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DANILO PINTO LIMA

CARACTERIZAÇÃO E DIFERENCIAÇÃO MORFOLÓGICA E FUNCIONAL DA
PLACA
DENTÁRIA DOS REPRESENTANTES DA FAMÍLIA POTAMOTRYGONIDAE
(ELASMOBRANCHII: MYLIOBATIFORMES)

JOÃO PESSOA

2025

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(ELASMOBRANCHII: MYLIOBATIFORMES)**

Dissertação apresentada ao Programa de Pós-Graduação em Ciências Biológicas (Zoologia) da Universidade Federal da Paraíba, como requisito parcial para a obtenção do título de Mestre em Ciências Biológicas.

Orientador: Prof. Dr. João Paulo Capretz Batista da Silva

Coorientadora: Dra. Aline Nayara Poscai

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Ao(s) vinte e sete dias do mês de junho de dois mil e vinte e cinco, às 14:00 horas, no(a) Ambiente Virtual, da Universidade Federal da Paraíba, reuniram-se, em caráter de solenidade pública, membros da banca examinadora para avaliar a dissertação de mestrado de **Danilo Pinto Lima**, candidato(a) ao grau de Mestre(a) em Ciências Biológicas. A banca examinadora foi composta pelos seguintes membros: **Dr. João Paulo Capretz Batista da Silva (Orientador- UFPB/PB); Dr. Aléssio Datovo (MZUSP/SP) e a Dra. Akemi Shibuya (INPA/AM).** Compareceram à solenidade, além do(a) candidato(a) e membros da banca examinadora, alunos e professores do PPGCB. Dando início à sessão, a coordenação fez a abertura dos trabalhos, apresentando o(a) discente e os membros da banca. Foi passada a palavra ao(à) orientador(a), para que assumisse a posição de presidente da sessão. A partir de então, o(a) presidente, após declarar o objeto da solenidade, concedeu a palavra a **Danilo Pinto Lima**, para que dissertasse, oral e sucintamente, a respeito de seu trabalho intitulado **“Caracterização e diferenciação morfológica e funcional da placa dentária dos representantes da família Potamotrygonidae (Elasmobranchii: Myliobatiformes)”**. Passando então a discorrer sobre o aludido tema, dentro do prazo legal, o(a) candidato(a) foi a seguir arguido(a) pelos examinadores na forma regimental. Em seguida, passou a Comissão, em caráter secreto, a proceder à avaliação e julgamento do trabalho, concluindo por atribuir-lhe o conceito **APROVADO**. Perante o resultado proclamado, os documentos da banca foram preparados para trâmites seguintes. Encerrados os trabalhos, nada mais havendo a tratar, eu, orientador(a), como presidente, lavrei a presente ata que, lida e aprovada, assino juntamente com os demais membros da banca examinadora.

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In memoriam a Enésia dos Santos Lima.

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“The morphology of elasmobranch teeth continues to be a vital systematic character that should not be neglected when describing a new living species.”

Guinot *et al.*, 2018.

RESUMO

A família Potamotrygonidae consiste em um grupo único de raias neotropicais. Englobam duas subfamílias compostas por algumas raias marinhas, e em sua maioria pela única linhagem bem estabelecida de raias de água doce. Tratam-se de quarenta espécies válidas, que se distribuem pela maioria dos rios que deságuam no Atlântico com exceção de parte do Nordeste, do Sudeste e parte do Sul brasileiro. Apesar de serem bem conhecidas pelas comunidades locais e pelo aquarismo, as interrelações de parentesco entre as espécies são complicadas, de modo que diversas proposições divergentes foram elaboradas desde a primeira descrição do grupo. Neste contexto, dados de anatomia interna e externa também são escassos ou foram mal explorados, de modo que dados sobre a morfologia dentária para o grupo são escassos ou ausentes. Do mesmo modo, dados sobre a alimentação e sua relação com a morfologia dentária também são escassos. O presente estudo, portanto, tem como objetivos realizar uma descrição morfológica e comparativa da placa dentária dos representantes da família Potamotrygonidae, otimizar os caracteres dentários propostos em uma árvore filogenética combinada para entender sua evolução dentro do grupo e correlacionar os caracteres levantados com os hábitos alimentares conhecidos na literatura. Ao todo 42 exemplares de 21 espécies foram avaliados. A placa dentária foi removida com o auxílio de materiais de dissecação, e os exemplares foram avaliados com auxílio de micro-CT e de uma lupa estereoscópica. 54 caracteres morfológicos foram levantados, e a partir destes uma análise filogenética combinada com dados moleculares foi executada. Também foi realizada uma pesquisa bibliográfica dos hábitos alimentares disponíveis na literatura. Estes foram correlacionados com a morfologia dentária em uma reconstrução histórica em cima da árvore filogenética resultante. Resultados da análise filogenética corroboram com algumas relações de parentesco previamente levantadas, com dois clados principais em Potamotrygoninae compostos por *Heliotrygon* e *Paratrygon* + *Plesiotrygon* e *Potamotrygon*, e a possibilidade de *Potamotrygon* ser parafilético sem a inclusão de *Plesiotrygon*. A reconstrução histórica dos hábitos alimentares demonstrou especializações de *Heliotrygon* e *Paratrygon* a uma morfologia mais adaptada a piscivoria, de espécies como *Potamotrygon jabuti* e *Potamotrygon motoro* a predação de alimentos mais duros, e uma adaptação ao esmagamento de presas para a maioria dos Potamotrygoníneos.

