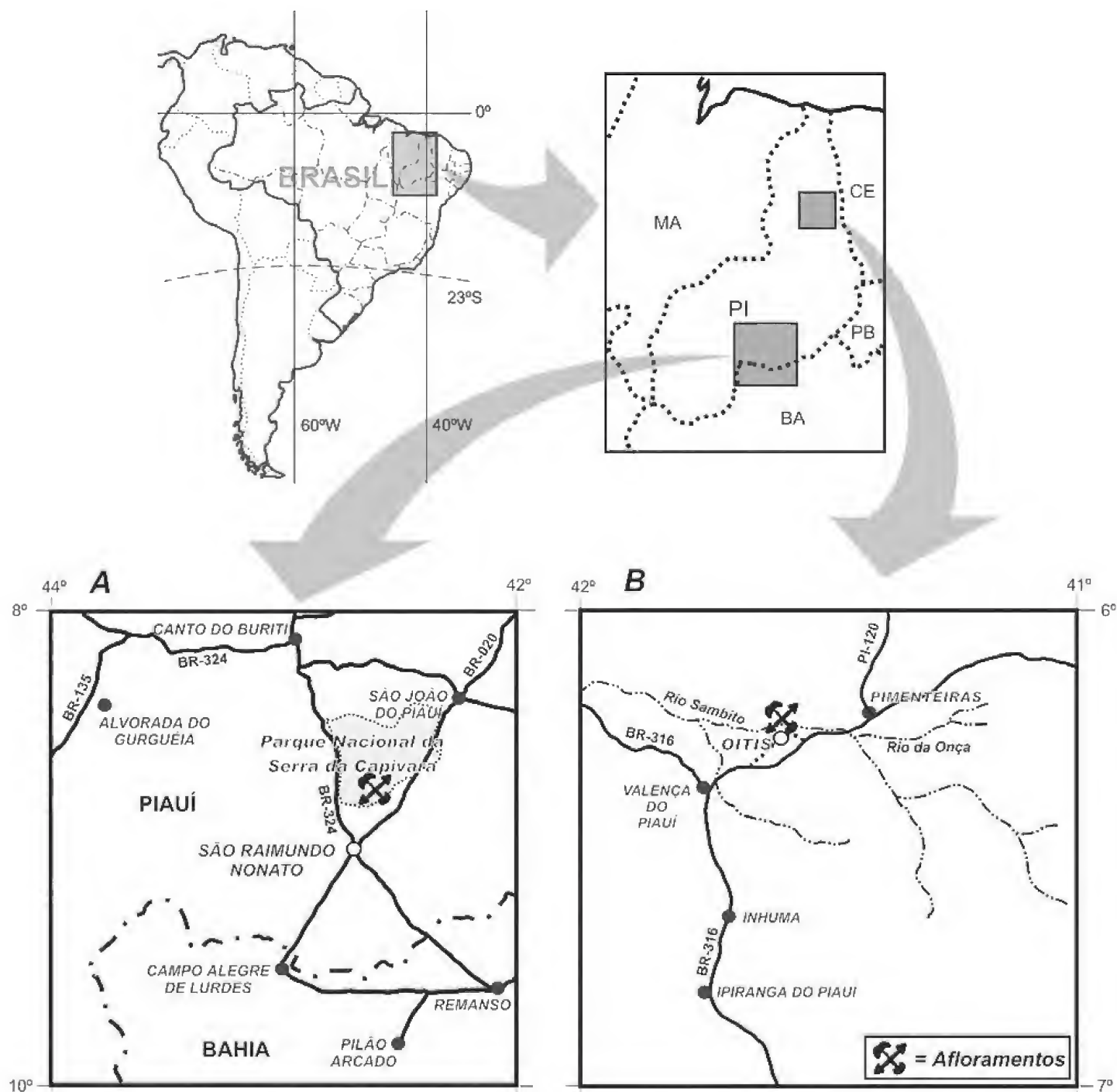


Fig. 1- (A) localização do afloramento de São João Vermelho, no Município de São Raimundo Nonato e (B) dos afloramentos situados nas margens do rio Sambito, Município de Pimenteiras, Estado do Piauí.



Fig.2- (A) vista geral do afloramento em São João Vermelho, com destaque em primeiro plano para o nível arenítico superior onde se encontram os exemplares de *Bifungites munizi* isp.nov.; (B) vista geral das exposições de arenitos da Formação Pimenteira nas margens do rio Sambito, próximo à localidade de Oiti.

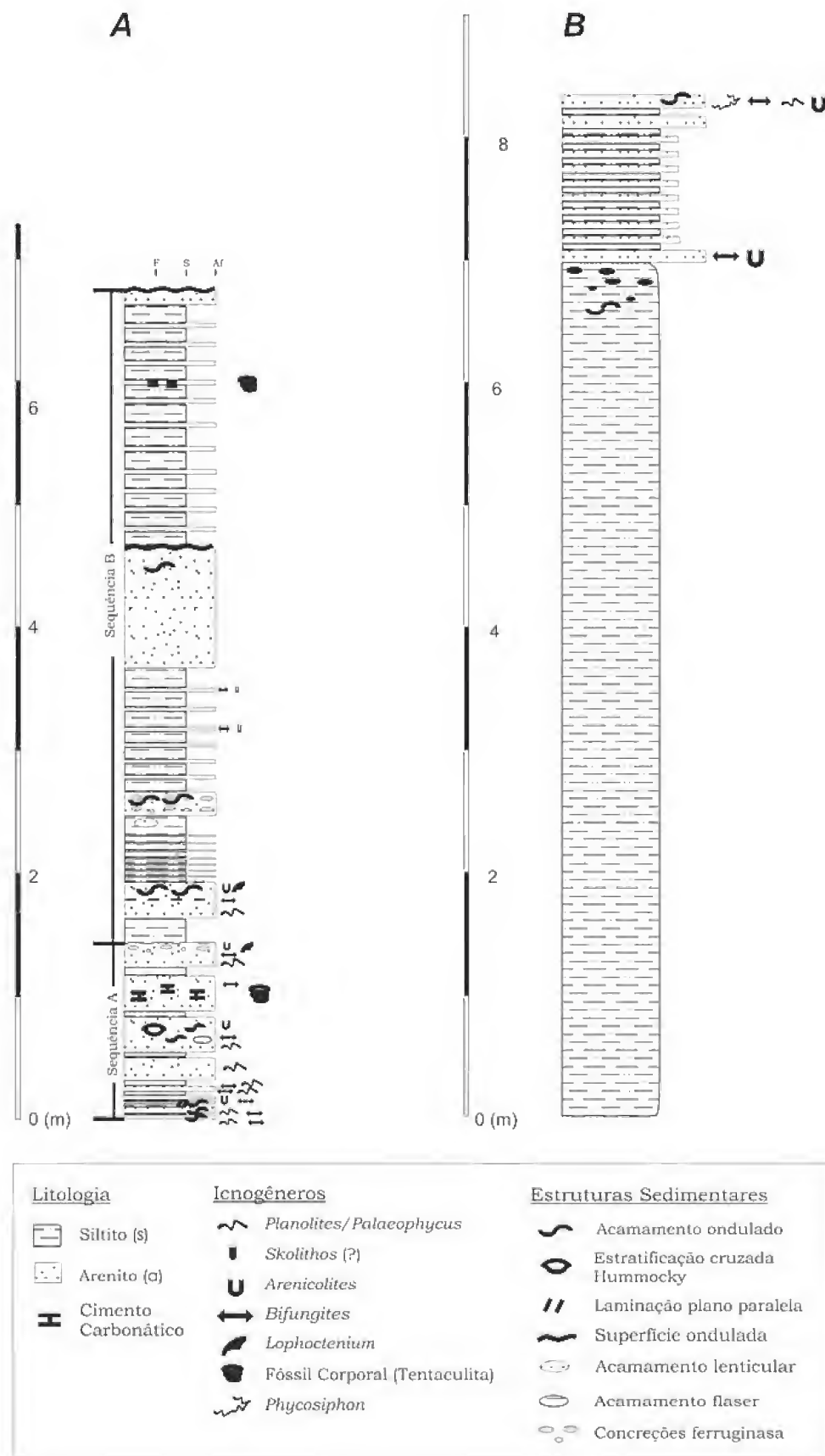


Fig.3- (A) seção estratigráfica do afloramento de São João Vermelho e (B) do afloramento no rio Sambito, próximo à localidade de Oiti.

classificação icnogênica, *Bifungites* não deve ser colocado como um sinônimo júnior de *Diplocraterion*. Caso se comprovasse a presença de tubos verticais no material-tipo de *Bifungites* (ressalta-se que o material-tipo se perdeu durante a Segunda Guerra Mundial), este seria considerado mais bem como um sinônimo júnior de *Arthriaria*. Caso os exemplares previamente atribuídos a *Bifungites* possuam tubos verticais sem *spreiten* entre si, estes deveriam ser renomeados como um icnogênero novo e distinto. Até que tal material se torne disponível para análise, FILLION & PICKERILL (1984) consideram as escavações em U ou em π invertido, sem *spreiten* entre os tubos, como *Bifungites*. Este icnogênero ocorre na icnofácies *Cruziana* e distribui-se do Cambriano Inferior ao Carbonífero (TURNER & BENTON, 1983). No Brasil, *Bifungites* foi registrado por NETTO (2000) para a Formação Santa Bárbara (pré-cambriana, da Bacia de Camaquã), mas cuja identificação foi equivocada, segundo comunicação pessoal de Renata Guimarães Netto (UNISINOS); para as formações Inajá (devoniana, da Bacia de Jatobá; MUNIZ, 1976, 1979), Ponta Grossa (devoniana; FERNANDES, 1996, 2001; FERNANDES & MELO, 1985), Rio Bonito/Palermo e Rio do Sul (permianas; BALISTIERI & NETTO, 2001; BALISTIERI, NETTO & WEINSCHUTZ, 2001), que posteriormente revelou-se tratar de exemplares de *Diplocraterion*, de acordo com comunicação pessoal de Renata Guimarães Netto, da Bacia do Paraná; e nas formações Pimenteira (AGOSTINHO & VALENÇA, 1999; AGOSTINHO, CORRÊA & FERNANDES, 2003; AGOSTINHO, VIANA & FERNANDES, 2003; ASSIS & FERNANDES, 1980; CAMPELO & VIANA, 2003; FERNANDES, AGOSTINHO & VIANA, 2003; FERREIRA & FERNANDES, 1983; SILVA, 1999) e Longá (MUNIZ, 1982), ambas devonianas, da Bacia do Parnaíba. Entre os espécimens estudados, entretanto, foram reconhecidas formalmente somente duas icnoespécies: *B. cruciformes* Muniz, 1982 e *B. paranaensis* Fernandes & Melo, 1985, ficando os demais registros referenciados como *Bifungites* isp.

Bifungites munizi isp.nov.
(Fig.4a-d)

Holotypus – DG-CTG-UFPE 5.689.

Paratypi – DG-CTG-UFPE 5.690 e 5.691.

Locus typicus – Os três exemplares foram coletados em afloramento localizado nos arredores do povoado de São João Vermelho (coordenadas

08°34'57"S e 42°26'55,2"W), no Município de São Raimundo Nonato, na área compreendida pelo Parque Nacional da Serra da Capivara (Fig.1a). O acesso à cidade de São Raimundo Nonato pode ser feito pelas rodovias BR-020 (que liga São Raimundo Nonato a Coronel José Dias e São João do Piauí) e BR-324 (também PI-140, que liga São Raimundo Nonato a Canto do Buriti); a localidade de São João Vermelho situa-se a 26km de Coronel José Dias, percorrendo-se 8 km a partir desta cidade pela BR-020 até a guarita 020, também conhecida como guarita do desfiladeiro e, a partir dela, em estrada de terra por 18km até o afloramento próximo ao povoado. O afloramento (Fig.2a) encontra-se representado por uma seqüência de arenitos silticos laminados e arenitos finos intercalados, apresentando marcas de onda de crista reta e laminação sub-horizontal (Fig.3a). Nos arenitos, além dos exemplares de *Bifungites munizi* isp.nov., são observadas outras formas de *Bifungites*, além de prováveis espécimens de *Phycosiphon incertum* von Fischer-Ooster, 1858 e amostras com exemplares que podem ser atribuídos aos icnogêneros *Arenicolites*, *Lockeia* e *Palaeophycus/Planolites*.

Stratum typicum – Arenitos finos a silticos finamente laminados da Formação Pimenteira.

Derivatio nomini – Em homenagem a Geraldo da Costa Barros Muniz, professor da Universidade Federal de Pernambuco que se dedicou ao estudo dos icnofósseis das bacias do Nordeste brasileiro.

Diagnosis – Um corpo terminal maior em forma de âncora em uma das extremidades e outro menor de contorno circular na extremidade oposta, interligados por um eixo central retilíneo de seção semi-cilíndrica.

Diagnosis – *Burrows preserved as convex epireliefs (epichnia) with a horizontal, straight, and subcircular shaft between two different terminations, the bigger one being reniform-like and the other, smaller in size, is dumbbell-like.*

Descrição – Exemplares completos preservados em hiporrelevo convexo, representados pelos corpos terminais e pelo eixo central. Os corpos terminais apresentam diferenças morfológicas e de dimensões entre si, sendo o maior em forma de âncora e, o menor, de contorno circular. O eixo central é retilíneo, subcilíndrico, sem variação de largura ao longo de seu comprimento. As dimensões em milímetros como comprimento total (C), comprimento do eixo central (c), diâmetro do eixo (d), distância entre as extremidades do corpo

terminal em forma de âncora (D1), distância entre as extremidades do corpo terminal de contorno circular (D2), comprimento do corpo terminal em forma de âncora (cct1) e de contorno circular (cct2), e as relações C/c, D1/d e D2/d, do holótipo e dos parátipos encontram-se relacionadas na tabela 1. Não foram observadas marcas de inserções dos tubos verticais nos corpos terminais.

Discussão – Os exemplares de *Bifungites munizi* isp.nov. apresentam morfologia e dimensões acentuadamente diferentes dos demais exemplares de *Bifungites* presentes no mesmo afloramento, bem como das icnoespécies de *Bifungites* já descritas em formações brasileiras. No primeiro caso, os exemplares associados apresentam corpos terminais triangulares ou em forma de seta, ou com contorno arredondado (Fig.4a), identificados como *Bifungites* isp. O exemplar de *Bifungites* isp., descrito por ASSIS & FERNANDES (1980) da Formação Pimenteira, do Estado de Goiás, é uma forma de dimensões menores, apresentando C/c = 1,55 e D/d = 1,75 e possuindo terminações cuja morfologia, em virtude da sua má preservação, varia de globular a triangular. *Bifungites munizi* isp.nov. difere também de *B. piauiensis* isp.nov. por esta última icnoespécie apresentar corpos terminais bem definidos em forma de seta, os quais possuem ainda algumas variações em sua forma e também com índices em grande parte com dimensões menores. Por outro lado, um confronto descritivo entre *B. munizi* isp.nov. e *B. paranaensis* permite também diferenciá-los pelo fato de *B. paranaensis* possuir corpos terminais bem definidos em forma de seta, os quais apresentam uma base plana, embora suas relações C/c e D/d aproximem-se de *B. munizi* isp.nov. *Bifungites cruciformis*, outra icnoespécie devoniana, mas descrita para a Formação Longá, difere por sua vez de *B. munizi* isp.nov. por apresentar terminações tipicamente em forma de

cruz em ambas extremidades, que possuem eixo e braços subcilíndricos e de contorno subarredondado. É preciso ressaltar que a icnoespécie ora proposta possui variação de forma nos corpos terminais em um mesmo exemplar (um em forma de âncora ou reniforme e outro subesférico), variação que não é observada em nenhuma das icnoespécies citadas acima. Exemplares portadores de terminações reniformes também são conhecidos na literatura estrangeira. OSGOOD (1970) atribuiu os exemplares do Ordoviciano Superior de Cincinnati (Estados Unidos) à icnoespécie *Corophioides biclavata* (Miller, 1875) e MÉLOU & PLUSQUELLEC (1975) descreveram espécimens do Ordoviciano Superior da França como *?Bifungites* isp. Os exemplares descritos por OSGOOD (1970), entretanto, possuem as terminações semelhantes, mais aproximadas à forma de halteres, sendo assim definidas pelo autor e o eixo central acentuadamente mais estreito ou de menor diâmetro que os exemplares de *B. munizi* isp.nov.; por outro lado, os exemplares descritos por MÉLOU & PLUSQUELLEC (1975), apesar de apresentarem corpos terminais morfologicamente diferentes entre si, possuem as terminações reniformes com contornos menos circulares com projeções laterais mais acentuadas, diferindo significativamente da forma apresentada pelas terminações reniformes de *B. munizi* isp.nov. SEILACHER (1983) atribuiu ambas as ocorrências à icnoespécie *Bifungites biclavatus* (Miller, 1875), assinalando que as formas com terminações reniformes seriam características do Ordoviciano Superior, enquanto que as dotadas de terminações em forma de seta, identificadas como *B. fezzanensis* Desio, 1940, seriam características do Devoniano, estendendo-se ao Carbonífero. A ocorrência de *B. munizi* isp.nov. em São João Vermelho (PI), portanto, estende a distribuição estratigráfica das formas dotadas de terminações reniformes ao Devoniano Médio.

Tabela 1. Dimensões (mm) dos exemplares de *Bifungites munizi* isp.nov.

EXEMPLARES	C	c	d	D1	D2	cct1	cct2	C/c	D1/d	D2/d
Holótipo										
DG-CTG-UFPE 5.689	35,85	18,92	6,95	19,77	15,23	7,97	9,55	1,89	2,84	2,19
Parátipos										
DG-CTG-UFPE 5.690	34,74	18,65	5,35	18,87	12,78	7,18	7,82	1,86	3,52	2,38
DG-CTG-UFPE 5.691	30,16	15,80	5,89	18,67	14,10	8,54	6,72	1,90	2,83	2,39

(C) comprimento total; (c) comprimento do eixo; (d) diâmetro do eixo; (D1) distância entre as extremidades do corpo terminal em forma de âncora; (D2) distância entre as extremidades do corpo terminal em forma de halteres; (cct1) comprimento do corpo terminal em forma de âncora; (cct2) comprimento do corpo terminal em forma de halteres. Índices de relações: C/c, D1/d e D2/d.

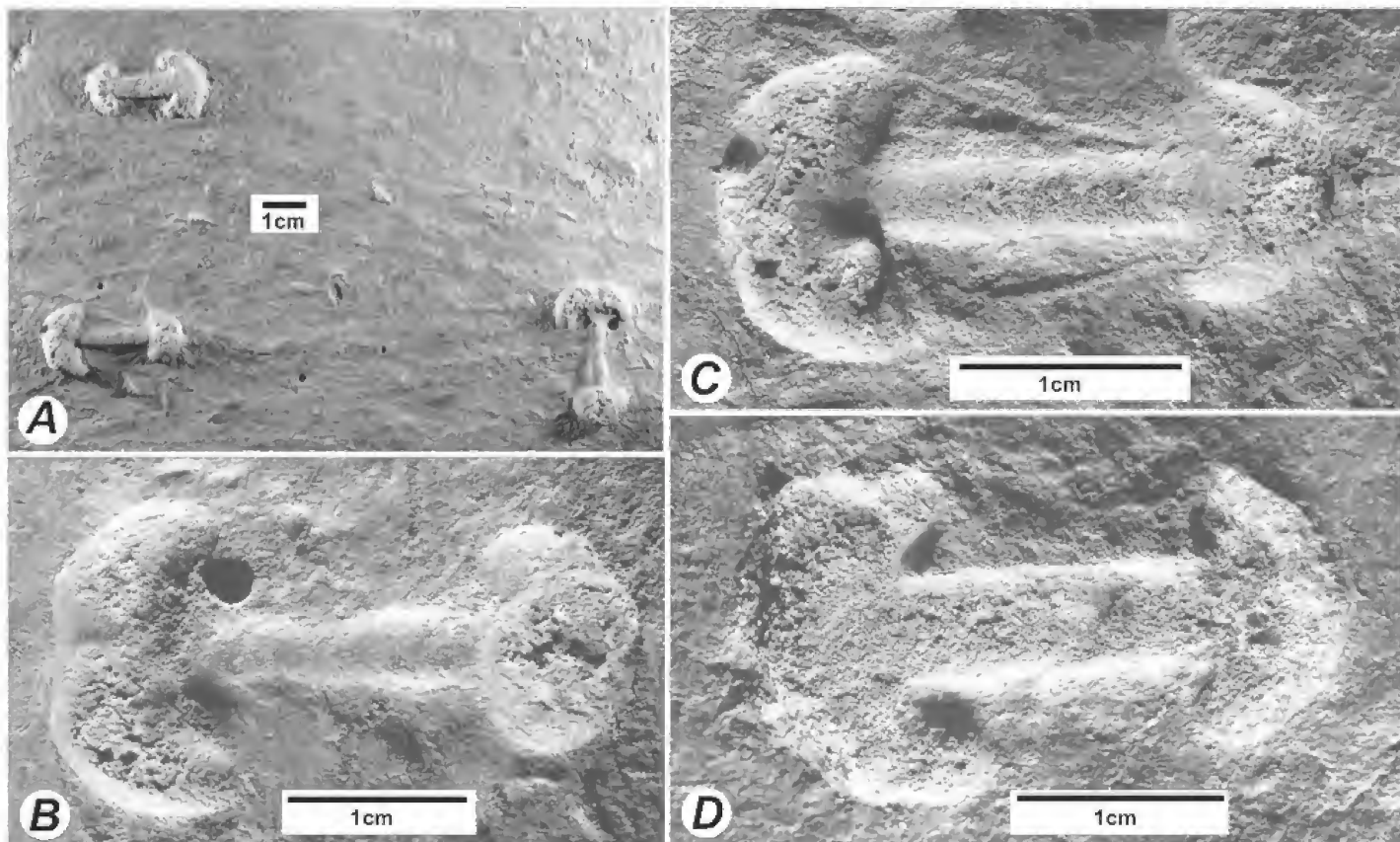


Fig.4- *Bifungites munizi* isp.nov.: (A) aspecto geral da amostra com os três exemplares estudados; (B) holótipo, exemplar DG-CTG-UFPE 5.689; (C) parátipo, exemplar DG-CTG-UFPE 5.690; (D) parátipo, exemplar DG-CTG-UFPE 5.691.

Bifungites piauiensis isp.nov.
(Fig.5a-c)

Holotypus – DG-CTG-UFPE 5.654.

Paratypi – DG-CTG-UFPE 5.647, 5.664, 5.665 e 5.652.

Locus typicus – Os exemplares foram coletados nos afloramentos situados na localidade de Oiti, Município de Pimenteiras, com as coordenadas de 06° 16'S e 41° 35'W (Fig.1b). Nessa localidade, um meandro do rio Sambito forma uma cachoeira com cerca de 200m de extensão em rochas da Formação Pimenteira (Fig.2b), as quais estão representadas por arenitos finos a silticos que se intercalam (Fig.3b) e exibem um rico conteúdo icnofossilífero. No afloramento foram também observados exemplares de *Asteriacites stelliforme* (Miller & Dyer, 1878), *Diplichnites* isp., ?*Granularia* isp., *Lophoctenium* isp., *Palaeophycus tubularis* Hall, 1847, *Planolites beverleyensis* (Bilings, 1862) e *Scolicia* isp., além de tentaculítídeos (AGOSTINHO & VIANA, 2001; CAMPELO & VIANA, 2003; SILVA, 1999).

Stratum typicum – Arenitos finos a silticos, finamente laminados, da Formação Pimenteira.

Designatio nominis – Em virtude de ser procedente do Estado do Piauí.

Diagnosis – Escavações preservadas em epirrelevo convexo (*epichnia*) com eixo central retilíneo, aparentemente subcilíndrico, com corpos terminais em forma de setas, cujas bases apresentam projeções para trás com ângulos de 10° a 35°.

Diagnosis – *Burrows preserved as convex epireliefs (epichnia) with a horizontal, straight, and subcircular shaft, with double arrow-shaped terminations, which bases have projections with angles of 10° to 35°.*

Descrição – Normalmente preservados como epirrelevos convexos (*epichnia*), dos cinco espécimes completos mensurados (Tab.2), quatro deles apresentaram comprimento compreendido entre 60mm e 73mm, e o restante medindo 40mm. Os corpos terminais apresentam-se freqüentemente em forma de seta. Ainda nos mesmos cinco

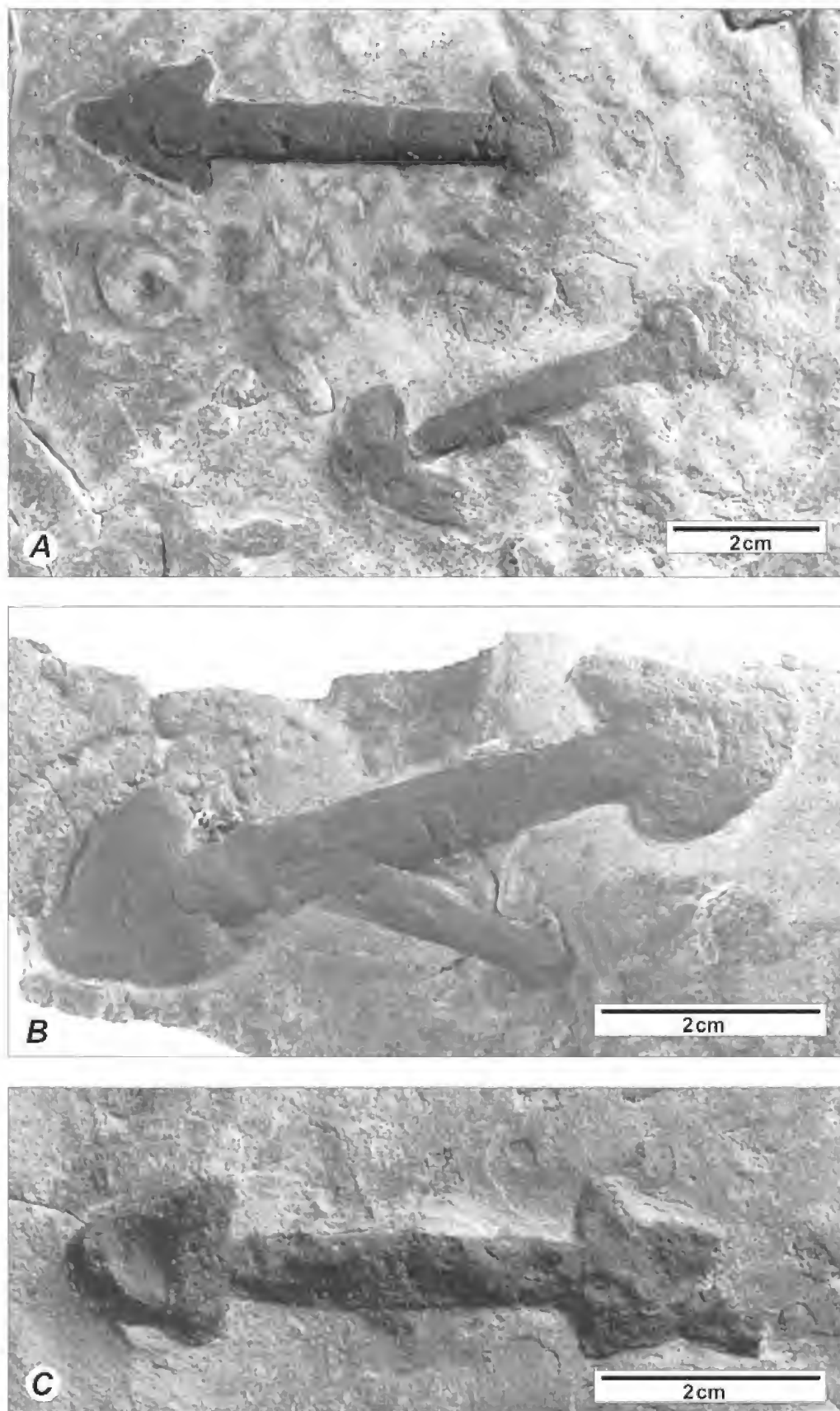


Fig.5- *Bifungites piuiensis* isp.nov.: (A) holótipo (exemplar superior) e parátipo (exemplar inferior), amostra DG-CTG-UFPE 5.654; (B), parátipo, amostra DG-CTG-UFPE 5.647; (C) parátipo, amostra DG-CTG-UFPE 5.664.

exemplares medidos os valores do índice C/c oscilaram no pequeno intervalo de 1,78 e 1,94, enquanto que D/d também oscilou no reduzido intervalo de 2,14 a 2,33.

Discussão – Dentre as formas de *Bifungites* registradas e descritas para as bacias sedimentares brasileiras, *Bifungites* isp., exemplar referenciado por ASSIS & FERNANDES (1980) para a Formação Pimenteira no Estado de Goiás, é uma forma de dimensões menores e com índices dimensionais diferentes representados por C/c = 1,55 e D/d = 1,75. Um confronto descritivo entre *B. piauiensis* isp.nov. e *B. paranaensis*, permite verificar que a icnoespécie ora proposta possui variação de forma em seta dos corpos terminais, bem como intervalo de variação do índice D/d, medido em cinco espécimes, significativamente maior que o índice D/d que caracteriza *B. paranaensis*, igual a 2,80. Por outro lado, as terminações tipicamente em cruz da icnoespécie *B. cruciformis* da Formação Longá, fazem-na também divergir morfológicamente do material agora focalizado. A comparação de *B. piauiensis* isp.nov. com as três icnoespécies (*B. bisagittula*, *B. bisagitta* e *B. bieurysagitta*) propostas por GUTSCHICK & LAMBORN (1975) para o Devoniano Superior-Mississipiano inferior dos Estados Unidos, e *B. fezzanensis*, registrado para o Devoniano Superior (DESIO, 1940; DUBOIS & LESSERTISSEUR, 1964) e Paleozóico superior do norte da África (SEILACHER, 1983) mostra que essas icnoespécies, embora também caracterizadas pela presença de corpos terminais em forma de seta, são claramente de dimensões menores. A icnoespécie *B. biclavatus*, registrada em rochas do Ordoviciano Superior da América do Norte (MILLER,

1875; OSGOOD, 1970) e da França (MÉLOU & PLUSQUELLEC, 1975), difere de *B. piauiensis* isp.nov. por apresentar corpos terminais reniformes. Cabe ressaltar que SILVA (1999) estudou a icnoespécie ora descrita, atribuindo-lhe uma designação que não é válida à luz do Código Internacional de Nomenclatura Zoológica (International Commission on Zoological Nomenclature) de 1985, para o qual documentos como teses não constituem publicações.

CONCLUSÕES

O presente trabalho descreve duas novas icnoespécies para a Formação Pimenteira, *Bifungites munizi* isp.nov. e *Bifungites piauiensis* isp.nov. Suas características morfológicas e dimensões permitiram diferenciá-las das demais formas conhecidas na literatura, acrescentando desse modo novos *ichnotaxa* às duas icnoespécies de *Bifungites* já conhecidas para o Devoniano no Brasil. Particularmente no caso de *Bifungites munizi* isp.nov., sua determinação vem auxiliar na distribuição estratigráfica das formas de *Bifungites* dotadas de terminações reniformes, estendendo-as ao Devoniano Médio.

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Tabela 2. Dimensões (mm) dos espécimes de *Bifungites piauiensis* isp.nov.

EXEMPLARES	C	c	d	D	C/c	D/d
Holótipo DG-CTG-UFPE 5.654	68,0	38,0	8,5	19,0	1,79	2,24
Parátipo DG-CTG-UFPE 5.647	73,0	38,0	8,0	18,5	1,92	2,31
Parátipo DG-CTG-UFPE 5.664	60,0	31,0	7,0	15,0	1,94	2,14
Parátipo DG-CTG-UFPE 5.665	41,0	23,0	4,5	10,5	1,78	2,33
Parátipo DG-CTG-UFPE 5.652	68,0	35,5	7,0	16,0	1,91	2,29

Foram calculadas as relações entre comprimento total (C) e comprimento do eixo basal (c), bem como entre a largura máxima dos corpos terminais (D) e largura do eixo basal (d). Índices de relações: C/c e D/d.

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A NEW ACTINOPTERYGIAN FISH
FROM THE LATE PERMIAN OF THE PARANÁ BASIN, SOUTHERN BRAZIL ¹
(With 5 figures)

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ABSTRACT: *Angatubichthys mendesi* gen. et sp. nov., an early actinopterygian fish from the Upper Permian of Paraná Basin (Corumbataí Formation), is described from four complete and articulated specimens preserved in a reddish siltstone obtained in an outcrop in Angatuba municipality, State of São Paulo. It is a small fish distinguished from the other palaeoniscoids by a combination of features: short and deep head; wrinkled median postrostral; nasal and dermosphenotic not in contact; suboperculum larger than operculum; conspicuous radiating ridges of ganoin on cleithrum and supracleithrum; longitudinal bands of ganoin on dentalosplenic; maxillary canal present; ethmoidal commissure on rostromaxilloantorbital; reduced number of branchiostegal rays; rows of deep smooth rhomboidal scales on flanks; and caudal fin heterocercal, deeply forked with almost equal-sized lobes. *Angatubichthys mendesi* gen. et sp. nov. appears to be more advanced than the so-called basal actinopterygians (*Cheirolepis*, *Mimia*, *Moythomasia*, *Polypterus*) due to various anatomical features (e.g., absence of pineal plate, presence of dermopterotic, deep scales on the flanks, presence of suborbitals, reduction of the number of branchiostegal rays, and reduced number of pectoral fin rays) but it wants synapomorphies of platysomid and neopterygian fishes.

Key words: *Angatubichthys mendesi* gen. et sp. nov., actinopterygian fish, Upper Permian, Paraná Basin.

RESUMO: Um novo peixe actinoptérgio do Neopermiano da Bacia do Paraná, Sul do Brasil

Angatubichthys mendesi gen. et sp. nov., um primitivo peixe actinoptérgio do Neopermiano da Bacia do Paraná (Formação Corumbataí), é descrito com base em quatro espécimes completos e articulados preservados em siltito avermelhado que aflora no município de Angatuba, Estado de São Paulo. Trata-se de um peixe de pequeno porte distinto de outros palaeoniscóides por uma combinação de caracteres: cabeça curta e alta; pós-rostral mediano de superfície enrugada; nasal e dermoesfenótico sem contato; subopérculo maior que o opérculo; conspicuas estrias radiantes de ganoína sobre o cleitro e supracleitro; faixas longitudinais de ganoína sobre o dentalo-esplênico; presença de comissura etmoideana e canal maxilar; número reduzido de raios de branquiostégios; fileiras de escamas rômbricas e lisas nos flancos; nadadeira caudal heterocerca profundamente bifurcada, com lobos de tamanho aproximadamente igual. *Angatubichthys mendesi* gen. et sp. nov. parece ser mais avançado que actinoptérgios basais (*Cheirolepis*, *Mimia*, *Moythomasia*, *Polypterus*) devido a presença de vários aspectos anatômicos (e.g., ausência de forame pineal, presença de dermopterótico, escamas altas nos flancos, presença de suborbitais, redução do número de raios de branquiostégios e número reduzido de raios da nadadeira peitoral), mas carece de sinapomorfias para platissomídeos e neoptérgios.

Palavras-chave: *Angatubichthys mendesi* gen. et sp. nov., peixe actinoptérgio, Neopermiano, Bacia do Paraná.

INTRODUCTION

The Brazilian Paleozoic paleoichthyofauna is relatively diversified but the record of well-preserved specimens is extremely meager (RICHTER, 1991; DIAS, 1995). Concerning the actinopterygian fishes, most of the specimens are represented by scales, bony fragments, and isolated teeth (e.g., RICHTER, 1985; MEZZALIRA, 1989).

Few studies were based on almost complete and articulated fishes (DUNKLE & SCHAEFFER, 1956; BELTAN, 1978; MALABARBA, 1988; RICHTER, 1991; SANTOS, 1991; DIAS, 1995; FIGUEIREDO, DIAS & COSTA-CARVALHO, 1998; VEGA, DIAS & RAGONHA, 1997; VEGA-DIAS, DIAS & RICHTER, 2000; and RICHTER, 2002) and most of these fossil material were obtained from the Brazilian portion of the Paraná Basin.

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SANTOS (1991) reported the occurrence of actinopterygian fishes for the Permian of the State of São Paulo. The material consists of a poorly preserved platysomid fish from the Tatuí Formation (see FIGUEIREDO, DIAS & COSTA-CARVALHO, 1998), and nearly complete palaeoniscoid fishes from the Corumbataí Formation. PETRI (2001) pointed out that the latter material is remarkable due to the quality of preservation and taxonomic novelty. Unfortunately, the late paleontologist Rubens da Silva Santos (1918-1996) passed away without formally describing it.

In this paper, we describe the ray-finned fish from the Corumbataí Formation originally reported by Silva Santos (SANTOS, 1991), comparing it with other South American taxa and briefly discussing its affinities.

GEOLOGICAL SETTING

The Paraná Basin is an extensive rock unit placed at the Central-Southeastern South America, covering part of the political territories of Brazil, Argentina, Uruguay, and Paraguay and encompassing an area of about 1,200,000km² (MILANI *et al.*, 1998). Sedimentation took place during the Paleozoic and Mesozoic, and the stratigraphic record ranges from the Late Ordovician to the Late Cretaceous (LAVINA, 1991).

The following stratigraphic groups are recognised in the Paraná Basin: Paraná (Devonian); Tubarão (Upper Carboniferous-Middle Permian); Passa Dois (Upper Permian); São Bento (Triassic-Jurassic); and Bauru (Jurassic-Cretaceous) (ALMEIDA & MELO, 1981; PETROBRAS, 1998).

SCHNEIDER *et al.* (1974) argued that the Passa Dois Group is composed in the southern Paraná Basin by the Irati, Serra Alta, Teresina, and Rio do Rasto formations, and in the States of São Paulo, Goiás, and Mato Grosso, by the Irati and Corumbataí formations.

In São Paulo, the Corumbataí Formation corresponds to the Serra Alta, Teresina, and Serrinha (in part) formations. It consists of mudstone, siltstone, and shale of dark grey colour in the basal portion and reddish in the top (SCHNEIDER *et al.*, 1974; ALMEIDA & MELO, 1981; MILANI, FRANÇA & SCHNEIDER, 1994).

The predominant climatic conditions during sediment deposition of the Corumbataí Formation were dry, with low rainfall, which gradually produced scattered water pools (RAGONHA,

1989a). The paleoenvironment was probably transitional from neritic to lacustrine (MILANI, FRANÇA & SCHNEIDER, 1994).

The fossil record of the Corumbataí Formation is rich in bryophytes, pteridophytes, gymnosperms, sponges, mollusks, crustaceans, reptiles, and fish remains (MENDES, 1952; FÚLFARO, 1970; MEZZALIRA, 1989). Regarding the latter, it is common to find stratigraphic levels with a considerable amount of disarticulated bones, dipnoan dental plates, petalodontid teeth, palaeoniscoid scales, xenacanthid and hybodontid remains, besides ctenacanthid spines and coelacanth teeth (RAGONHA, 1989b; TOLEDO, BRITO & BERTINI, 1997). At the moment, the palaeoniscoid fish *Tholonotus braziliensis* Dunkle & Schaeffer, 1956 is the only relatively complete and articulated vertebrate known from that formation (DUNKLE & SCHAEFFER, 1956).

MATERIAL AND METHODS

The fossil fish material herein studied consists of four specimens preserved in a reddish siltstone. All specimens are housed at the Paleozoological Collection of the Departamento de Biologia Animal e Vegetal of the Universidade do Estado do Rio de Janeiro and are referred in this paper by the abbreviation Pz.DBAV.UERJ followed by the catalogue number.

The specimens were mechanically prepared with sharp steel needles and consolidated with PARALOID 67 dissolved in ethyl acetate. Casts of the specimens were made using CAF 73 (a silicone rubber). The specimens and casts were coated with a smoke of ammonium chloride to enhance skeletal details for photographs. Observations were made using a binocular microscope Olympus SZ 40. Line drawings were made from magnified photographic prints.

The anatomical terminology mainly follows GARDINER & SCHAEFFER (1989). The scale series formula follows WESTOLL (1944): D/P, A, C1, C2, where, D is the number of scale series anterior to the origin of the dorsal fin; P, number of scales series anterior to the pelvic fin; A, number of scale series anterior to the anal fin; C1, number of scale series anterior to origin of the caudal peduncle and C2, the number of scale series anterior to the end of the epichordal lobe of the caudal fin.

As far as possible, problems concerning homologies are discussed along the text. The

proposed diagnosis is based on the unique combination of primitive and derived characters that, although not rigorously in accordance with cladistic principles, this allows the identification of individual taxa when autapomorphies are wanting (ARRATIA, 1997).

Anatomical Abbreviations – r and l are used before anatomical terms to indicate right and left side respectively. (ANG) angular; (APR) anterior postrostral; (AUP) pars autopalatina of palatoquadrate; (ba.s.) basal shield; (BBR) basibranchial; (BR.R) branchiostegal rays; (CH) ceratohyal; (CL) cleithrum; (CLA) clavicle; (DH) dermohyal; (DPAL) dermopalatine; (DPT) dermopterotic; (DSPH) dermosphenotic; (DSPL) dentalosplenic; (e.ps.a.) canal for efferent pseudobranchial artery; (ENPT) endopterygoid; (f.e.a.) fenestra exonarina anterior; (ep. f.) epaxial fulcra; (ethm.c.) ethmoidean commissure; (f.e.p.) fenestra exonarina posterior; (FR) frontal; (fr.f.) fringing fulcra; (HBR1) first hypobranchial; (HP) hypohyal; (iorb.s.c.) infraorbital sensory canal; (JU) jugal; (l.l.s.c.) lateral line sensory canal; (LA) lachrymal; (LEXS) lateral extrascapular; (LG) lateral gular; (md.s.c.) mandibular sensory canal; (MEXS) medial extrascapular; (MG) median gular; (MPR) median postrostral; (MX) maxilla; (mx.c.) maxillary canal; (NA) nasal; (OP) operculum; (p.pl.) posterior pit-line of parietal bone; (PA) parietal; (PAS) parasphenoid; (PO) postorbital; (POP) preoperculum; (pop.s.c.) preopercular sensory canal; (PSCL) presupracleithrum; (PT) post-temporal; (QJ) quadratojugal; (R+PMX+ANT) rostromaxilloantorbital; (S) symplectic; (SCL) supracleithrum; (scl.b.) sclerotic bone; (SO) suborbital; (SOP) suboperculum; (sorb.s.c.) supraorbital sensory canal; (st.c.) supratemporal commissure; (t) teeth; (t.c.) temporal sensory canal; (t.pl.) transverse pit-line of parietal bone; (v.pl.) vertical pit-line of quadratojugal.