Palaeras-chave: Batoidea; Neotropical; Potamotrygoninae; raias; Styracurinae; dente.

ABSTRACT

The family Potamotrygonidae consists of a unique group of Neotropical stingrays. It includes two subfamilies composed of a few marine species, and the only well-established lineage of freshwater stingrays. The group comprises forty valid species distributed across most river basins that flow into the Atlantic Ocean, except for a few parts of northeastern, southeastern, and southern Brazil. Although the group is well known by local communities and the aquarium trade, the phylogenetic relationships among its species are complex, and several divergent hypotheses have been proposed. In this context, data on internal and external anatomy are scarce or poorly explored, and information on dental morphology within the group is limited or absent. Likewise, data on feeding habits and their relationship with dental morphology are also scarce. Therefore, the present study aims to conduct a morphological and comparative description of the dental plate of representatives of the family Potamotrygonidae, to optimize the proposed dental characters in a combined phylogenetic tree to understand their evolution within the group, and to correlate the identified dental characters with known feeding habits reported in the literature. A total of 42 specimens representing 21 species were examined. The dental plates were removed using dissection tools, and the specimens were analyzed using micro-CT scanning and a stereomicroscope. 54 morphological characters were identified, and a combined phylogenetic analysis including molecular data was conducted. A literature review of feeding habits was also performed, and this information was correlated with the dental morphology through a historical reconstruction on the resulting phylogenetic tree. The phylogenetic analysis supports some previously proposed relationships, revealing two main clades within Potamotrygoninae: one composed of *Heliotrygon* and *Paratrygon* + *Plesiotrygon*, and *Potamotrygon*, with the possibility that *Potamotrygon* is paraphyletic without the inclusion of *Plesiotrygon*. The historical reconstruction of feeding habits indicated that *Heliotrygon* and *Paratrygon* exhibit specializations toward an adapted morphology to piscivory, that species such as *Potamotrygon jabuti* and *Potamotrygon motoro* are more adapted to consuming harder prey, and most Potamotrygonines show adaptations for crushing prey.

Keywords: Batoidea; Neotropical; Potamotrygoninae; stingrays; Styracurinae; teeth.

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LISTA DE ABREVIATURAS E SIGLAS

Apx - apex;

Acus - accessory cusp;

Cus - cusp;

Lae - labial edge;

Lie - lingual edge;

Maa - marginal edge;

Mlr - mesial lingual ridge;

Scus - second transversal cusp

Trc - transversal crest.

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1 INTRODUÇÃO

A família Potamotrygonidae atualmente consiste em um clado composto por representantes de raias neotropicais que possuem distribuição pela América Central e América do Sul, sendo composta por duas subfamílias, Styracurinae e Potamotrygoninae (Carvalho, Loboda & Silva, 2016; Silva & Loboda, 2019; Silva, Junior & Rech, 2022). Styracurinae incorpora as raias previamente denominadas como *Himantura* anfi-americanas (Lovejoy, 1996; Aschliman, Claeson & McEachran, 2012), com um único gênero e duas espécies marinhas, *Styracura schmardae* (Werner 1904) e *Styracura pacifica* (Beebe & Tee-Van 1941) (Carvalho, Loboda & Silva, 2016; Silva, Junior & Rech, 2022).