SYSTEMATIC PALEONTOLOGY

Osteichthyes Huxley, 1880
Actinopterygii Woodward, 1891
Actinopteri Cope, 1871
Family indeterminate

Angatubichthys gen.nov.

Diagnosis – Fusiform palaeoniscoid fish of small size recognised by the following combination of features: head length contained about five times

in the maximum body length; short and obtuse snout; operculum smaller than suboperculum; broad and spatulate median postrostral, ornamented with delicate rugae on the anterior border; ethmoidean commissure included into the rostromaxilloantorbital; maxillary canal present; nasal separate from dermosphenotic; presence of dermopterotic; circumorbital ring including postorbital, jugal, lachrymal and two suborbitals; laniform teeth on the oral border of jaws; six branchiostegal rays; subequal medial and lateral extrascapular bones; suspensorium vertically inclined; post-temporal and cleithrum ornamented with conspicuous ridges; presupracleithrum present; dentalosplenic ornamented with fine longitudinal ridges; endopterygoid separated; pectoral fin twice as long as the pelvic fin; rows of smooth rhombic scales along the lateral side of the body, anteriormost ones three times as high as long; caudal fin heterocercal with almost equal-sized lobes; fin-rays closely articulated and fulcra are present along the leading edges of all fins.

Type-species – *Angatubichthys mendesi* sp.nov.

Etymology – A combination of the name of the type-locality (Angatuba) and the Greek word, *ichthys*, fish.

Angatubichthys mendesi sp.nov.
(Figs.1, 2a, 2b, 3-5)

Diagnosis – As for the genus (by monotypy).

Holotype – Pz.DBAV.UERJ 059, a complete specimen, 66mm maximum length (ML); Westoll Formula (WF): 26/11, 20, 39, 53.

Etymology – The specific epithet is in honor of the late Brazilian paleontologist Josué Camargo Mendes, from the Instituto de Geociências of the Universidade de São Paulo, Brazil, who collected the material.

Additional material – Pz.DBAV.UERJ 60, complete specimen, 93mm ML [WF: 27/11, 20, 41, 57]; Pz.DBAV.UERJ 61 a (part) and b (counterpart), incomplete specimen, 57,9mm estimated ML [WF: 27/12, 21, 38, 5]; Pz.DBAV.UERJ 58, complete specimen 37mm ML.

Horizon and type-locality – Upper third of the Corumbataí Formation; Upper Permian (Kazanian). The outcrop is located between kilometres 200 and 210 of the Raposo Tavares Highway (SP-270), about 6km south of the municipality of Angatuba, São Paulo State.

DESCRIPTION

Angatubichthys mendesi (Fig.1) reaches about 90mm of maximum length. The body is elegantly fusiform, laterally compressed and elongate, appearing to be subtrigonal in transverse section. The head is slightly longer than deep and the orbit is situated well forward. The cranium is brachycephalous and the dorsal profile is almost straight. The snout is obtuse, not projecting beyond the mouth opening. The dorsal fin is situated nearer to the caudal fin than to the head and its origin is approximately opposite to origin of the anal fin. The pelvic fin originates at about midway point between the pectoral and pelvic fin bases. The lateral line runs along the middle line of the body. There are 38 to 41 rows of rhombic and macromeric scales ahead of the hinge-line.

Most of the dermocranial bones have smooth surfaces, but show conspicuous growth lines apparently corresponding to concentric accretions of ganoin on the borders. Only rostromaxilloantorbital, median postrostral, dentalosplenic, and the bones of the pectoral girdle are ornamented conspicuously. The sensory canals are totally included in dermal bones and exit on the surface through minute pores.

The snout region is composed of the following bones: median postrostral, anterior postrostral, rostromaxilloantorbital, and nasal. The median postrostral (Figs.2b, 3-4; MPR) is a large spatulate bone forming most of the snout anterior to the orbit. This bone is long, about one third of head length. It lacks teeth and tubercles, but is ornamented with rugae on the anterior portion. In addition, there

are marked growth lines near the borders. The obtuse posterior border meets the frontals through an oblique and straight suture.

This bone meets the nasals laterally and the rostromaxilloantorbital anteroventrally. There is in its anterior third a lateral notch corresponding to the anterior limit of the fenestra exonarina anterior (Figs.2b, 3; f.e.a.).

In Pz.DBAV.UERJ 059 there is a small anamestic and reniform bone, slightly displaced from its anatomical position and lying anteriorly and below the median postrostral above the rostromaxilloantorbital. It was interpreted as an anterior postrostral (Fig.2b; APR). Probably this bone lies on a shallow depression between the anterior margins of the median postrostral and nasal. Its presence is not a regular feature in the specimens observed. This bone was observed by DUNKLE & SCHAEFFER (1956) in *Tholonotus braziliensis* and apparently corresponds to the lat-rostral of *Cheirolepis canadensis* Whiteaves, 1881 (see ARRATIA & CLOUTIER, 1996).

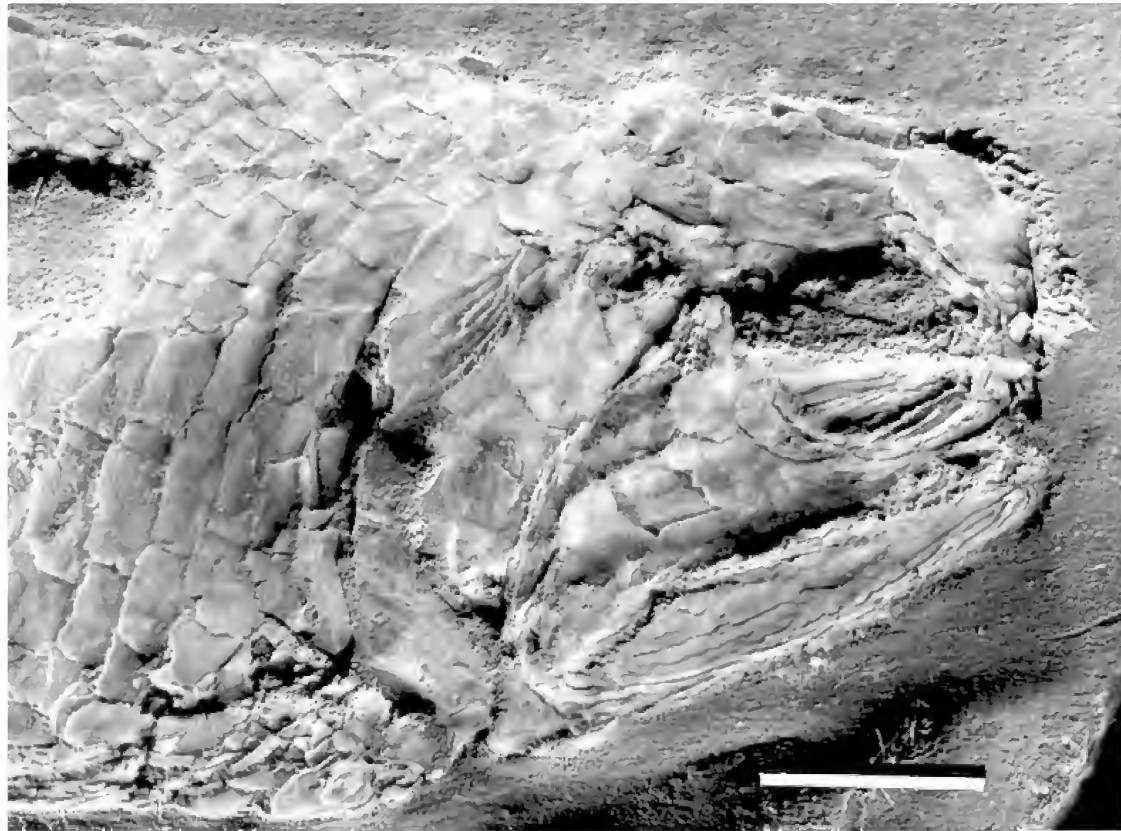
Presence of supranumerary bones in the rostral region is considered to be a primitive condition for actinopterygian fishes since it also occurs among sarcopterygian fishes and in the primitive *Cheirolepis* Agassiz, 1835. Therefore, the condition found in *Angatubichthys* (i.e., reduced number of bones in rostral region) is derived.

The rostromaxilloantorbital (Figs.2b, 3; R+PMX+ANT) is a small bone that forms the anterodorsal limit of the mouth opening. It is a complex and squarish bone, articulated dorsally with the median postrostral and nasal, and



Fig.1- *Angatubichthys mendesi* gen. et sp.nov. Holotype (Pz.DBAV.UERJ 059). Scale bar = 1cm.

A



B

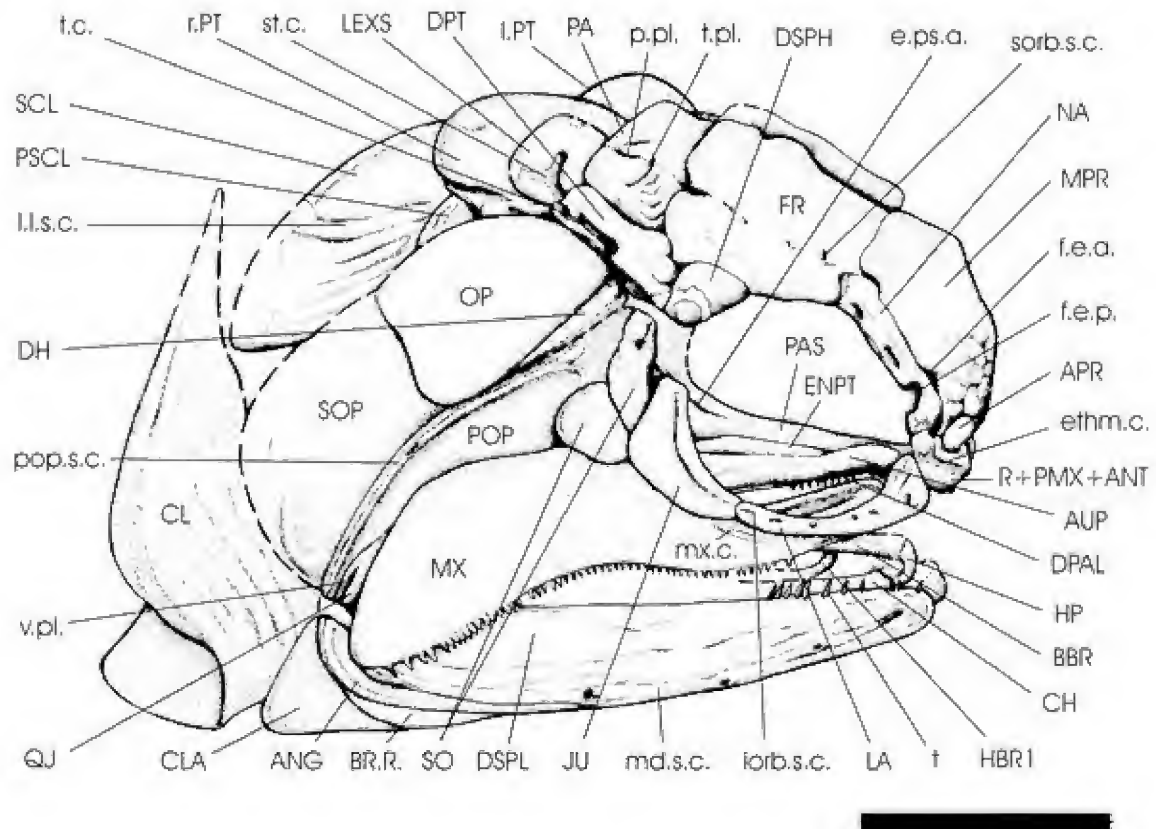


Fig.2- *Angatubichthys mendesi* gen. et sp.nov., skull of holotype (Pz.DBAV.UERJ 059): (A) photograph; (B) line drawing of A. Scale bar = 0.5cm.

posteriorly with the lachrymal above and maxilla below. It possesses a well developed neurodermal component marked by a tripartite pattern of sensory canals. The supraorbital and infraorbital sensory canals join together into the middle portion of the bone producing a well developed ethmoidean commissure (Figs.2b, 3; ethm.c.). The shape and arrangement of the bone correspond to that of *Rhadinichthys fusiformis* Lund & Poplin, 1997 (see LUND & POPLIN, 1997; POPLIN & LUND, 1997). In the holotype, there are in the oral margin of the rostromaxilloantorbital three round teeth-like structures, but we are unable to establish hitherto if they are true teeth or tubercles.

The nasal (Figs.2b, 3-4; NA) is a paired bone, straight and elongate, with length equal to that of the frontal. It meets the whole lateral margin of the median postrostral forming the anterodorsal limit of the orbit. It is inclined in relation to the basicranian axis meeting the frontal posteriorly through a limbate suture. The anterior third is capitate and in this region there is a notch corresponding to the posterior border of the fenestra exonarina anterior. In the orbital margin, another notch occurs, deeper than the anterior, for the fenestra exonarina posterior

(Figs.2b, 3; f.e.p.). The supraorbital sensory canal runs along the bone in the midline exiting on the surface through few minute pores. In *Cheirolepis* the nasal is divided into two bony elements. This condition is considered primitive to basal actinopterygians (POPLIN & LUND, 1995) whereas the condition of *Angatubichthys* is derived.

The frontal (Figs.2b, 3-4; FR) and postrostral are the largest bones of the skull roof. The frontal is subrectangular, with the longitudinal margins approximately parallel, and length equivalent to the orbital diameter. It is also wide, reaching the greatest width, near the dermosphenotic bone. Its width is about $\frac{2}{3}$ of its length.

The posterior margin of the frontal is slightly wider than the anterior. Posterodorsally, it meets the dermosphenotic, posteriorly with a small portion of the dermosphenotic, and medially with its antimeric. The bone slightly overlaps the anterior margin of the parietal bone. A rounded medial projection in the middle third of the bone shows that this bone was slightly asymmetrical in some individuals.

The supraorbital sensory canal (Figs.2b, 3-4; sorb.s.c.) runs the frontal totally bone enclosed, exiting on surface through at least three large pores.

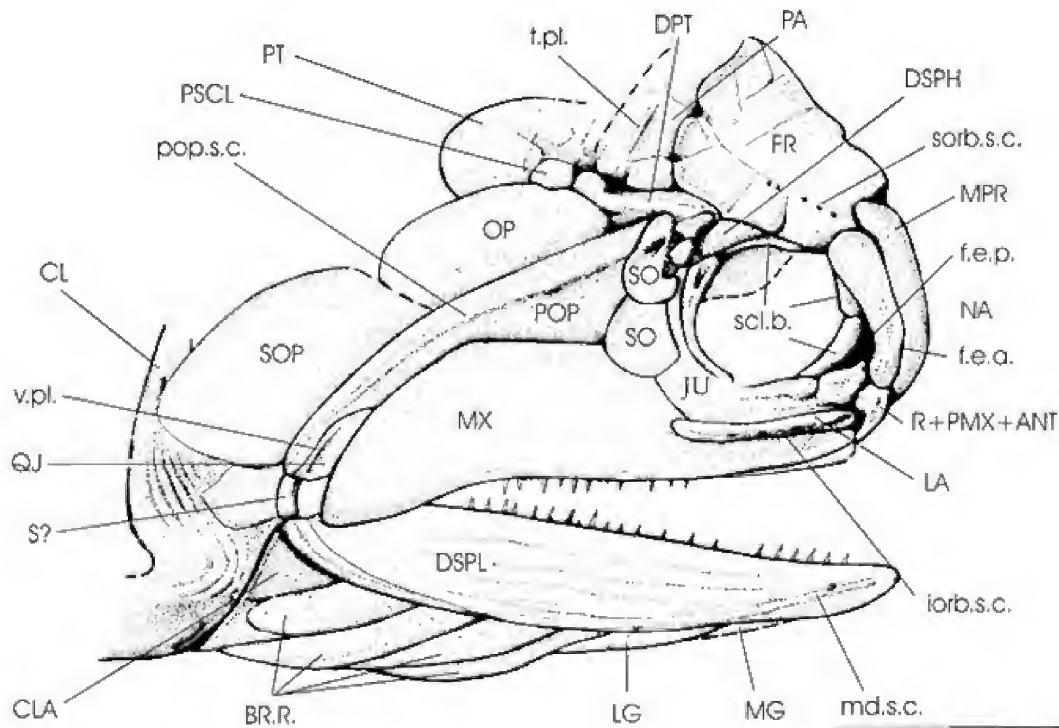


Fig.3- *Angatubichthys mendesi* gen. et sp.nov., skull of Pz.DBAV.UERJ 60. Scale bar = 0.5cm.

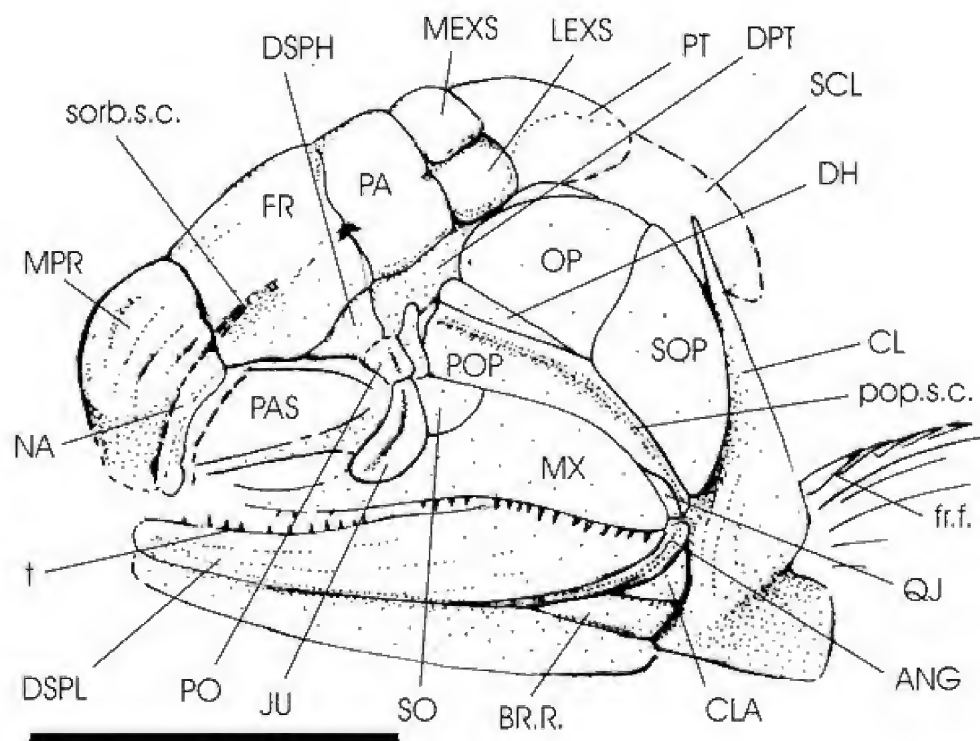


Fig.4- *Angatubichthys mendesi* gen. et sp.nov., skull of Pz.DBAV.UERJ 58. Scale bar = 0.25cm.

The frontal possesses a well-developed cleft, followed by a deep depression, in its posterior margin, corresponding to the projection of the supraorbital sensory canal into the parietal. This bone forms most of the dorsal margin of the orbit, separating the nasal from the dermosphenotic, as in *Polypterus* Lacepède, 1803, *Calamoichthys* Smith, 1865, and *Cosmoptychius* Traquair, 1877 and many other actinopterygians. Supraorbital bones are lacking.

The parietal bone (Figs.2b, 3, and 4; PA) is a paired and subquadrangular bone, about 1.5 times wider than long and 2.5 times shorter than the frontal. The lateral border is twice as long as the medial. Its surface is smooth, except near the anteroventral border, where there are conspicuous cuneiform striae. In the central portion of the bone there is a pair of pit-lines: an arciform transverse (Figs.2b, 3; t.pl.) and, a posterior one, running longitudinally in relation to the main body axis (Fig.2b; p.pl.), almost at right angle with the first. An anterior pit-line is lacking.

The parietal meets the dermopterotic laterally. Posteromedially, it joins the medial extrascapular and posterolaterally, the lateral extrascapular.

In *Cheirolepis* and in most of the sarcopterygian fishes, the parietal is a long bone, about the same length as the frontal. This condition is considered primitive to ray-finned fishes (POPLIN & LUND,

1995; ARRATIA & CLOUTIER, 1996). *Angatubichthys* and most of advanced actinopterygian fishes present derived condition.

The dermosphenotic (Figs.2b, 3, and 4; DSPH) is a small triangular bone that forms the posterodorsal limit of the orbit. The loop of the temporal sensory canal (otic branch) runs along the bone towards the postorbital. In most of the primitive actinopterygians there is an ypsiloid dermosphenotic. In *Angatubichthys*, the long orbital branch and the posterior process are lacking.