Já Potamotrygoninae é representada por um clado exclusivamente dulcícola, endêmico da América do Sul (Lasso *et al.*, 2013a, 2016; Last *et al.*, 2016; Silva, Junior & Rech, 2022). Atualmente é composta por quatro gêneros e 38 espécies válidas (Silva, Junior & Rech, 2022). Em relação aos gêneros, *Heliotrygon* é representada por duas espécies, *Paratrygon* por três espécies, *Plesiotrygon* por duas espécies, e as outras trinta e uma espécies pertencem ao gênero *Potamotrygon* (Carvalho & Lovejoy, 2011; Loboda *et al.*, 2021; Silva, Junior & Rech, 2022). Adicionalmente, representantes da subfamília se distribuem pelos rios da América do Sul que desaguam no Mar do Caribe e no Atlântico, com exceção da bacia do Rio São Francisco, rios que desaguam a partir da Mata Atlântica no Nordeste e Sudeste do Brasil, e rios ao Sul do Rio La Plata (Rosa & Lasso, 2013a; Last *et al.*, 2016; Silva, Junior & Rech, 2022). Dos quatro gêneros, *Potamotrygon* é o que possui maior distribuição pelo continente sul-americano (Rosa & Lasso, 2013a), enquanto *Paratrygon* possui representantes nas bacias do Amazonas e do Orinoco (Loboda *et al.*, 2021), *Plesiotrygon* possui representantes nas bacias do Amazonas e do Solimões (Rosa, Castello & Thorson, 1987; Carvalho & Ragno, 2011; Sánchez-Duarte *et al.*, 2013) e *Heliotrygon* é restrito apenas à bacia do Amazonas (Carvalho & Lovejoy, 2011; Carvalho *et al.*, 2013a; Carvalho *et al.*, 2013b).

Os potamotrygoníneos possuem uma grande variação de coloração dorsal do disco, aspecto muitas vezes crucial para a identificação e diferenciação das espécies (Silva & Carvalho, 2015; Last *et al.*, 2016). Esta característica resulta muitas vezes na identificação errônea destes animais, uma vez que existe uma grande variação de coloração intraespecífica, além de casos eventuais de hibridismo entre as espécies

(Lasso *et al.*, 2013a; Silva & Carvalho, 2015; Silva, Junior & Rech, 2022), demonstrando a necessidade de estudo de outros caracteres morfológicos para a resolução de problemas taxonômicos, com a correta identificação e diagnose das espécies.

Trabalhos mais recentes de descrição de novas espécies e de revisões taxonômicas vêm trazendo informações cada vez mais detalhadas a fim de resolver estas questões, a exemplo de Silva & Carvalho (2015), Carvalho, Rosa & Araújo (2016), Silva & Loboda (2019) e Loboda *et al.* (2021). Entretanto, estudos mais aprofundados com base em complexos anatômicos mais específicos ainda são escassos, sendo que apenas recentemente Araújo (2024) e Araújo *et al.* (2024) exploram a variação do neurocrânio de representantes da família Potamotrygonidae, levantando 60 caracteres morfológicos para o grupo. Isso demonstra claramente o potencial que estudos morfológicos mais acurados possuem para o entendimento da evolução desses animais.

Dentre os complexos explorados na família Potamotrygonidae, pouca atenção foi dada para a descrição das placas dentárias tanto em trabalhos mais antigos (e.g., Castelnau 1855) quanto de trabalhos mais recentes (e.g., Carvalho & Lovejoy, 2011) seguindo o exemplo que ocorre para outros grupos de elasmobrânquios (Guinot *et al.*, 2018). Para os elasmobrânquios, a dentição realiza um papel importante na alimentação através do manejo da presa, e possui importância reprodutiva visto que o macho utiliza do aparato bucal para agarrar a fêmea no momento da cópula (Paig-Tran *et al.*, 2022).