Medially, the dermosphenotic bone meets the frontal and posteriorly, the dermopterotic. In Pz.DBAV.UERJ 061 there is a gap between the dermosphenotic and the jugal, which is occupied by a postorbital bone.

The dermopterotic (Figs.2b, 3-4; DPT) is a subrectangular bone approximately three times as longer than wide. It forms the main part of the lateral border of the skull roof. The longitudinal margins are approximately parallel, except for the anterior third where the bone is wider and shows a crenulate border to the dermosphenotic and the frontal bones. A small space anteroventrally placed above the dermohyal is interpreted as a spiracular region. The temporal sensory canal pierces the bone along its longitudinal axis close to the lateral border.

Direct evidence from embryology of certain extant actinopterygians (*e.g.*, *Polypterus* Lacepède, 1803; *Polyodon* Lacepède, 1797; *Acipenser* Linnaeus, 1758; and *Amia* Linnaeus, 1766) shows that fusion of intertemporal with supratemporal occurs during early ontogeny (PEHRSON, 1922, 1940, 1944, 1947; JOLLIE, 1980, 1984; GRANDE & BEMIS, 1998) and this condition is considered derived for basal actinopterygians (GARDINER & SCHAEFFER, 1989). Based on that, a compound dermopterotic bone occurs in *Angatubichthys*.

There is a pair of subcircular extrascapulars, median and lateral, lying on the posterior limit of the skull roof. They are of same size, laminate and flat. The lateral extrascapular (Figs.2b, 3-4; LEXS) bears a tripartite outline due to the passage of sensory canals. The main sensory canal of the lateral line (Figs.2b, 3-5; l.l.s.c.) pierces this element producing a supratemporal commissure (Fig.2b; st.c.). It pierces the bone transversely crossing over to the medial extrascapular. Anteromedially, the lateral extrascapular meets the curved posterolateral border of the parietal bone and anterolaterally the dermopterotic. The lateral extrascapular also covers the anterolateral margin of the post-temporal bone.

Anteriorly, the medial extrascapular (Fig.4; MEXS) meets the parietal bone and laterally, the lateral extrascapular. Posteriorly, it overlaps the medial portion of the post-temporal bone.

The parasphenoid (Figs.2b, 4; PAS) is the only basicranial bone preserved. It is partially preserved in lateral view and can be seen within the orbit of the Pz.DBAV.UERJ 59 forming the floor of the anterior braincase. Laterally, it has a wing-shaped process that gradually tapers forwards. In the base of the ascending process there is a longitudinal groove for the pseudobranchial efferent artery (Fig.2b; e.ps.a.) as described by GARDINER (1973; fig.5, p.115; 1984) in *Mimia toombsi* Gardiner & Bartram, 1977 of the Gogo Formation, Australia.

The anteriormost portion of parasphenoid is laterally covered by the pars autopalatina of the palatoquadrate. The rest contacts the medial lamina of the endopterygoid bone.

There are fragments of an interorbital bony septum extending towards the parasphenoid in the posterodorsal corner of the orbit in Pz.DBAV.UERJ 059 and 060.

The anteriormost element of the circumorbital series, the lachrymal (Figs.2b, 3 LA), is a long and slightly arched bone occupying the

anteroventral corner of the orbit. Anteriorly, it is dilated, while slender rear.

The infraorbital sensory canal (Figs.2b, 3; iorb.s.c.) runs longitudinally through the median portion of the lachrymal. It is recognised on the surface of the bone by a delicate tubular inflated area and by the presence of at least three exiting pores.

Anteriorly, the lachrymal meets the rostromaxilloantorbital and posteriorly the jugal. The ventral border of lachrymal lies on a depression on the dorsal margin of the maxilla, hence the dorsal margin of the maxilla is partially covered.

The second element of the circumorbital series, the jugal (Figs.2b, 4; JU), is a crescent-shaped bone occupying of about $1/4$ of the posteroventral corner of the orbit. Its membranodermal component is large and laminate. The infraorbital sensory canal pierces the bone close to the orbital rim.

The jugal meets the postorbital dorsally and posteriorly, the dorsal and ventral suborbitals.

The third element, the postorbital (Fig.4; PO) is a small, roughly trapezoidal bone only preserved in Pz.DBAV.UERJ 61. This bone forms with jugal, the posterior limit of the orbit. The infraorbital sensory canal pierces it dorsoventrally. The postorbital also occurs in sarcopterygians (SCHULTZE, 1993) and some basal actinopterygians (*e.g.*, *Pteronisculus magnus* Nielsen, 1942; see NIELSEN, 1942). The bone preserved in *Angatubichthys* is homochiral to that of *Pteronisculus* White, 1937.

The suborbitals (Figs.2b, 3-4; SO) are two anamestic dermal plates lacking ornamentation. The dorsal suborbital is a guttate and laminate bone. Anteriorly, it abuts the postorbital; ventrally, the ventral suborbital, and posteriorly, the preoperculum. The ventral suborbital is an ovoid bone, with a convex posterior border and anterior border almost straight. Anteriorly, it meets the jugal, ventrally the maxilla and posteriorly the preoperculum. Two suborbital bones occur in the most primitive actinopterygians (*e.g.*, *Mimia* Gardiner & Bartram, 1977; *Moythomasia* Gross, 1950), showing what it seems to be the primitive condition (GARDINER & SCHAEFFER, 1989).

There are four partially preserved sclerotic bones in the orbital region (Fig.3; scl.b.) of examined specimens. As in other paleoniscoid fishes, they are flimsy and arched structures.

The dermohyal (Figs.2b, 4; DH) is a triangular and elongate dermal bone, lying obliquely between preoperculum and operculum. It covers the lateral

face of hyomandibula near to the spiracular region. Apparently, the primitive condition for basal actinopterygians is to bear two dermohyals (or two antopercular bones) (GARDINER & SCHAEFFER, 1989). In this case, *Angatubichthys* presents derived condition in relation to *Cheirolepis* and *Moythomasia*.

The maxilla (Figs.2b, 3-4; MX) is a large bone, laminate and triangular. As in other paleoniscoid fishes it has a shallow and elongate anterior suborbital portion and a high and well-developed postorbital portion. Posteriorly, it is very inclined, covering part of the posterior end of the lower jaw. The oral margin contains laniariform teeth in the outer row and apparently delicate conical teeth in an inner row.

There is in Pz.DBAV.UERJ 059 a very reduced longitudinal sensory canal on the maxilla lying beneath the lachrymal bone. It is interpreted herein as a maxillary canal (Fig.2b; mx.c.) because of its resemblance with the feature occurring in the semionotid *Lepidotes elvensis* Blainville, 1818 (THIES, 1989).

The preoperculum (Figs.2b, 3-4; POP) is a malleiform bone consisting of a dorsal and well-developed subhorizontal arm and a ventral and slender vertical arm. The morphological pattern is similar to that of primitive actinopterygians such as *Mimia* and *Moythomasia* (see GARDINER, 1984). The dorsal arm is projected towards the orbit. Anterodorsally, it meets the dorsal suborbital and below the ventral suborbital. At the level of the posterodorsal angle of the maxilla, the preoperculum becomes narrow and vertical. This vertical arm ends before the posteroventral angle of maxilla. The preopercular sensory canal (Figs.2b, 3-4; pop.s.c.) runs close to the posterior margin of the bone. The subhorizontal arm of the preoperculum meets the dermohyal posteriorly, and, in part, the operculum. The posterior margin of the vertical arm articulates throughout its extension with the suboperculum.

The operculum (Figs.2b, 3-4; OP) is a sub-rectangular bone. The anterior border is straight and contacts the dermohyal. The posterodorsal margin is convex and the ventral margin shows a sigmoidal contact with the suboperculum. It partially covers the anterior margin of presupracleithrum, supracleithrum, and part of the lateral border of the post-temporal.

The suboperculum (Figs.2b, 3-4; SOP) is roughly trapezoidal and slightly larger than the operculum.

The posteroventral margin is more developed, covering most of the vast smooth inner lamina of cleithrum and meeting the posteriormost branchiostegal ray ventrally.

There are six branchiostegal rays (Figs.2b, 3-4; BRR) lying in series below angular and dentalosplenic. Ahead of the anteriormost branchiostegal ray there is a pair of gular plates. The lateral gular (Fig.3; LG) is triangular and slender in lateral view. An imprint in front of the lateral gular is interpreted as the median gular (Fig.3; MG).

The dentalosplenic (Figs.2b, 3-4 DSPL) is the largest bone of lower jaw. It is an elongate and shallow bone preserved with the ypsilateral angular, forming with it the outer surface of the lower jaw. Oral margin is almost straight and the ventral border slightly convex. Its greatest depth corresponds to about $\frac{1}{5}$ of its length. Its anteriormost end is slightly rounded.

There are laniariform teeth (Figs.2b, 4; t) along the oral border of the dentalosplenic. In Pz.DBAV.UERJ 058A, interpreted as a young fish, apparently there is a double series of teeth. The inner series appears to consist of very small conical teeth, while more acuminate teeth form the outer. The dentalosplenic is densely ornamented on the outer surface with bands apparently corresponding to the sinuous accretion of ganoin. The mandibular sensory canal (Figs.2b, 3-4; md.s.c.) runs across the bone close to the ventral margin. From that, spaced and minute pores exit on surface.

The angular (Figs.2b, 3-4; ANG) is a fistuliform dermal bone that forms the posteroventral margin of the lower jaw. It typically carries in its midline the posterior section of the mandibular sensory canal.

The mandibular suspensorium is roughly triangular, large, and somewhat inclined. It is approximately as long as the maxilla. Considering shape and arrangement of preoperculum, the articular region between hyomandibula and otic endocranium is almost vertical. In Pz.DBAV.UERJ 059, the quadrate portion of palatoquadrate was partially preserved behind suboperculum. This portion appears to possess a large and convex articular area to lower jaw as in the acrolepid *Namaichthys schroederi* Gardiner, 1962. The contact zone with the lower jaw lies just behind the orbit. The design of the bones and their relationship with the parasphenoid follow the

pattern in *Australosomus kochi* Nielsen, 1949 (see NIELSEN, 1949).

The pars autopalatina (Fig.2b; AUP) of palatoquadrate is slender and narrow. Its anteriormost end is capitate. Most of the medial border abuts against the endopterygoid (Fig.2b; ENPT) that appears through the orbital space, as a narrow and elongate bone.

A dentigerous plate with pointed teeth meeting the ventral face of the pars autopalatina is interpreted as a dermopalatine (Fig.3b; DPAL). It is similar to that described by GARDINER (1962) in *Namaichthys schroederi*.

In Pz.DBAV.UERJ 060 the articular area of the palatoquadrate is poorly preserved, but among bone remains there is a nodular bone between ventral extremity of the vertical branch of preoperculum and the dorsal end of angular tentatively interpreted as a symplectic (S?, Fig.3). The presence of this bone among early actinopterygians is questioned by certain authors (GARDINER & SCHAEFFER, 1989) that claim this is a synapomorphy of Neopterygii. However, other (e.g., OLSEN, 1984; VÉRAN, 1988) have been surveying anatomical evidences that indicate its early occurrence among primitive actinopterygians.

A small bone identified as quadratojugal (Figs.2b, 3-4; QJ) lies between the end of the vertical arm of the preoperculum and the posteroventral border of the maxilla. It is a triangular bone with a sharp dorsal extremity and a large base bearing conspicuous vertical pit-line (Figs.2b, 3; v.pl.). A vertical pit-line on quadratojugal was considered a relevant feature by BRITO (1997) to recognize that bone in various lineages of actinopterygians.

The following bones of the hyobranchial apparatus are preserved: dermohyal (seen above), ceratohyal, hypohyal, basibranchial, and hypobranchial.

The hypohyal (Fig.2b; HP) and the ceratohyal (= neocerato-hyal of VÉRAN, 1988; Fig.2b, CH) are partially preserved in lateral view in Pz.DBAV.UERJ 059. The first is a small triangular bone, slightly arched, with the round extremities synchondrally joined with the basibranchial plate. The second is seemingly a slender and long bone, but only its proximal capitate end can be seen.

Concerning the branchial apparatus, a basibranchial plate (Fig.2b; BBR) and the first hypobranchial (Fig.2b; HBR1) are preserved, in lateral view, in the gape of Pz.DBAV.UERJ 059. Both bones are somewhat elongate, the basibranchial being a wide and depressed plate and the hypobranchial slightly arched in the proximal portion.

The post-temporal (Figs.2b, 3-4; PT) is an ovoid and laminate dermal bone. The main sensory canal of the lateral line runs along a reduced portion of bone close to ventral margin. Anteroventrally, it is joined with the presupracleithrum and dorsoventrally with supracleithrum.

The presupracleithrum (Figs.2b, 3-4; PSCL) is preserved in all specimens. It is a small triangular bone lying on the anterodorsal corner of supracleithrum. Typically, it belongs to the pectoral girdle (see BJERRING, 1985) and not to the spiracular series as argued by certain authors (e.g., LEHMAN, 1966). It occurs homoplastically in certain taxa of primitive actinops such as *Pteronisculus* White, 1937, *Paramblypterus* Sauvage, 1888, *Watsonulus* Piveteau, 1934, *Boreosomus* Stensiö, 1925 (*passim* LEHMAN, 1966).

The supracleithrum (Figs.2b, 3; SCL) is spatulate, well ossified and deep (1.8 times the height of the frontal and 1.2 times the height of the operculum). Ventrally, it is articulated with the dorsal process of the cleithrum. The bone is partially covered by operculum and suboperculum and is densely ornamented with radial ridges on the anterior margin. The main sensory canal of the lateral line crosses the supracleithrum obliquely, running from the anterodorsal region to the median point of the convex posterior margin of the bone.

The cleithrum (Figs.2b, 3-4; CL) is the largest dermal bone of the pectoral girdle. It is slightly sigmoid and typically bears a well-developed spine-shaped dorsal process. The portion below the spine-shaped process corresponding to the external lamina of the cleithrum is arched and ornamented with radial ridges. This rounded prominence covers the radials and the proximal portion of the lepidotrichia of the pectoral fin. It projects medially into a concave margin that is covered by the suboperculum. Its posterior margin is sinuous, convex below the spine-shaped process and concave ventrally. This last portion projects backwards in an outer lamina. The anteriormost part of cleithrum contacts the clavicle through an oblique suture.

The clavicle (Figs.2b, 3-4; CLA) is triangular and projected forwards; it is partially hidden by the posterior corner of lower jaw and branchiostegal rays. In primitive actinopterygians the clavicles are in close contact along the ventral midline. A narrow interclavicle is distinguished behind gulars (LUND, POPLIN & McCARTHY, 1995). In *Angatubichthys* we were not able to determine the presence of an interclavicle, probably because it is hidden by the

clavicle in all specimens examined.

The pectoral fin is directly associated with the cleithrum. It is relatively long, and the largest ray reaches the eighth scale row counting from the posterior margin of the cleithrum. It is approximately twice as long as the pelvic fin. It carries at least ten segmented and distally ramified rays. A reduced number of fin-rays (<25) in the pectoral fin is considered derived condition for basal actinopterygians (TAVERNE, 1997). Small and sharp fringing fulcra (Fig.4; fr.f.) are present along the leading edge of the fin.

The pelvic girdle is not visible. The pelvic fin is very small and triangular. Its base is relatively short; the length of the anterior margin corresponds to the half the length of anterior margin of anal fin. We counted at least 12 segmented rays. The pelvic fin is preceded by a modified subcircular scute.

The dorsal fin is triangular and moderate in size. The anterior margin is equivalent to the anterior border of the anal fin. The base of dorsal fin is approximately equal to the length of the anterior margin of pelvic fin. We count 21 segmented and distally ramified rays. The largest one bears about 11 articulate segments. Fringing fulcra occur on anterior border of fin preceded by at least three basal sagittate scutes. It was not possible to observe

any endoskeletal supports for the dorsal fin because it is hidden by rows of scales.

The anal and dorsal fins are placed at the posterior half of the body; the base of the anal fin is 1.5-2 times longer than the anterior margin of the pelvic fin. It carries at least 31 segmented and distally ramified rays. The anterior margin is covered with small fringing fulcra and the base is preceded by a small basal sagittal scute. Support elements were not observed.

The caudal fin (Fig.5) bears at least 50 distally ramified and segmented rays. In its dorsal margin there are 13-16 epaxial fulcra (Fig.5; ep.f.). They are long rod-like structures that progressively decrease in size toward the tail end. In the caudal base there are three basal sagittate scutes (Fig.5; ba.s.).

In the base of ventral hypochordal lobe there are two basal scutes and a series of small fringing fulcra (= "anterior lepidotrichia" of PEARSON & WESTOLL, 1979; fr. f., Fig.5).

The body is entirely covered with ganoid scales of smooth surface. In epaxial area scales are rhombic and equilaterals (4 longitudinal rows starting from back), the same for hypoaxial area (3 longitudinal rows up from abdomen). At the midline of body scales are higher than longer decreasing gradually in size backwards.

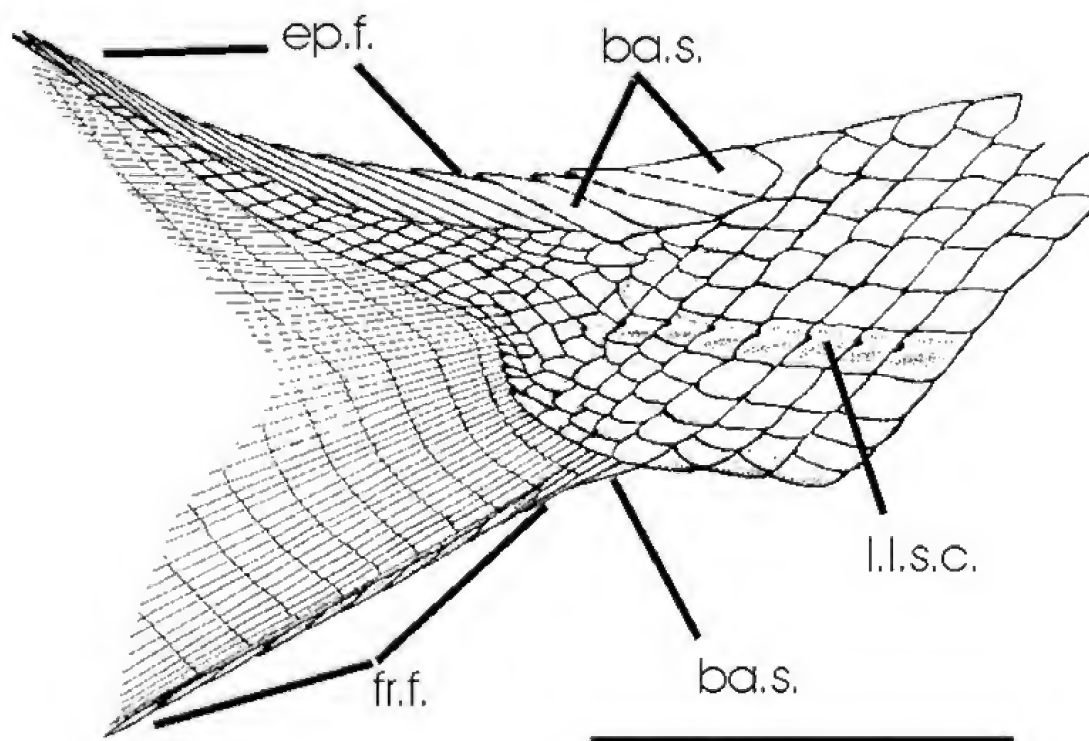


Fig.5- *Angatubichthys mendesi* gen. et sp.nov., caudal skeleton of holotype (Pz.DBAV.UERJ 59). Scale bar = 1cm.

The row of scales immediately above and two immediately below the lateral line are similar in size. Behind the pelvic fin the scales that compose these three rows gradually become equilateral toward hinge line, where they are small and elongated.

The lateral line scales are crossed at midline by the sensory canal which is totally enclosed. Their anterior and posterior borders show a moderately developed notch. There are about 38-41 middle flank scales, at least 30 of which are from lateral line. Anteriorly they are rhombic and deep and more equilateral near caudal peduncle.

Posterior to the hinge line there is a gradual change of direction and shape of scales in relation to the main longitudinal body axis (Fig.5). They become inclined and lozenge-shaped.

There are about 24 modified sagittal dorsal fin scales in the back, from the occiput to the origin of the dorsal fin.

DISCUSSION AND CONCLUSIONS

Angatubichthys mendesi and other South American palaeoniscoid fishes

Comparisons between *Anagatubichthys mendesi* and palaeoniscoid fishes previously described from Brazil on the basis of either nearly complete or well-preserved specimens, indicate that *Tholonotus braziliensis* (?Acrolepididae) shares an amount of general similarities. However, it can be distinguished from *Angatubichthys* by the presence of the following features: an arched dorsal profile (semionotid-like); large frontals with narrow anterior portion and excluded from the orbit; small postrostral; dermosphenotic obliquely truncated in its anterior portion, but with a posterolateral expansion; dermosphenotic covering the orbit and contacting the nasal; operculum larger than suboperculum; weak or absent dentition; pectoral and anal fins with 17 rays; dorsal fin placed in the middle of the body and anterior to anal fin; and scales ornamented with wrinkles.

Tholonosteon santacatarinae Beltan, 1978, is a large palaeoniscoid from the Upper Carboniferous of the State of Santa Catarina, about which few anatomical structures relevant to systematics are known, mainly due to the fact that skull is lacking. But this species can be easily distinguished from *Angatubichthys mendesi* by suitable features such as: an arched dorsal profile; 36 soft rays in pectoral fin; dorsal fin with base longer than deep, rising in

the middle of the body and composed of 25 rays; caudal fin deeply forked and bearing 68 rays, besides the presence of 20 dorsal scutes and scales along the body ornamented with delicate longitudinal rugae.

Additionally to describing *Tholonosteon santacatarinae*, BELTAN (1978) reported the occurrence of various species of palaeoniscoid fishes from the Upper Carboniferous of Uruguay based on partially complete specimens. Among those taxa, *Gondwanichthys maximus* Beltan, 1978 (Acrolepididae) and *Carbinolepis uruguayensis* Beltan, 1978 (Acrolepididae) promptly differ from *Angatubichthys* for their supranumerary extra-scapular and grooved scales; *Mesonichthys antipodus* Beltan, 1978 (Acrolepididae), for a fenestra exonarina anterior higher on snout and operculum larger than suboperculum; *Elonichthys macropercularis* Beltan, 1978 (Elonichthyidae), for the presence of ornamented scales, oval rostral and large number of branchiostegal rays (15); *Rhadinichthys rionigher* Beltan, 1978 (Rhadinichthyidae), for a dermosphenotic contacting the nasal and scales with parallel grooves; *Itararichthys microphthalmus* Beltan, 1978 (Pygopteroidea), for a reduced orbit, a single sclerotic bone, and supranumerary extrascapulars; *Daphnaechelus formosus* Beltan, 1978 (Amblypteroidea), for skull higher than long, small or lacking rostral, operculum larger than suboperculum, and triangular and small parietal.

Furthermore, BELTAN (1989) erected two new monotypical palaeoniscoid families: Monesedeiphidae and Irajapintoseidae. The first includes *Monesedeiphus* Beltan, 1989, an aberrant palaeoniscoid recognised mainly for the presence of 15 extrascapulars and 12 branchiostegal rays, five suborbitals, and skull roof bones ornamented with tubercles and rugae of ganoin. The family Irajapintoseidae includes *Irajapintoseidon* Beltan, 1989, that possesses a robust postrostral with V-shaped posterior suture, nasal in contact with the dermosphenotic, operculum twice as large as suboperculum, 12 extrascapulars, and scales ornamented. Therefore, both differ considerably from *Angatubichthys mendesi* in various diagnostic anatomical features.

Santosichthys mafrensis Malabarba, 1988 (?Elonichthyidae) is known mainly from a skull cast. It differs from *Angatubichthys mendesi* mainly by the presence of a prominent snout; narrow frontals ornamented with rugae; long dermosphenotic forming a digitate projection towards the frontal; well-developed trapezoidal dermosphenotic forming the posterodorsal limit of the orbit; narrow and

slender maxilla; presence of supraorbital bone; high number of branchiostegal rays (16); and rhomboid scales ornamented with wrinkles and indented posterior border.

RICHTER (1991) pointed out the occurrence of eight new palaeonisciform fishes mostly from Santa Catarina State, not yet formally described. Examining restorations made by her, we are unable to find any remarkable similarities with *Angatubichthys mendesi*. The pattern of the dermal bones skull, particularly the non-contacting condition between nasal and dermosphenotic is enough to separate these fishes from *Angatubichthys*.

COX & HUTCHINSON (1991) pointed out the presence of an early actinopterygian fish to the Late Permian of Pedra do Fogo Formation: *Brazilichthys macrognathus* Cox & Hutchinson, 1991. It is represented by a poorly preserved cranium which can be distinguished from that of *Angatubichthys* by the presence of skull bones ornamented with ridges and tubercles, large maxilla with convex orbital portion, two rows of large teeth on maxilla and mandible, the inner row bearing stout and spaced fang-like teeth; unusual premaxilla, and nasal contacting dermosphenotic bone.

VEGA, DIAS & RAGONHA (1997) registered the occurrence of palaeonisciform fishes for the Rio do Rasto Formation, Permo-Triassic of the Paraná Basin, district of Santo Antônio da Platina, State of Paraná. The material consists of seven incomplete fishes preserved on the same bedding plane. In all specimens most of the skull bones are lacking, constraining an accurate identification. Three different morphotypes were described suggesting new taxa (VEGA-DIAS, DIAS & RICHTER, 2000). A high number of scale rows separate these taxa from *Angatubichthys*.

BORDAS (1944) reported the occurrence of the following species from the Triassic of Argentina: *Pseudobeaconia bracaccinii* Bordas, 1944 and *Pseudobeaconia elegans* Bordas, 1944 (Redfieldiidae), *Cleithrolepis cuyana* Bordas, 1944 (Cleithrolepididae), and *Mendocinichthys (=Mendocinia) brevis* (Bordas, 1944) (Perleidiidae). All these taxa share a deep body and arched dorsal profile as in various so-called "subholostean" fishes, therefore differing from *Angatubichthys mendesi*.

More recently, RICHTER (2002) described a complete palaeoniscoid fish from Late Permian of the State of Santa Catarina (Rio do Rasto Formation): *Rubius*

pascoalensis Richter, 2002. The fish possesses an anvil-shaped dermosphenotic meeting the nasal and the intertemporal does not reach the nasal. In addition, the operculum is larger than the suboperculum. These features are enough to separate *Rubius* Richter, 2002 from *Angatubichthys*. Other palaeoniscoid fishes were reported from the Paleozoic of the Paraná Basin. Some remains were tentatively identified as belonging to *Acrolepis* Agassiz, 1833 and *Elonichthys* Giebel, 1848 (BELTAN, 1978; RICHTER, 1985). However, these are based on fragmentary material consisting of isolated bones, scales, and teeth, limiting adequate identification and comparisons. But, *Angatubichtys mendesi*, when compared with well known oversea species of Acrolepididae and Elonichthyidae such as *Acrolepis sedgwicki* Agassiz, 1834 and *Elonichthys robisoni* Agassiz, 1843, shares only plesiomorphous similarities. Otherwise, the families Acrolepididae and Elonichthyidae, presumably represented in the Brazilian Paleozoic strata, are hitherto paraphyletic assemblages (GARDINER & SCHAEFFER, 1989). Their scales have been reported to get three times higher than long as in the flanks of *Angatubichthys mendesi*. It is probable that many scales assigned to taxa of these families belong to representatives of several non related groups.

The early actinopterygian scale structure is, in general, conservative (retaining many plesiomorphies). An attempt by ALDINGER (1937) to define groups based on certain patterns of canaliculi distribution and ornamentation have been recently questioned (GARDINER & SCHAEFFER, 1989, SCHULTZE, 1996; but see RICHTER & SMITH, 1995 for a new approach to assess scale features of actinopterygians). We assume that the current knowledge of the morphological diversity of scales is still in its infancy and will not allow a correct assessment of isolated scales of most of taxa.

Taking all of the current information about anatomy and systematics of South American palaeoniscoids there is little doubt that they are poorly known. Probably most of taxa form paraphyletic assemblages waiting for instant review. In addition, there is large amount of missing data to generate noise in a premature cladistic analysis. For similar reasons, *Angatubichthys mendesi* does not fit any species diagnosis within palaeoniscoid families described for the Paleozoic of Africa too (BROUGH, 1931; GARDINER, 1962, 1969; JUBB & GARDINER, 1975).

Comments on the phylogenetic relationships of *Angatubichthys*

The most influent approach concerning phylogenetic classification of lower actinopterygian fishes is that by GARDINER & SCHAEFFER (1989). In order to tentatively place *Angatubichthys* in this system, the characters used by them are discussed independently, but not integrated into a cladistic analysis because of the large amount of missing data.

In this context, based on the available morphological data, *Angatubichtys mendesi* seems to occupy a more derived position in relation to various actinopterygians below the Chondrostei-Neopterygii divergence. For instance, the presence of dermopterotic bone (synapomorphy for the node H of GARDINER & SCHAEFFER, 1989, Fig.10) places it in a derived position in relation to assemblages such as “*Pteronisculus* group”, “*Boreosomus* group”, and “*Watsonichthys* group”. A reduced number of branchiostegal rays and a dermosphenotic contacting less than $\frac{1}{3}$ of the dermopterotic (synapomorphies for the node I of GARDINER & SCHAEFFER, 1989, Fig.10) place it in a polytomy with a clade formed by “*Redfieldius* group” + “*Hoplolepis* group” and another, formed by “*Mesopoma* group” + (“*Aeduella* group” + (“*Platysomus* group” + (“*Bobasatrania* group” + “*Dorypterus* group”))). *Angatubichthys mendesi* lacks the skeletal apomorphies listed for the first clade (node J of GARDINER & SCHAEFFER, 1989, Fig.12), or for the second (node K of GARDINER & SCHAEFFER, 1989, Fig.12). It seems to be closer to the group where *Canobius* is included (“*Mesopoma* group”).

The “*Mesopoma* group” of GARDINER & SCHAEFFER (1989) that includes *Mesopoma* Traquair, 1890, *Canobius* Traquair, 1881 and *Styracopterus* Aldinger, 1937 is defined by the presence of an almost vertical suspensorium, reduced preoperculum, reduced posterodorsal processes of maxilla, suboperculum subequal or larger than the operculum, and T-shaped dermosphenotic (in *Mesopoma* and *Styracopterus*). No formal taxonomy was given for this group. Despite of general resemblances shared, only the presence of a suboperculum larger than operculum suggests putative relationship of *Angatubichthys* with taxa of this clade.

Unfortunately, due to the preservation of the specimens examined, the correspondence between the number of dermal rays and endoskeletal

supports of the fins, very important to clarify the systematic position of a fish as a stem actinopteran or a neopterygian (PATTERSON, 1982; COATES, 1999) was inaccessible to direct observation.

More recently, COATES (1999) tested the hypotheses of phylogenetic relationships for lower actinopterygians of GARDINER & SCHAEFFER (1989) including new anatomical data and additional taxa. The trees obtained are similar in various aspects to those of GARDINER & SCHAEFFER (1989). Most of the morphological features used in his analysis were observed in well-preserved specimens showing details of endocranium and brain. Such exceptional preservation is found in relatively few fossil taxa. Unfortunately, the available morphological data of *Angatubichthys* permits only comparisons of dermal elements of the skull, scales and fins.

In sum, the phylogenetic relationships of various taxa of lower actinopterygians have not yet been resolved. Considering an array of current phylogenetic approaches (KAZANTZEVA, 1971; KAZANTSEVA-SELEZNEVA, 1981; LONG, 1988; GARDINER & SCHAEFFER, 1989; LUND, POPLIN & McCARTHY, 1995; TAVERNE, 1997; COATES, 1998; 1999), *Angatubichthys mendesi* appears to be more advanced in relation to so-called basal actinopterygians (e.g., *Cheirolepis* Agassiz, 1835; *Mimia* Gardiner & Bartram, 1977; *Moythomasia* Gross, 1950; *Osorioichthys* Casier, 1952; *Howqualepis* Long, 1988; *Polypterus* Lacepède, 1803). It is suggested by several derived skeletal features (e.g., absence of plate pineal, presence of dermopterotic and suborbitals, high scales on the flanks, reduced number of branchiostegals and pectoral fin rays). Nevertheless, *Angatubichthys mendesi* wants synapomorphies of more advanced actinopterygian fishes of the platysomid and neopterygian clades.

It is hoped that additional informative specimens will allow the phylogenetic position of *Angatubichthys* and other lower actinopterygians from South America to be refined in the future.

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ON A NEW MANIRAPTORAN DINOSAUR (THEROPODA) FROM THE UPPER CRETACEOUS OF NEUQUÉN, PATAGONIA, ARGENTINA ¹

(With 41 figures)

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ABSTRACT: The “Futalognko” site, situated at the margins of the Los Barreales lake about 90 km northwest of Neuquén city (Patagonia), revealed several new dinosaur specimens, all from the Portezuelo Formation (Turonian-Early Coniacian). Among those are the remains of new theropod dinosaur referable to a new species of the maniraptoran *Unenlagia*, *Unenlagia paynemili* n. sp. The material is represented by a pubis, humerus, ilium, and a dorsal vertebra, plus a pedal phalanx and a claw that tentatively referred to this new species. It shares with *Unenlagia comahuensis* a posteriorly oriented distal end of the pubis that shows a convex anterior margin and differs by possessing more gracile bones, angle between the anterior rim of the deltopectoral crest and the humerus shaft more closed, the presence of a small anterior process on the distal end of pubis, and the distal end of the postacetabular blade of ilium broader and rounded, with a shallower *brevis fossa*.

Key words: Dinosauria, Maniraptora, Portezuelo Formation, Patagonia, Argentina

RESUMO: Sobre um novo dinossauro Maniraptora (Theropoda) do Cretáceo Superior de Neuquén, Patagônia, Argentina.

Novos materiais de dinossauros, todos procedentes da Formação Portezuelo (Turoniano-Coniaciano Inferior), foram encontrados nos últimos anos na localidade denominada de “Futalognko”, situada às margens do lago Barreales a cerca de 90 km noroeste da cidade de Neuquén (Patagonia). Entre estes se destaca uma nova espécie do maniraptora *Unenlagia*, denominado aqui de *Unenlagia paynemili* n. sp. O material é representado pelo úmero, púbis, ílio e uma vértebra dorsal, além de uma falange e uma ungueal, atribuídos por tentativa a essa nova espécie. A principal característica compartilhada com *Unenlagia comahuensis* é a margem anterior convexa do púbis, com a parte distal orientada posteriormente. As principais diferenças observadas na nova espécie são os ossos mais gráteis, o ângulo entre a crista deltopeitoral e eixo do úmero mais fechado, a presença de uma projeção anterior no púbis, e a porção pós-acetabular do ílio mais larga e arredondada, com a *brevis fossa* mais rasa.

Palavras-chave: Dinosauria, Maniraptora, Formação Portezuelo, Patagônia, Argentina

INTRODUCTION

In 2000, the team of the National University of Comahue has discovered an important fossil deposit about 90km northwest of the Neuquén city (Patagonia), Argentina (CALVO *et al.*, 2002b). Called the Futalognko site, this quarry is placed at Costa Dinosaurio Locality, northern coast of the Barreales lake. Due to the richness of fossils a new Paleontological Center of the National University of Comahue was built there. Today, this complex is named Barreales Lake Paleontological Center

(CePaLB) and consists the first permanent educational paleontological site in South America fully dedicated to field research in vertebrate paleontology.

The fossiliferous beds of the Futalognko site are from the Turonian- Early Coniacian Portezuelo Formation of the Rio Neuquén Group (LEANZA & HUGO, 2001) and yielded several important vertebrate fossils. Among those are titanosaurid sauropods (CALVO *et al.*, 2001, CALVO & GRILL, 2003), new material from the theropod *Megaraptor namunhuaiquii* Novas, 1998 (CALVO *et al.*, 2002a;

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PORFIRI & CALVO, 2003), theropod teeth (POBLETE & CALVO, 2003; VERALLI & CALVO, 2003) ornithopods (PORFIRI & CALVO, 2002), turtles, osteichthyan fishes (GALLO, CALVO & KELLNER, 2003), crocodylomorphs, pterosaurs (KELLNER *et al.*, 2004), and plants (PRÁMPARO *et al.*, 2003).

During the field season of 2002, another interesting material was recovered from this site. It consists of isolated remains, including the left humerus and left pubis that share several features with the maniraptoran *Unenlagia comahuensis* Novas & Puerta, 1997 (CALVO, PORFIRI & KELLNER, 2003). The latter was found at the Sierra del Portezuelo, about 50km south of the Futalognko site (NOVAS & PUERTA, 1997). In 2003, one dorsal vertebra and the posterior end of one right ilium, also sharing several features with *Unenlagia comahuensis*, were recovered from that site. The purpose of this paper is to report this material, which is referred to a new species of *Unenlagia* (*U. paynemili* n.sp.). An isolated phalanx and ungual, also recovered from the site, are tentatively referred to the new taxon, which is described here.

GEOLOGICAL SETTING

The Neuquén Basin of western Argentina has deposits ranging from the Upper Triassic to the Tertiary. These deposits include a sequence of marine and continental strata, including the Neuquén Group, which is composed of sediments formed in a continental, fluvial environment that range from Albian to Campanian age (ULIANA & DELLAPE, 1981; LEGARRETA & GULISANO, 1989; CALVO, 1991; CALVO & SALGADO, 1995).

The material of the new species, *Unenlagia paynemili* n.sp., comes from continental deposits from the top of the Portezuelo Formation, Río Neuquén Subgroup, Neuquén Group (CAZAU & ULIANA, 1973; LEANZA, 1999). The Río Neuquén Subgroup is composed of two formations, at the base the Portezuelo and at the top the Plottier formations. The Portezuelo Formation is characterized by yellowish sandstones, red and green claystones with a poor participation of conglomerates, which have been interpreted as Turonian - Early Coniacian (LEANZA & HUGO, 2001). The depositional environment is interpreted as a meandering river system that runs over a flattened area by an exuberant vegetation in humid climate conditions (SÁNCHEZ *et al.*, 2003). Fossils were recovered from a fine conglomerate and are mostly unarticulated.

SYSTEMATIC PALEONTOLOGY

Theropoda Marsh, 1881
 Coelurosauria Gauthier, 1986
 Maniraptora Gauthier, 1986
Unenlagia Novas & Puerta, 1997

Type-species – *Unenlagia comahuensis* Novas & Puerta, 1997

Unenlagia paynemili n.sp.

Etymology – In honor to Maximino Paynemil, the chief of the Paynemil Indian community that lives in the region of Loma de La Lata, where the Futalognko site is situated.

Holotype – Left humerus and left pubis, regarded as belonging to the same individual, housed at the Museo de Geología y Paleontología de la Universidad Nacional del Comahue under the number MUCPv-349.

Referred specimens – A dorsal vertebra (MUCPv-416) and the posterior end of a right ilium (MUCPv-409). Tentatively, a pedal phalanx (MUCPv-415) and a pedal claw (MUCPv-343) are also referred to this species.

Locality and horizon – Futalognko site at the Centro Paleontológico Lago Barreales situated about 90km northwest of the Neuquén city, Neuquén province, Patagonia, Argentina; Portezuelo Formation (Turonian-Early Coniacian), Río Neuquén Group.

Diagnosis – Species of *Unenlagia* distinguishable from *Unenlagia comahuensis* by possessing more gracile bones, the angle between the anterior rim of the deltopectoral crest and the humerus shaft about 116° (opposed to 140° of *Unenlagia comahuensis*), a small anterior process on the distal end of pubis, and the distal end of the postacetabular blade of ilium broader and rounded, and a shallower brevis fossa.