Para a taxonomia, a morfologia dentária em alguns casos é utilizada como característica diagnóstica para a separação de espécies aparentemente semelhantes (e.g., *Rhinoptera brasiliensis* e *Rhinoptera bonasus* em Last *et al.*, 2016). Também, possuem um papel crucial para a sistemática e inferências de hábitos em animais extintos, visto que na maioria dos casos são as únicas estruturas que são preservadas no registro fóssil devido à baixa mineralização que o esqueleto dos Chondrichthyes possui em relação as placas dentárias (Cappetta, 2012; Guinot *et al.*, 2018).

Além da ausência de dados de morfologia da placa dentária na família Potamotrygonidae, existem outras informações acerca do comportamento e ecologia destes animais que ainda não foram totalmente investigados e compreendidos (Shibuya, Zuanon & Carvalho, 2016; Shibuya, 2022). Sabe-se que a alimentação das raias está normalmente restrita a larvas, anelídeos, moluscos, crustáceos e alguns peixes ósseos

(Shibuya, Zuanon & Carvalho, 2016; Silva, Junior & Rech, 2022). Entretanto, diferentes estudos apontam para comportamentos distintos entre as espécies, de modo que algumas teriam uma preferência alimentar mais restrita, enquanto outras seriam oportunistas (Shibuya, 2022).

Dados sobre a morfologia dentária dos representantes da família podem ajudar a elucidar problemas de sistemática a exemplo semelhante ao de Araújo (2024) e Araújo *et al.* (2024). Visto que a morfologia dentária está diretamente associada ao estilo de alimentação do animal (Cappetta, 2012), entender a morfologia deste complexo também pode auxiliar no entendimento de espécies do grupo onde o conhecimento da alimentação é escasso ou inexistente.

2 REFERENCIAL TEÓRICO

A família Potamotrygonidae consiste em um clado único exclusivo da América do Sul, e engloba organismos importantes para diversas áreas do conhecimento humano. Ecologicamente são considerados de mesopredadores a predadores de topo (Shibuya, 2022) exercendo papéis importantes no controle populacional de diferentes organismos nos rios sul-americanos, como peixes ósseos, insetos, moluscos e crustáceos. Também são considerados de extrema relevância para a saúde pública devido à grande taxa de acidentes derivados da interação humana, principalmente em comunidades ribeirinhas. Estes acidentes são geralmente ocasionados pela ferroadada do animal utilizando-se de seu espinho caudal como um ato de defesa após ser capturado ou acidentalmente pisoteado. Por possuírem uma estrutura peçonhenta (ferrão), as regiões do corpo que possam vir a sofrer o trauma resultam em dores agudas e podem levar a necrose tecidual da área afetada (Haddad Jr. *et al.*, 2013). Também são animais que pela grande variabilidade de coloração inter- e intraespecífica, são altamente procurados para comércio entre aquaristas (Kyne & Lucifora, 2022).

2.1 Taxonomia, sistemática e biogeografia

Para a sistemática e biogeografia, os Potamotrygonideos são igualmente importantes, pois possuem a única grande linhagem de peixes cartilaginosos vivos com adaptações a uma vida exclusivamente dulcícola (Silva, Junior & Rech, 2022). Outras espécies de raias de ferrão extintas são reconhecidas por também terem habitado ambientes de água doce (e.g., †*Asterotrygon maloneyi* Carvalho, Maisey & Grande 2004), e alguns autores reconhecem ao menos sete espécies viventes de Dasyatidae consideradas como igualmente restritas ao ambiente dulcícola nos continentes Africano e Asiático (Grant *et al.*, 2019; Kyne & Lucifora, 2022). Entretanto, correspondem a espécies majoritariamente marinhas ou de estuário, de modo que os representantes da família Potamotrygonidae compreendem a única linhagem completamente estabelecida no ambiente dulcícola. Sendo assim, possuem um papel crucial e único para o entendimento evolutivo adaptativo dos Chondrichthyes a estes ambientes.