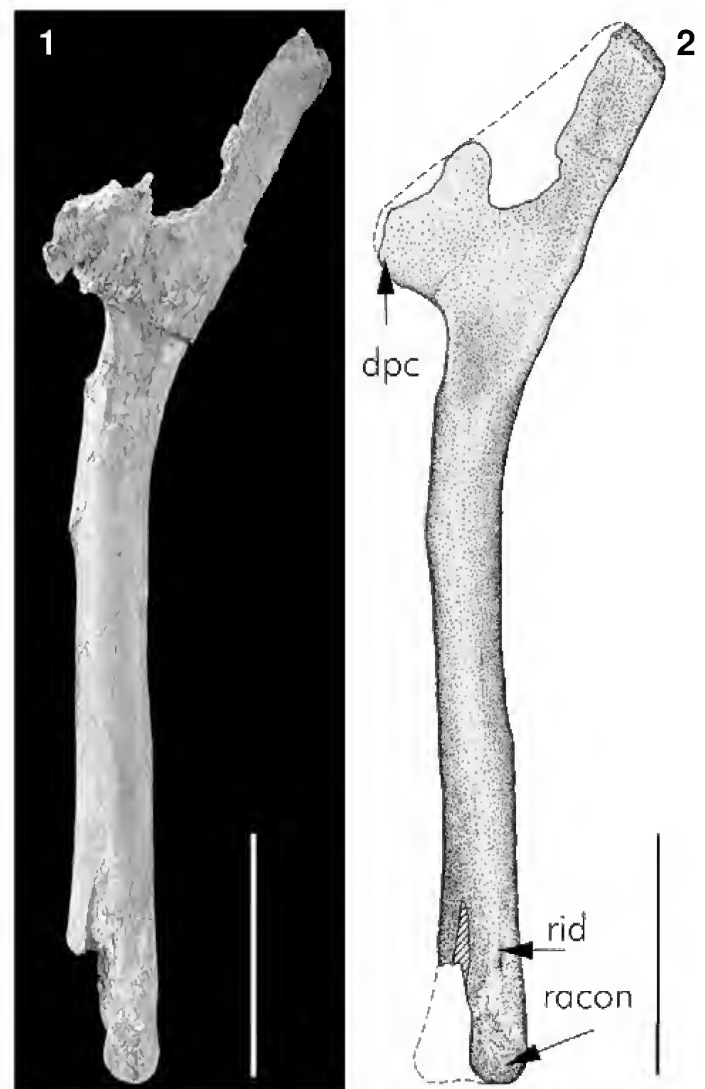
DESCRIPTIONS AND COMPARISONS

Since 2002 a quarry map of the Futalognko site showing the relation of all collected fossil remains is being made, including the elements attributed to *Unenlagia paynemili* n.sp., which were found isolated. The pubis and the humerus were lying about two and half meters from each other (close to the remains of the giant sauropod) and are regarded as belonging to the same individual due to their proximity in the quarry and similarity in size when compared to the material of the larger *Unenlagia comahuensis*. Furthermore, both bones have a

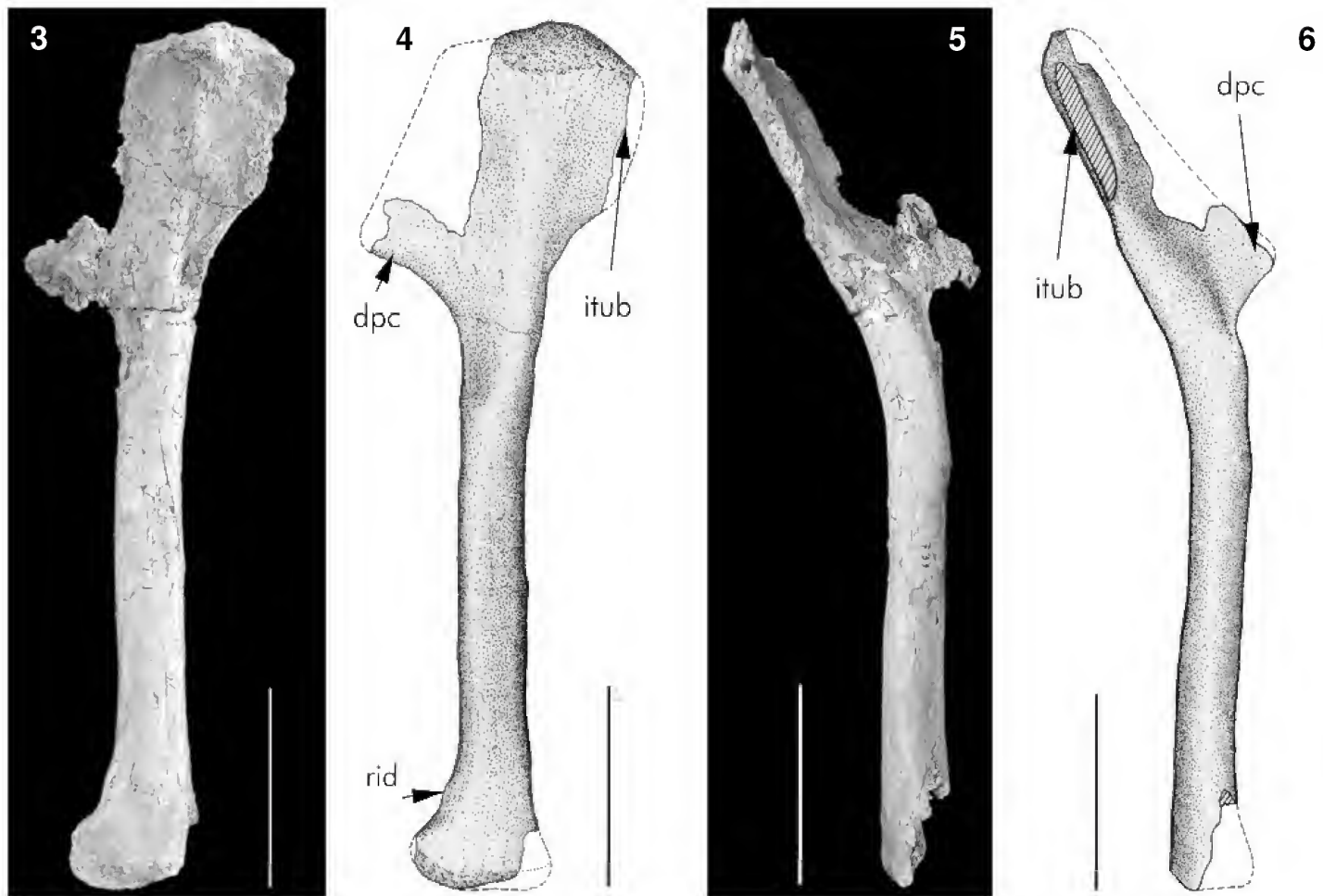
distinct brownish color, different from the other sauropod and theropod elements (*e.g.*, *Megaraptor namunhuaiquii*) collected at the site. Although the size of the ilium (and the bone color) is also compatible with the humerus and pubis, it was found more distant (ca. 23 meters from the pubis) and is regarded as belonging to a different individual. The last element attributed to *Unenlagia paynemili* n.sp. is an incomplete dorsal vertebrae that belongs to a proportionally larger individual (also larger than the type material of *Unenlagia comahuensis*) and was found in 2003 by surface collecting (probably washed out from the quarry during the flooding of the Barreales lake). Two more bones are described and are tentatively referred to *Unenlagia paynemili* n.sp.: a pedal phalanx and an ungual, also found isolated (respectively 5 and 12.5 meters from the pubis). Except for the humerus and pubis, all remaining specimens are numbered separately.

The humerus (MUCPv-349) belongs to the left side and except for some parts of the proximal and distal articulations is complete with a total length of 217mm (Figs.1-10). It is a long and slender pneumatic bone, with the thickness of the cortex around 2mm. The proximal part is flattened anteroposteriorly. The deltopectoral crest is expanded and restricted to the proximal third of the humerus, a condition common to other maniraptorans. It is thin and inclined about 116 degrees relative to the shaft. The preserved part of the internal tuberosity is anteroposteriorly compressed and longitudinally elongated as in *Unenlagia comahuensis*, *Deinonychus antirrhopus* Ostrom 1969, *Archaeopteryx lithographica* Meyer 1860, and some other maniraptorans (OSTROM, 1969a, b; WELLNHOFER, 1974; 1993; NOVAS & PUERTA, 1997). The shaft is essentially straight and long differing from the bowed condition present in some maniraptorans like *Deinonychus antirrhopus* (OSTROM, 1969b). It is slightly compressed anteroposteriorly with an oval cross section over most its length (middle part = 17.5 x 14mm) and gets more triangular closer to the distal articulation. A blunt longitudinal ridge (length 20mm) is observed above the radial condyle (partially preserved) at the dorsal margin close to the posterior surface (Figs.1-4, 7, 8). Overall, the humerus of *Unenlagia paynemili* n.sp. is similar to the one of *Unenlagia comahuensis* (Figs.9-10). Both have the proximal part, that includes the deltopectoral crest, strongly deflected relative to the shaft. The deltopectoral crest in those taxa is quadrangular in anterior view, similar to oviraptorids (BARSBOLD, MARYANSKA & OSMÓLSKA, 1990) and most dromeosaurids (OSTROM, 1969a, b), but differs

from the distinct and long deltopectoral crest of alvarezsaurids (*e.g.*, NOVAS, 1996) and the less pronounced condition reported in *Archaeopteryx lithographica* (WELLNHOFER, 1974; 1993) and in the Ornithomimosauria (BARSBOLD & OSMÓLSKA, 1990). The humerus of *Unenlagia paynemili* n.sp. differs from *Unenlagia comahuensis* mainly by being about 20% smaller and a more gracile element. Furthermore, the angle between the ventral margin of the deltopectoral crest in the new species is 116° while in *Unenlagia comahuensis* it is wider, about 140° (Figs.9-10). The latter also shows a developed blunt ridge on the dorsal margin posterior to the deltopectoral crest that is not observed in the new species (Figs.9-10).



Unenlagia paynemili n.sp., left humerus (MUCPv-349) in dorsal view – fig.1- picture; fig.2- drawing. (dpc) deltopectoral crest, (itub) internal tuberosity, (rad) radial condyle, (rid) ridge. Scale bars = 50mm.

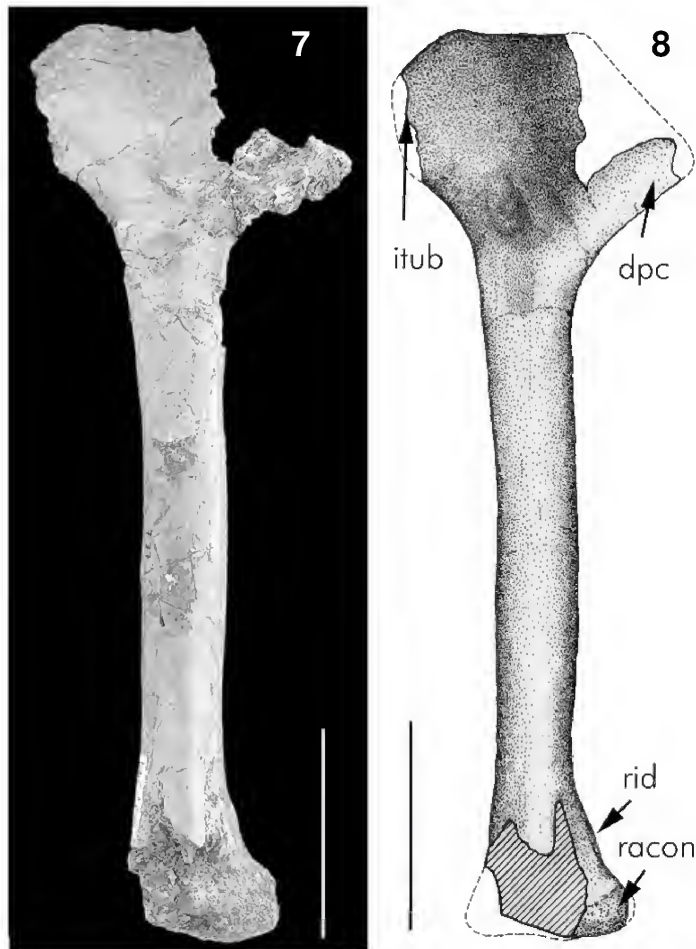


Uenlagia paynemili n.sp., left humerus (MUCPv-349) – fig.3- picture, posterior view; fig.4- drawing, posterior view; fig.5- picture, ventral view; fig.6- drawing, ventral view. (dpc) delto pectoral crest, (itub) internal tuberosity, (rid) ridge. Scale bars = 50mm.

The left pubis (MUCPv-349) of *Uenlagia paynemili* n.sp. is almost complete (length: 267mm) while the right one is represented only by a thin layer of bone at the tip of the distal half, forming the pubic boot (Figs.11-19). Overall, the pubis is a slender and comparatively thin bone, with an anteroposteriorly expanded proximal end that is slightly displaced medially (anterior view). In proximal view, the iliac articulation is slightly concave, long and narrow. The shaft has a convex anterior surface, with the distal part directed posteroventrally. In anteroposterior view, the lateral margin is sigmoidal, with the proximal half concave and the distal half convex. The distal end is expanded anteroposteriorly, with both pubes fusing in the midline forming a pubic boot, and showing a small anterior projection (Figs.11-16). The pubic apron is deflected posteriorly and extends for about 135mm, reaching half the public

shaft (Figs.13-18). Apparently this flange is too narrow to meet at the midline with the opposite element. Except for the proximal region, most of the pubic flange extends medially from the anterior margin of the shaft.

Although no complete ilium is available for *Uenlagia paynemili* n.sp., the comparisons with other maniraptorans, particularly *Uenlagia comahuensis* indicate that the pubes is positioned vertically. The pubic apron of the new form is extended for about half of the public shaft like in most maniraptorans but differing from the smaller pubic apron diagnostic of the Avialae (NORELL, CLARK & MAKOVICKY, 2001). Contrary to some other maniraptorans (e.g., *Velociraptor* Osborn, 1924), the opposite flange forming the pubic apron apparently does not meet in the midline, a condition also reported in *Uenlagia comahuensis* (NOVAS & PUERTA, 1997).



Unenlagia paynemili n.sp., left humerus (MUCPv-349) - fig.7-picture; fig.8- drawing. (dpc) delto pectoral crest; (itub) internal tuberosity; (rad) radial condyle; (rid) ridge. Scale bars = 50mm.

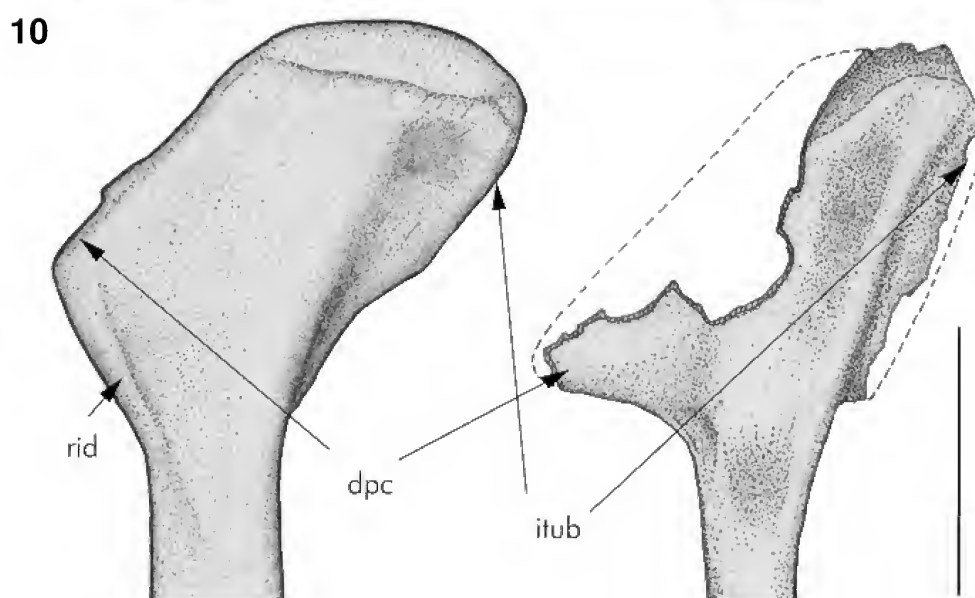
The comparisons of the pubes of *Unenlagia paynemili* n.sp. with other maniraptorans show that it is more similar to *Unenlagia comahuensis*, both sharing at least one feature: the posteriorly oriented distal end of the pubis that shows a convex anterior margin (Figs.20-21). Although NOVAS & PUERTA (1997) reconstructed the pubis of *Unenlagia comahuensis* in a straight fashion in lateral view, a closer examination of the holotype indicates that the pubis (particularly the left one) had the distal part directed posteriorly as in *Unenlagia paynemili* n.sp., this character is considered a synapomorphy of *Unenlagia*. This feature differs from the straight pubes found in most other theropods and from the anteriorly curved distal pubic end of the oviraptorids (BARSBOLD, MARYANSKA & OSMÓLSKA, 1990).

The main difference between the pubes of *U. paynemili* n.sp. and *U. comahuensis* is the presence of an anterior component in the pubic boot in the new

species absent in the latter. More basal theropods such as *Carnotaurus* Bonaparte, 1985 (BONAPARTE, NOVAS & CORIA, 1990), *Pycnonemosaurus* Kellner & Campos, 2002 (KELLNER & CAMPOS, 2002), *Sinraptor* Currie & Zhao, 1993 (CURRIE & ZHAO, 1993) and many coelurosaurs like the Oviraptorosauria (BARSBOLD, MARYANSKA & OSMÓLSKA, 1990) have the anterior portion of the pubes more developed. Other maniraptorans like *Velociraptor* also show a small anterior extension of the pubic boot (NORELL & MAKOVICKY, 1999) but differ from *Unenlagia paynemili* n.sp. by being dorsoventrally expanded.

In posterior view, the shaft is bowed at the third distal end as in *Unenlagia comahuensis*, differing from other maniraptorans where the lateral margin is bowed more proximally like *Velociraptor mongolensis* Osborn, 1924 (NORELL & MAKOVICKY, 1999); or straight like *Achillobator giganticus* Perle, Norell & Clark, 1999 (PERLE, NORELL & CLARK, 1999); *Tyrannosaurus rex* Osborn, 1905 (OSBORN, 1905; BROCHU, 2003); *Avimimus portentosus* Kurzanov, 1981; Coelurosauria indet. (MARTILL *et al.*, 2000). This character is just present in *Unenlagia comahuensis* and *Unenlagia paynemili* n.sp. and it might be another synapomorphy uniting those taxa.

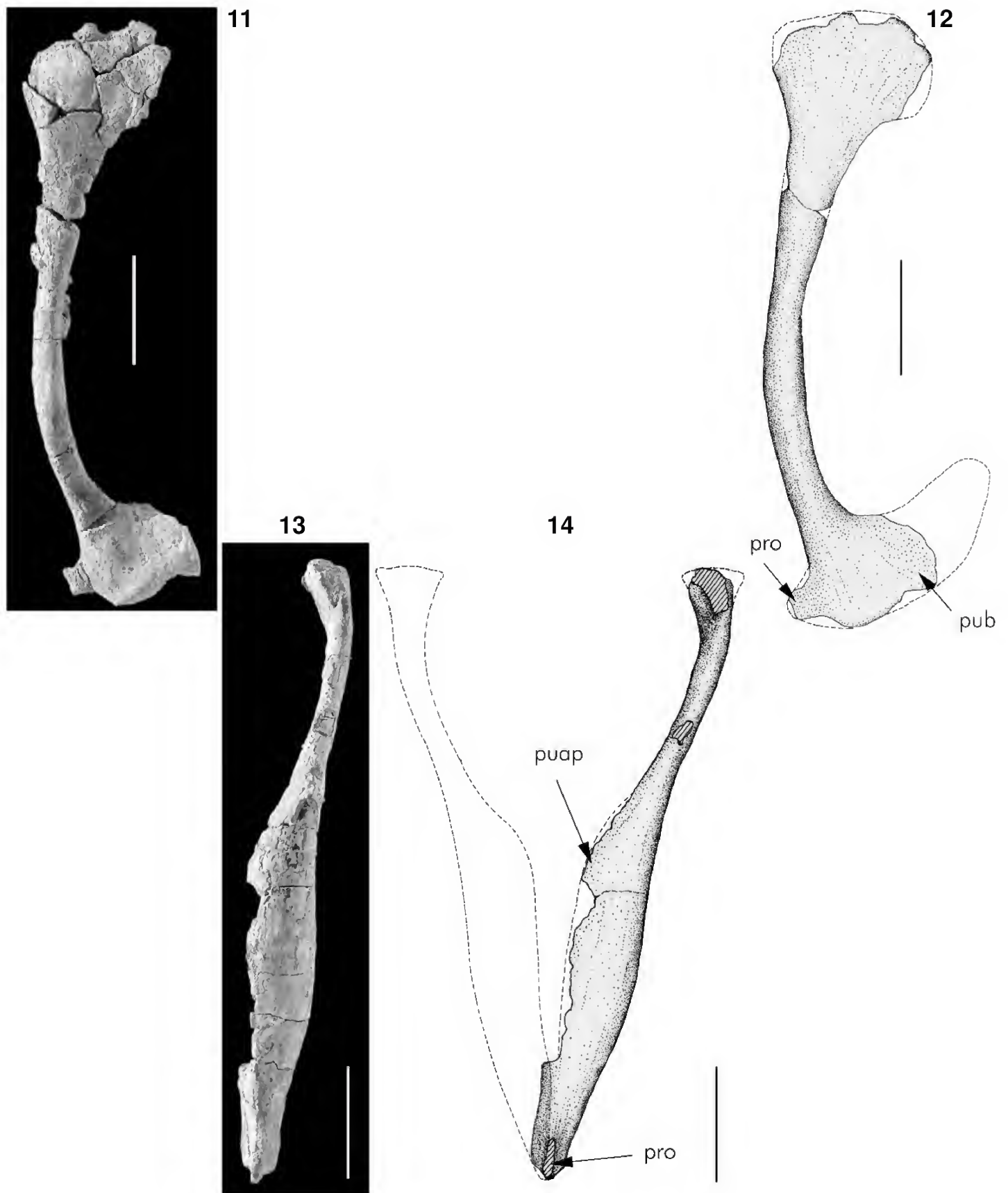
Only the posterior portion of the right ilium (MUCPv-409) was found (length of preserved portion: 103mm), including the posterior part of the acetabulum (Figs.22-31). In dorsal view, the dorsal margin of the preserved part is sigmoid, with the posterior end displaced laterally (Figs.24-25). The postacetabular blade forms a thin lamina of bone that shows a strong lateral concavity corresponding to a medial convexity. Overall it is short and acuminate, showing a marked inflection on the dorsal margin posterior to the acetabulum. The lateral surface is smooth. Close to the dorsal margin before the beginning of the inflected border of the postacetabular portion a rugose area is present; two distinct knob-like structures are present, possibly for muscle attachment. Some weakly grooves and ridges, likely for muscle scars, are also present at the most posterior end (on the lateral and medial surfaces). Ventrally, the brevis fossa is narrow and shallow. Medially a marked ridge forms the medial shelf of the brevis fossa that is directed posterodorsally running divergent from the ventral margin of the postacetabular blade. A rounded depression is present above the posterior part of the acetabulum. The preserved surface of the acetabulum forms a rugose surface that broadens posteriorly, ending in a thick posterior edge ("lip") that is part of the ischiadic peduncle.