Atualmente cinco gêneros são reconhecidos dentro da família Potamotrygonidae: *Styracura* Carvalho, Loboda & Silva 2016; *Heliotrygon* Carvalho & Lovejoy 2011; *Paratrygon* Duméril 1865; *Plesiotrygon* Rosa, Castello & Thorson 1987 e *Potamotrygon* Garman 1877 (Carvalho, Loboda & Silva, 2016; Silva, Junior & Rech, 2022). *Heliotrygon*, *Paratrygon*, *Plesiotrygon* e *Potamotrygon* formam uma subfamília denominada Potamotrygoninae e acredita-se que compartilham um ancestral comum marinho com os integrantes do gênero *Styracura*, que sozinhos compõem a subfamília Styracurinae (Lovejoy, 1996; Marques, 2000; Carvalho, Loboda & Silva; Fontenelle *et al.*, 2021a). Várias hipóteses sobre a origem das raias de água doce já foram levantadas (Brooks, Thorson & Mayes, 1981; Rosa, 1985; Lovejoy, 1996; Hoberg *et al.*, 1998; Marques, 2000; Carvalho, Maisey & Grande, 2004) de modo que a mais aceita atualmente sugere que o grupo divergiu a aproximadamente 26 Ma, durante a transição entre o Oligoceno e o Mioceno (Fontenelle, 2021b). Durante este período houveram diversas incursões do ambiente marinho no continente sul-americano, relacionadas ao sistema Pebas, o que teria permitido a invasão do grupo no continente. Com a formação do Istmo do Panamá e o isolamento do ambiente marinho, os potamotrygoníneos teriam se diversificado ao longo do tempo em um ambiente transitório entre água salobra e dulcícola (Lovejoy, 1996; Fontenelle, 2021b).

A primeira descrição formal de um representante do grupo foi feita no século XIX referente à espécie *Potamotrygon hystrix* (Müller & Henle, 1839) na época alocada no gênero *Trygon*. Outras espécies dentro da subfamília também foram previamente alocadas em gêneros de representantes marinhos [e.g., *Paratrygon aiereba* (Müller & Henle, 1841)] (Rosa, 1985). Tal condição se modificou apenas em 1877, quando Garman realizou uma primeira subdivisão de representantes das raias de água doce em um grupo separado dos seus congêneres marinhos, nomeado na época de Potamotrygones (Garman, 1877). Porém foi somente no início do século XX que Garman, 1913 realocou todos os representantes descritos em uma família exclusiva de água doce denominada Potamotrygonidae. Até o final do século XX, 17 das espécies consideradas válidas atualmente foram descritas, com uma espécie atribuída ao gênero *Paratrygon* (*P. aiereba*) e todas as outras 16 espécies ao gênero *Potamotrygon*.

Apesar de todas as modificações realizadas para a família até então, boa parte das descrições feitas para os seus representantes careciam de informações importantes, como a falta de descrições morfológicas mais acuradas da morfologia interna e externa. Nesse contexto, Rosa (1985) realizou uma revisão sistemática baseada em dados morfológicos de todos os táxons conhecidos até o momento, sendo uma das mais importantes revisões feitas para o grupo, e a última revisão mais abrangente para a família. Neste trabalho, também foi descrita uma nova espécie pertencente a um novo gênero, publicada posteriormente por Rosa, Castello & Thorson, 1987 (*Plesiotrygon iwamae*). No início do século XX Carvalho & Lovejoy, 2011 descreveram formalmente o gênero mais recente para a subfamília Potamotrygoninae, incluindo duas espécies (*Heliotrygon gomesi* e *H. rosai*). No mesmo ano Silva & Carvalho, 2011a realizaram a redescrição morfológica e taxonômica de *Potamotrygon falkneri* Castex & Maciel 1963, que resultou na sinonímia de dois nomes até o momento considerados válidos (*Potamotrygon castexi* Castello & Yagolkowski 1969; *Potamotrygon menchacai* Castex & Maciel 1963), e na descrição de uma nova espécie (*Potamotrygon tatiana* em Silva & Carvalho, 2011b). Posteriormente, Loboda & Carvalho (2013) realizaram a revisão sistemática da espécie *Potamotrygon motoro* (Müller & Henle 1841) da Bacia do Paraná-Paraguai, com a descrição de duas novas espécies morfológicamente semelhantes (*P. pantansensis* e *P. amandae*).