Comparison of the proximal part of the left humerus of *Unenlagia comahuensis* (MCF PVPH 78 - left) and *Unenlagia paynemili* n.sp. (MUCPv-349 - right) – fig.9- picture, fig.10- drawing. (dpc) delto pectoral crest, (itub) internal tuberosity, (rid) ridge. Scale bars = 50mm.

Comparing the preserved part of the ilium with other coelurosaurs, *Unenlagia paynemili* n.sp. shows the postacetabular part of the ilium acuminate, a feature considered synapomorphic of the Maniraptora (NORELL, CLARK & MAKOVICKY, 2001) that contrasts to the more square outline observed in other theropods such as *Sinraptor* (CURRIE & ZHAO, 1993). The brevis fossa is shelf-like, a common feature within Maniraptora. Among coelurosaurs, *Unenlagia paynemili* n.sp. shares one feature, at the ilium, with *Unenlagia*

comahuensis – the marked inflection of the dorsal margin of the postacetabular blade that is here considered a diagnostic feature of the genus *Unenlagia*. The main differences between those species are the more rounded (and less) acuminate posterior edge and the shallower brevis fossa of *Unenlagia paynemili* n.sp. that also has a narrower and more open posterior portion of the acetabulum. Furthermore *Unenlagia comahuensis* shows a well developed ridge dividing the brevis fossa that is absent in *Unenlagia paynemili* n.sp.

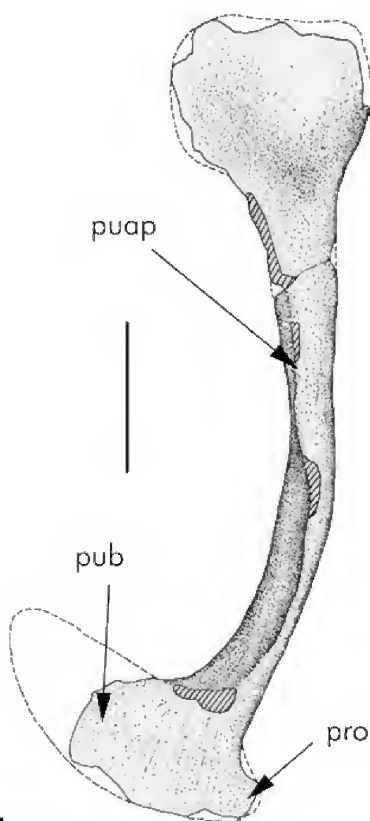


Unenlagia paynemili n. sp., left pubis (MUCPv-349) – fig. 11- picture, lateral view; fig. 12- drawing, lateral view; fig. 13- picture, anterior view; fig. 14- drawing, anterior view. (pro) bone projection, (puap) pubic apron, (pub) pubic boot. Scale bars = 50mm.

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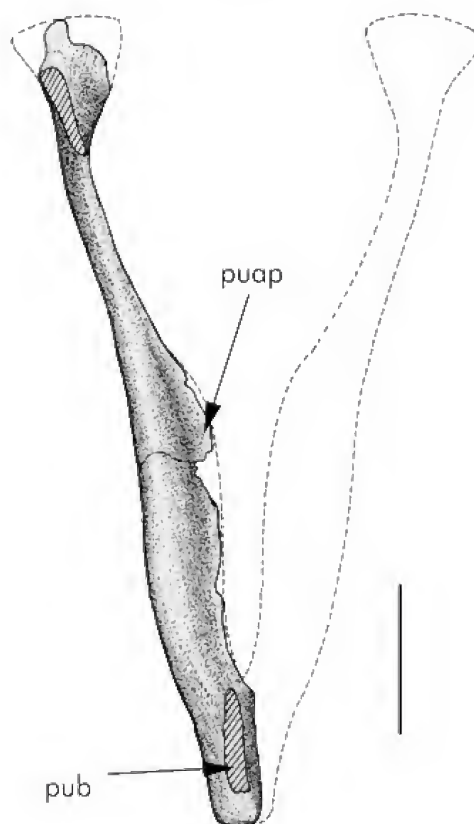
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Unenlagia paynemili n.sp., left pubis (MUCPv-349) – fig.15- picture, medial view; fig.16- drawing, medial view; fig.17- picture, posterior view; fig.18- drawing, posterior view. (pro) bone projection, (puap) pubic apron; (pub) pubic boot. Scale bars = 50mm.

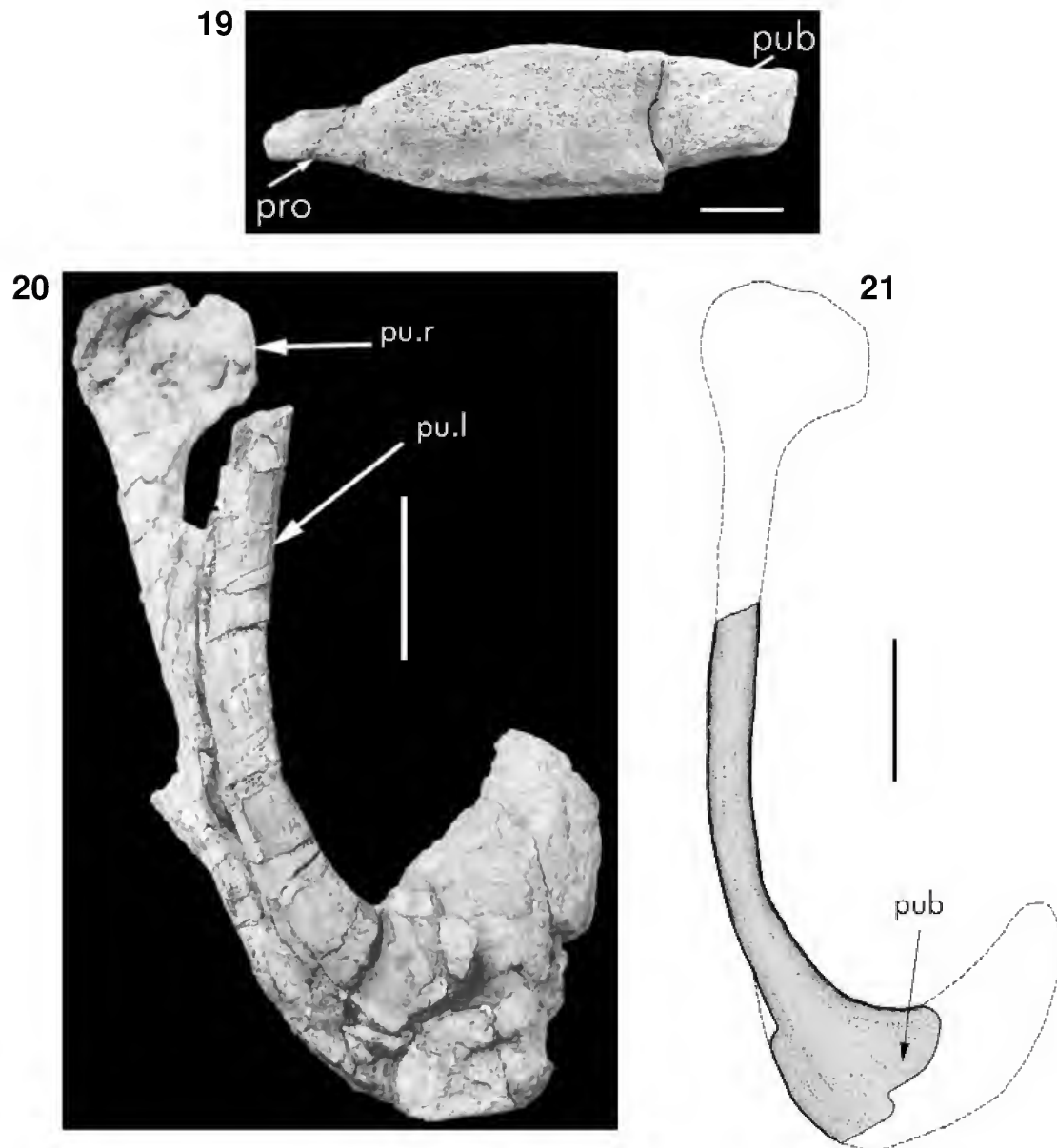
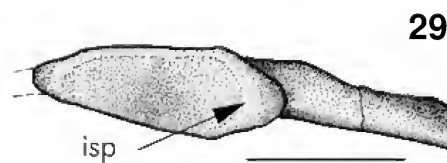
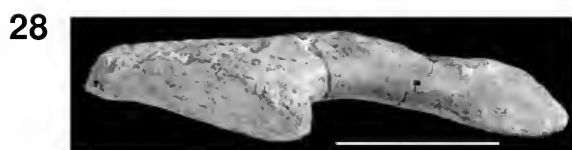
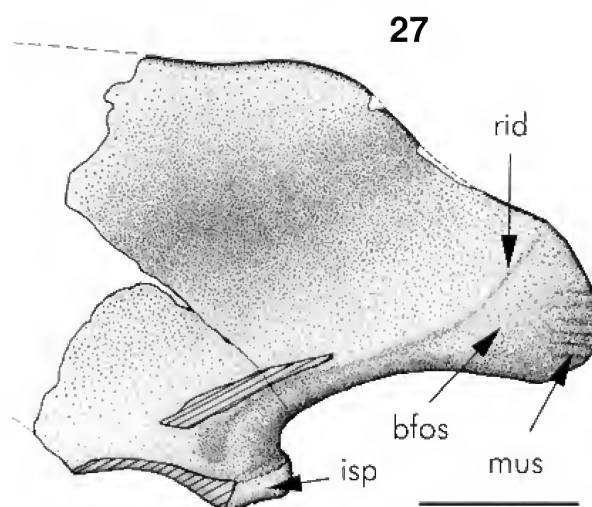
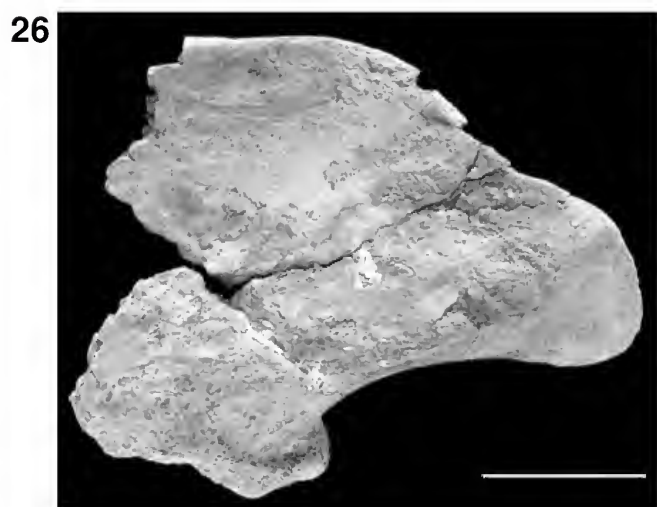
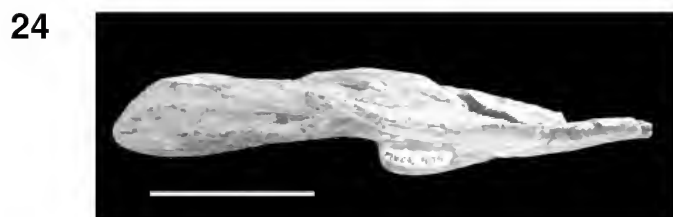
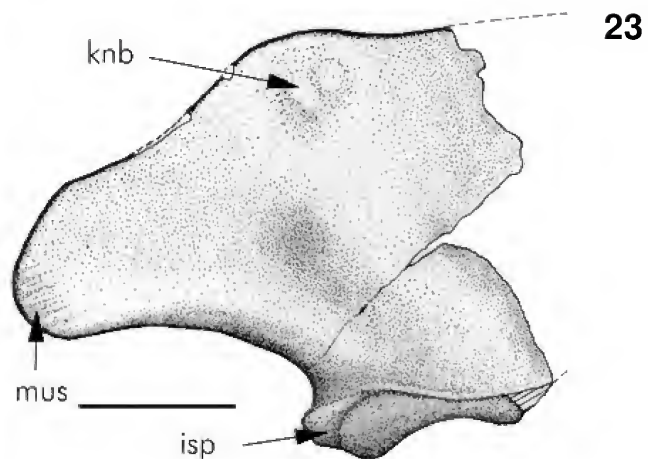
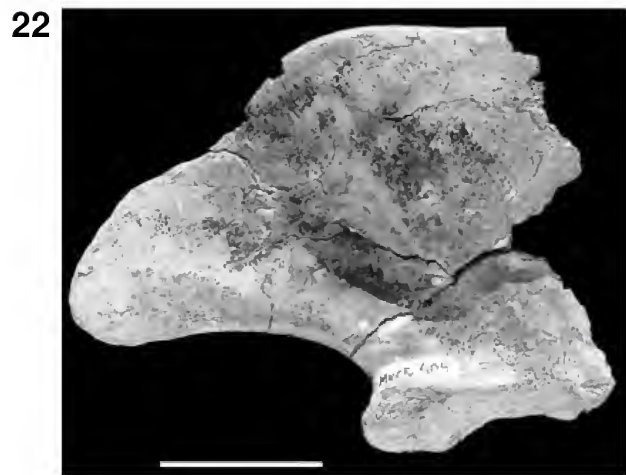


Fig.19- *Unenlagia paynemili* n.sp., picture of the distal part of the left pubis (MUCPv-349) showing the pubic boot and the anterior projection. Scale bar = 10mm. *Unenlagia comahuensis* (MCF PVPH 78) – fig.20- picture of the pubia, fig.21- drawing of the left pubis (MUCPv-349) in lateral view. Scale bar = 50mm. (pro) bone projection, (pub) pubic boot, (pu.l) left pubis, (pu.r) right pubis.

Only one dorsal vertebra (MUCPv- 416) was found. It shows the centrum and part of the neural arch, lacking the neural spine and most of the zygapophyses (Figs.32-35). Neural arch and the centrum are fused. One deep lateral pit on the basal portion of the neural spine is present on each side (Figs.34-35). Other more laterally placed openings (two on the right and one of the left side) are also observed and were possibly situated at the ventral base of the transverse processes that are broken in this specimen (Figs.32-33). The basal part of the

postzygapophyses is preserved and indicates that they are placed lateral to the neural canal and separated by a groove for the interspinous ligaments. Although present, hyposphenes are not sufficiently preserved to determine if they are separated, a feature present in *Unenlagia comahuensis* and in most Maniraptora (NORELL, CLARK & MAKOVICKY, 2001). The parapophyses are situated on the neural arch. The last one is not complete; although, they are clearly projected outward, a common feature present in dromeosaurids (and alvarezsaurids).

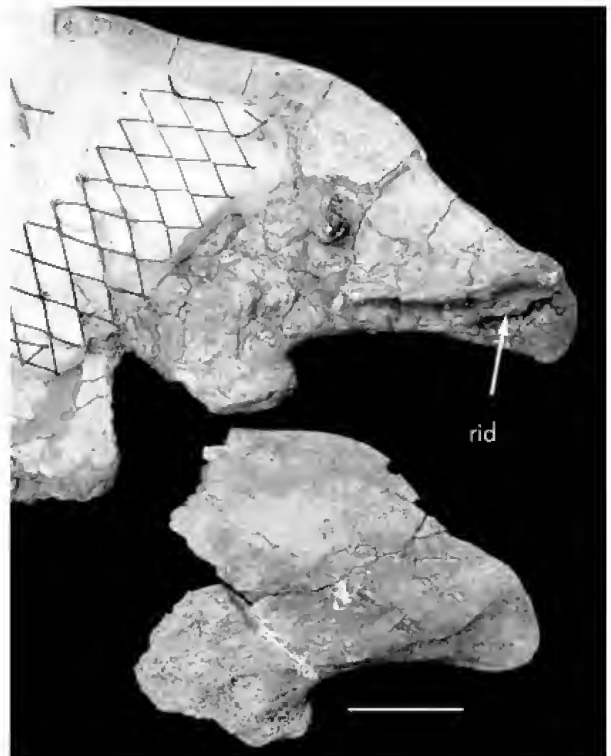


Unenlagia paynemili n.sp., right ilium (MUCPv-409) – fig.22- picture, lateral view; fig.23- drawing, lateral view; fig.24- picture, dorsal view; fig.25- drawing, dorsal view; fig.26- picture, medial view; fig.27- drawing, medial view; fig.28- picture, ventral view; fig.29- drawing, ventral view. (bfos) brevis fossa, (isp) ischiadic peduncle; (knb) knob-like protuberance; (mus) muscle scars, (rid) ridge. Scale bars = 30mm.

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Picture comparing the posterior part of the right ilium of *Unenlagia comahuensis* (MCF PVPH 78 - top) and *Unenlagia paynemili* n.sp. (MUCPv-409 - bottom) – fig.30- lateral view, fig.31- medial view. (rid) ridge. Scale bars = 30mm.

The centrum is amphiplatyan, with the anterior articulation surface rounded and the posterior surface slightly wider than higher. Close to the contact with the neural arch, one pleurocoel followed by a small depression is present on each side. A shallow groove followed by a small foramen is present on the ventral side of the centrum.

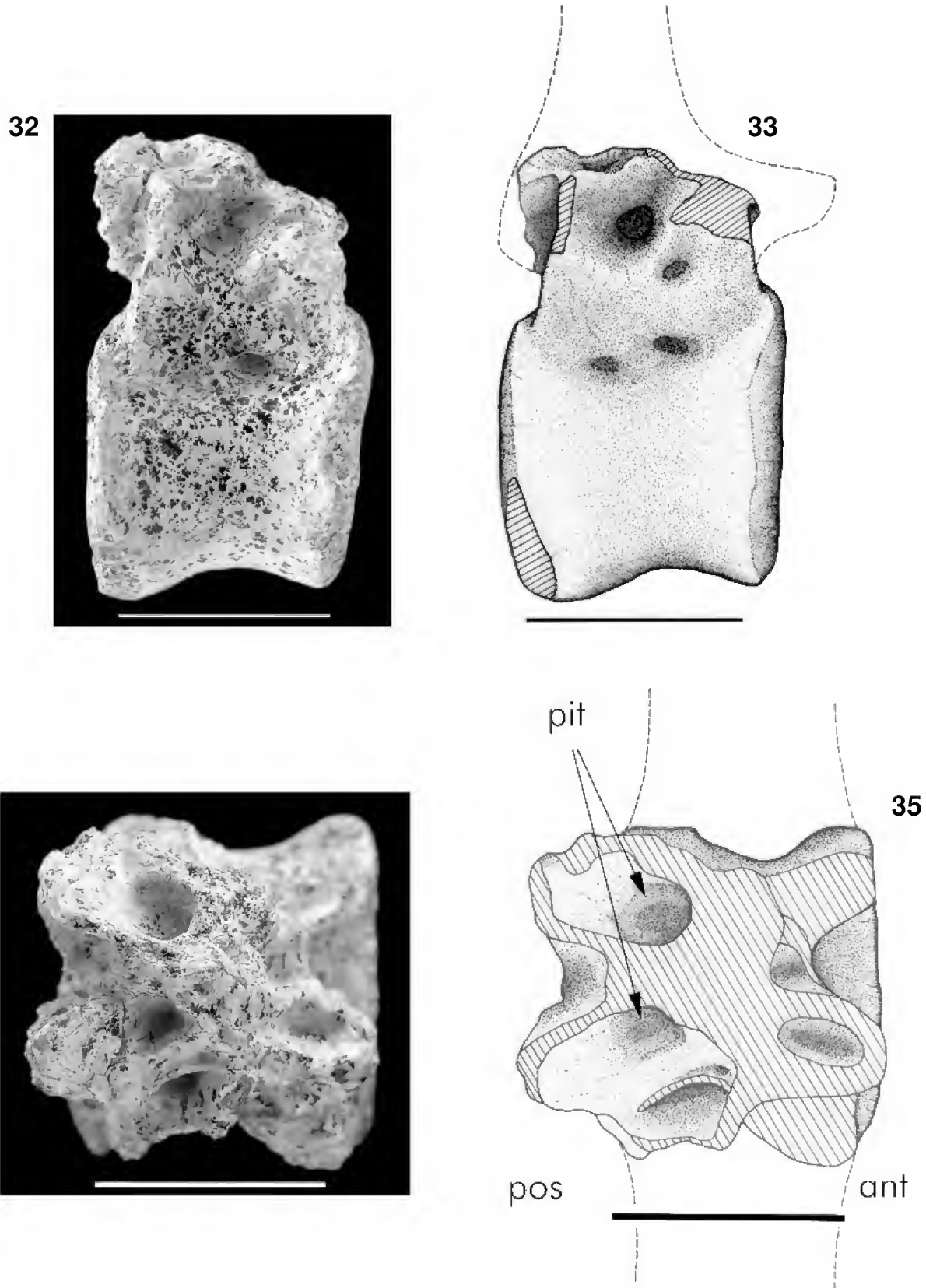
The most interesting feature of the MUCPv- 416 is the presence of a lateral pit close to the base of the neural spine, which has been reported in the posterior dorsals of *Unenlagia comahuensis* (NOVAS & PUERTA, 1997). Other dorsals of the holotype of this species, however, do not show this feature (pers. obs.)

A complete pedal phalanx (MUCPv-415) was also found in the same quarry and is tentatively referred to *Unenlagia paynemili* n.sp. (Figs.36-37). The specimen is complete and represents the first phalanx of the right digit I. The distal condyles are asymmetric and are separated by a marked groove. The lateral condyle shows a developed sub-circular fossa (possible for ligaments) while in the medial condyle this fossa is less developed. Proximally the articulation with the metatarsal is formed by two asymmetric surfaces separated by a blunt ridge, with the lateral one larger than the medial. Dorsally a bony ridge is positioned on the medial side. It

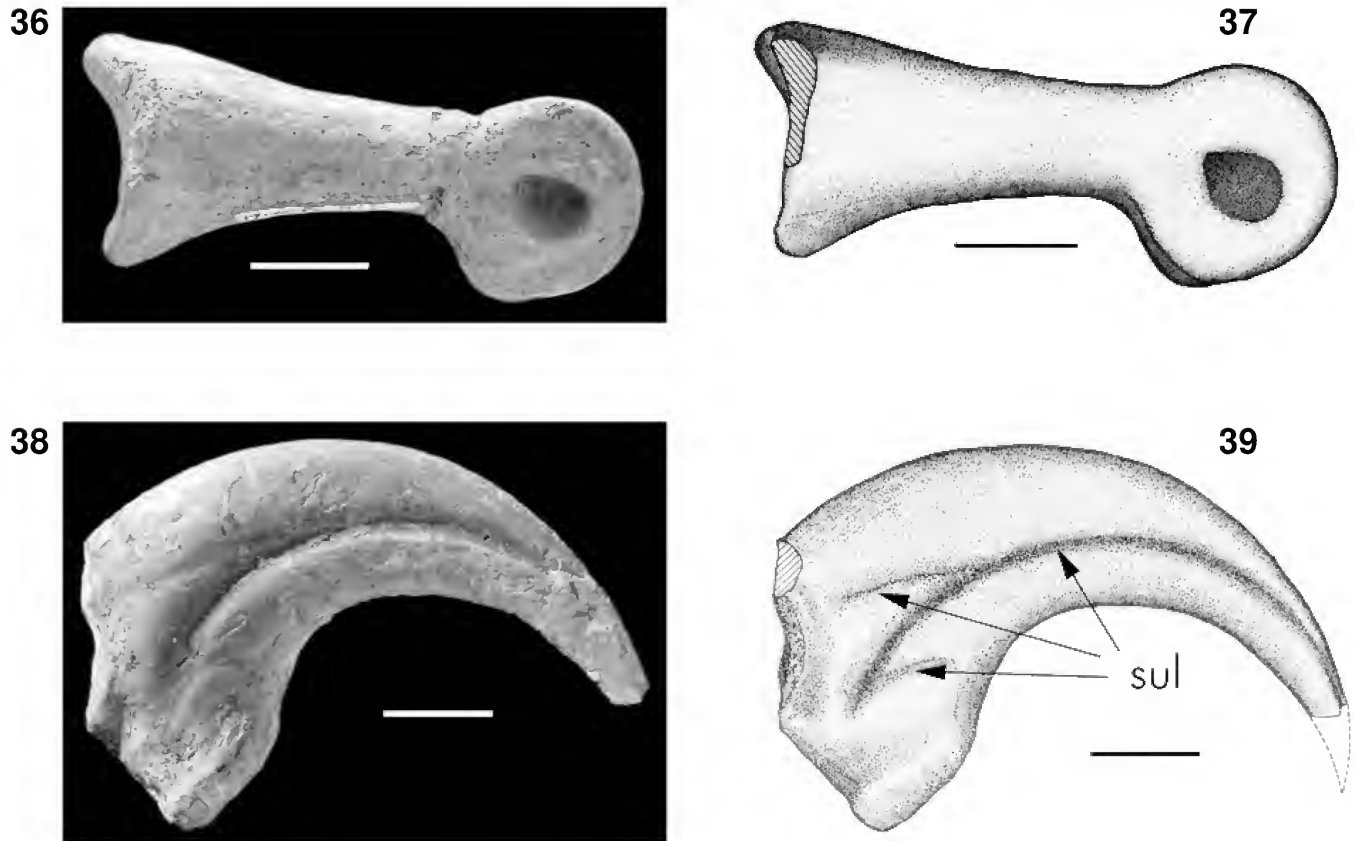
extends about one third of the total length of the phalanx, and it was likely the attachment surface for a muscle or ligament.

An ungueal phalanx (MUCPv-343) is also tentatively referred to *Unenlagia paynemili* n.sp. (Figs.38-39). It is strongly curved and laterally compressed, 65mm long on the dorsal border, and about 29mm high at the proximal end. On each side there is a groove that runs on the middle part of the claw, starting proximally close to the basal portion, reaching the dorsal margin close to the tip. Two additional parallel sulcus are present on one side. The upper sulcus runs from the proximal region, near the articular facets up to the middle groove. The lower sulcus starts at the base of the middle groove and reaches the ventral region of the claw anterior to the flexor tubercle. The ventral rim is lateroventrally rounded. It presents a flexor tubercle well developed placed below the articular facets, the latter being asymmetrical.

The lateral compression and the curvature of the *Unenlagia paynemili* n.sp. claw resemble that present in digit I of *Rahonavis* Forster, Sampson, Chiappe, & Krause, 1998. Although no foot is known from *Unenlagia comahuensis*, it should be noted that FORSTER *et al.* (1998) suggest that *Unenlagia comahuensis* should have had a similar claw to *Rahonavis*.



Unenlagia paynemili n.sp., dorsal vertebra (MUCPv-416) – fig.32- picture, right lateral view; fig.33- drawing, right lateral view; fig.34- picture, dorsal view; fig.35- drawing, dorsal view. (ant) anterior, (pit) lateral pit, (pos) posterior. Scale bars = 30mm.



Pedal phalanx (MUCPv-415), which is tentatively referred to *Unenlagia paynemili* n.sp. – fig.36- picture, fig.37- drawing, lateral view. Ungual (MUCPv-343), which is tentatively referred to *Unenlagia paynemili* n.sp. – fig.38- picture, fig.39- drawing, lateral view. (sul) sulcus. Scale bars = 10mm.

DISCUSSION

The dinosaur material collected from the Futalogno site includes articulated and isolated material. As common in paleontology, it is always difficult to associate isolated bones to one taxon, which is also the case of the material of *Unenlagia paynemili* n.sp. However, each of the main bones – the humerus, pubis, ilium and vertebra shows features attributed to *Unenlagia* (NOVAS & PUERTA, 1997). Based on the proportions and proximity in the quarry, the humerus and pubis are regarded as belonging to the same individual. Although the ilium might also belong to the same individual as the former, its position in the quarry lead us to cautiously regard it as belonging to a different animal of the same species. The dorsal vertebra definitively belongs to another much larger individual, but the presence of deep lateral pits in the base of the neural spines suggests that it belongs to an *Unenlagia*-type taxon and is therefore referred to *Unenlagia paynemili* n.sp.

In order to assess the phylogenetic position of the Barreal taxon, we used the comprehensive phylogenetic analysis of coelurosaurian relationship presented by NORELL, CLARK & MAKOVICKY (2001), consisting of 44 taxa (including *Unenlagia comahuensis*) and 205 characters. They used the algorithm NONA v. 1.9 through the WinClada interface and obtained 1065 equally parsimonious trees with a length of 554 steps, consistency index (CI) of 0.45 and a retention index of (RI) 0.73. We used the same data set and run it through PAUP 4.0b10 for Microsoft Windows, using the general heuristic search option (SWOFFORD, 2000). Characters were given equal weight and 11 were ordered, *Allosaurus* and *Sinraptor* were used as outgroups, following NORELL, CLARK & MAKOVICKY (2001). The consensus tree was further analyzed by MacClade 3.04 (MADDISON & MADDISON, 1992).

Differing from the previous study, PAUP encountered a much larger number of equally parsimonious trees (170.100; CI: 0.4554; RI:

0.7150) with a shorter length of 549 steps. The consensus tree also differs from the one published by NORELL, CLARK & MAKOVICKY (2001), by recovering a monophyletic Dromaeosauridae (including *Unenlagia comahuensis*) in sister group relationship with the Avialae (compare figures 40 and 41). Within Dromaeosauridae, PAUP recovered a trichotomy formed by *Unenlagia*, *Sinornithosaurus* and all other dromaeosaurids (which in the previous study formed a polytomy). Furthermore, PAUP resolved the relationship between Troodontidae, with *Sinornithoides* followed stepwise by *Byronosaurus*, *Troodon* and *Saurornithoides*.

The next step was to include the information available for *Unenlagia paynemili* n.sp. using the same data matrix and run it through PAUP. Only 10 characters could be scored for the new species (141/ 162/ 180: state 0; 105-106/ 160/ 176-178: state 1; 179: state 2), all remaining are unknown (1-104/ 107-140/ 142-159/ 161/ 163-175/ 181-205: ?). We also changed character 179, concerning the pubic shaft, which according to NORELL, CLARK & MAKOVICKY (2001) could vary from being straight (state 0) or curved anteriorly (state 1). The direct observation of the holotype of *Unenlagia comahuensis*, as well as the Barreal specimen, leads us to include a third state: distal end of pubis curved posteriorly (state 2). This modified data set was run through PAUP and obtained the same number of equally parsimonious trees which were expectedly one step longer (550 steps; CI: 0.4564; RI: 0.7158). The topology of the tree did not change, and differed only by showing a monophyletic grouping formed by *Unenlagia comahuensis* and the Barreal specimen (Fig.41). Based on the comparisons and phylogenetic analysis, we opted to consider the Barreal specimen congeneric with *Unenlagia comahuensis*, proposing the new species *Unenlagia paynemili* n.sp. Although it is quite possible that a generic differentiation might be applied in the future for the Barreal taxon, we prefer to wait until more complete and articulated material comes to light. According to the hypothesis of coelurosaurian relationships published by NORELL, CLARK & MAKOVICKY (2001), *Unenlagia paynemili* n.sp. presents two maniraptoran synapomorphies: the acuminate postacetabular ala of the ilium and vertical placed pubis (proximal part). The new Barreal taxon also shows a synapomorphy that unites all maniraptoran except *Ornitholestes*: the brevis fossa shelf-like. It further has a comparatively

small anterior projection of the pubic boot also absent or slightly projected in Avialae and Dromaeosauridae opposed to the well anterior projection known in most other theropods (e.g., *Allosaurus*, *Deinonychus antirrhopus*). *Unenlagia paynemili* n.sp. does not have at least one synapomorphy of the Avialae: reduced pubic apron. Furthermore it shares one synapomorphic feature with *Unenlagia comahuensis*: the posteriorly oriented distal end of the pubis.

Among the diagnostic features of *Unenlagia comahuensis*, NOVAS & PUERTA (1997) point out the presence of lateral pits at the base of the neural spines of the posterior dorsals and anterior sacrals and the inflected margin of postacetabular iliac blade. Those features are present in the referred specimens of *Unenlagia paynemili* n.sp. and might be considered two additional synapomorphies uniting those taxa. It should be noted, however, that the two additional dorsal vertebrae of the holotype of *Unenlagia comahuensis* lack lateral pits. The main differences between *Unenlagia comahuensis* and the new Barreal taxon is the different angle of the distal margin of the deltopectoral crest, the more rounded posterior edge of the ilium and the projection on the anterior part of the pubis. Furthermore the postacetabular portion of the ilium of *Unenlagia paynemili* n.sp. has a shallower brevis shelf with a smooth surface lacking the ridge present in *Unenlagia comahuensis*.

CONCLUSIONS

The new Barreales lake species shares one synapomorphy with *Unenlagia comahuensis*: the particular posterior inclination of the distal end of the pubis. One more character is shared by those taxa and is regarded as a potential synapomorphy of *Unenlagia*: the inflected dorsal margin of the postacetabular iliac blade. Although the dorsal vertebra of the Barreal species also shows the lateral pits at the base of the neural spine observed in *Unenlagia comahuensis* (NOVAS & PUERTA, 1997), this feature is absent in the additional two dorsal vertebrae of the type material and has to be seen with caution. Although the Barreales lake material possibly represents a new genus, we regard classify this species within the genus *Unenlagia* until more material allowing a better characterization is found. The several observed anatomical differences, however, lead us to propose a new species, *Unenlagia paynemili* n.sp.

The phylogenetic position of *Unenlagia* is disputed

with some authors regarding this taxon in sister group relationships with the Avialae (NOVAS & PUERTA, 1997) member of the Avialae (FORSTER *et al.*, 1998) or a dromeosaurid not closely related to Avialae (NORELL & MAKOVICKY, 1999; NORELL, CLARK & MAKOVICKY, 2001). Unfortunately the incomplete nature of the *Unenlagia paynemili* n.sp. does not resolve this dispute. Since we used the data basis of NORELL, CLARK & MAKOVICKY (2001), we end up as having both species of *Unenlagia* as members of the Dromeosauridae (Fig.41). Although

the analysis of the coelurosaurian phylogenetic hypothesis published by NORELL, CLARK & MAKOVICKY (2001) is not the purpose of the paper, the fact that PAUP produced different results than NONA, particularly recovering shorter and more resolved parsimonious trees is somewhat intriguing and should be object of further studies.

In any case, the discovery of this new species of *Unenlagia* indicates a higher diversity of those enigmatic *Unenlagia*-type maniraptorans.

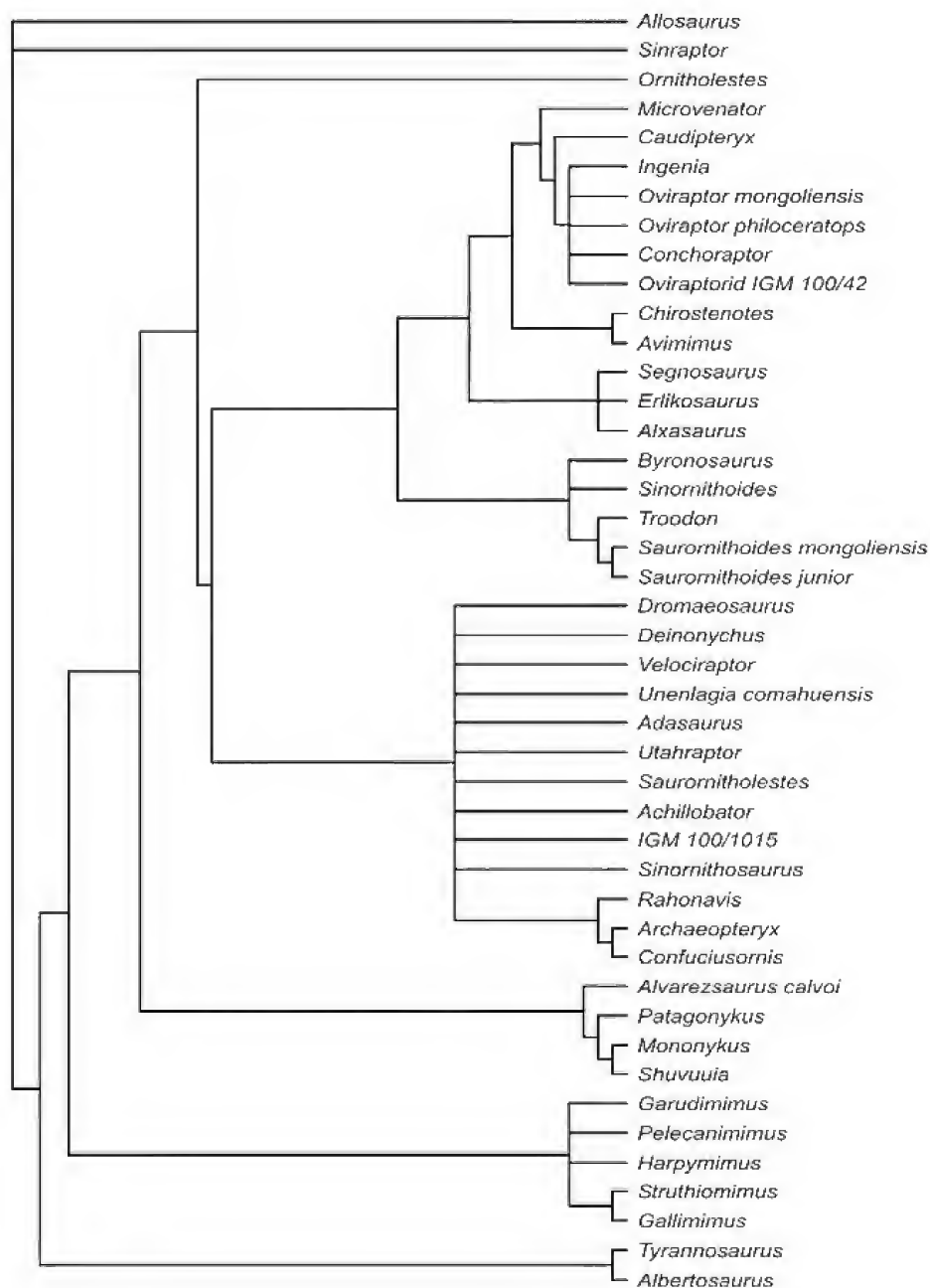


Fig.40- Strict consensus cladogram published by NORELL, CLARK & MAKOVICKY (2001).

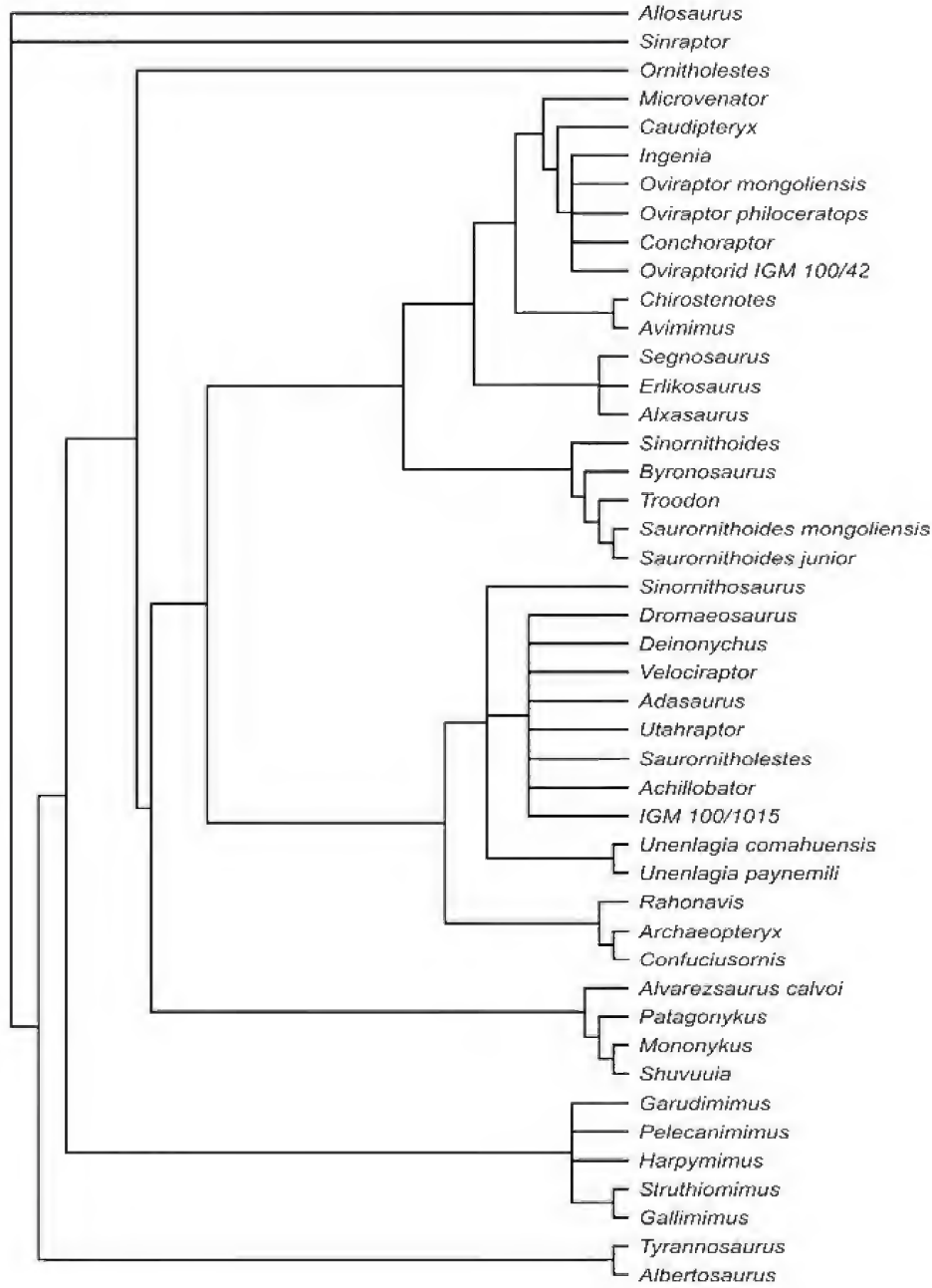


Fig.41- Strict consensus cladogram based on the data set of NORELL, CLARK & MAKOVICKY (2001) run through PAUP 4.0b10, including the *Unenlagia paynemili* n.sp. See text for details.

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