Fontenelle (2013) realizou a revisão taxonômica de *Potamotrygon scobina* Garman, 2013, que resultou na descrição de quatro novas espécies morfológicamente

semelhantes: *Potamotrygon limai* Fontenelle, Silva & Carvalho, 2014 e *P. adamastor*; *P. amazona*; e *P. garmani* em Fontenelle & Carvalho (2017). Posteriormente, Silva & Carvalho (2015) realizaram a revisão sistemática de *Potamotrygon orbignyi* (Castelnau, 1855) onde duas espécies previamente válidas foram sinonimizadas [(*Potamotrygon reticulata* (Günther, 1880); *Potamotrygon dumerilii* (Castelnau, 1855)]. Por fim, Carvalho, Loboda & Silva (2016) rearranjaram a família Potamotrygonidae e a subdividiram em duas subfamílias, sendo uma exclusiva para as duas espécies marinhas previamente alocadas no gênero *Himantura* (Styracurinae) no novo gênero (*Styracura*). Neste contexto, as raias de água doce foram incluídas exclusivamente na subfamília Potamotrygoninae, sendo essa a classificação atual conhecida para o grupo. Desde a revisão feita por Rosa, 1985, outras 11 espécies foram descritas (Deynat, 2006; Rosa, Carvalho & Wanderley, 2008; Carvalho & Ragno, 2011; Carvalho, Sabaj-Perez & Lovejoy, 2011; Carvalho, 2016a, 2016b; Carvalho, Rosa & Araújo, 2016; Silva & Loboda, 2019; Loboda *et al.*, 2021), totalizando 40 espécies atualmente válidas.

Passados 40 anos da última revisão sistemática de todos os integrantes da família Potamotrygonidae, recentemente Araújo (2024) realizou a descrição e análise comparativa do neurocrânio de 28 espécies da família, resultando na proposição de 60 caracteres morfológicos para o grupo. Uma análise filogenética combinada (morfológica e molecular) foi realizada, resultando nas relações de parentesco mais recente para a família até o momento.

Na contramão da falta de trabalhos de sistemática filogenética baseados exclusivamente em dados morfológicos para o grupo, apenas trabalhos de análises probabilísticas com dados moleculares foram propostos desde a obra de Rosa (1985). No início do século XX, Marques (2000) averiguou as interrelações dos integrantes do grupo através da análise molecular de parasitas intraespecíficos. Posteriormente, Toffoli *et al.* (2008) e Garcia *et al.* (2016) realizaram análises de 7 e 6 espécies, respectivamente, sendo seguidos por, Fontenelle *et al.* (2021a) que realizaram a análise molecular mais completa até então, incluindo 35 espécies válidas.

Em todos os trabalhos aqui citados, a monofilia da família Potamotrygonidae é amplamente aceita. Entretanto, o mesmo não pode ser dito sobre as interrelações do grupo (Rosa & Lasso, 2013). As relações dentro de Potamotrygoninae normalmente são recuperadas com *Heliotrygon* e *Paratrygon* mais proximamente relacionados, a mesma relação de *Plesiotrygon* e *Potamotrygon*. Desde que foi descrita, *Heliotrygon*

normalmente é recuperada como grupo irmão de *Paratrygon*, com alguns trabalhos propondo este clado como grupo irmão de *Plesiotrygon* + *Potamotrygon* (Carvalho & Lovejoy, 2011; Fontenelle *et al.*, 2021a; Araújo, 2024) e outros trabalhos sugerindo este clado como grupo irmão sucessivo de *Plesiotrygon* e *Potamotrygon* (Araújo *et al.*, 2024). Entretanto outras hipóteses recuperam *Heliotrygon* como táxon irmão de todos os outros Potamotrygonininos, e consequentemente *Paratrygon* compartilhando ancestralidade em comum com o clado *Plesiotrygon* + *Potamotrygon* (García, Lasso & Villanil, 2013; García *et al.*, 2016). As relações entre *Plesiotrygon* e *Potamotrygon* são igualmente problemáticas, com trabalhos mais recentes recuperando *Potamotrygon* como um grupo parafilético sem a inclusão de *Plesiotrygon* (Marques, 2000; Toffoli *et al.*, 2008; Fontenelle *et al.*, 2021a; Araújo, 2024), ou com *Potamotrygon* sendo recuperado como grupo irmão de todos os outros potamotrygoníneos dentro do cenário proposto por Araújo *et al.* (2024).

O motivo de tantos trabalhos de sistemática filogenética resultarem em hipóteses conflitantes está no conhecimento escasso existente acerca do grupo em áreas de morfologia, anatomia comparada e genética (Silva, Junior & Rech, 2022). Desde que o grupo foi inicialmente descrito, os dados mais destacados em descrições e chaves de identificação é o padrão de coloração do disco do animal (Silva, Junior & Rech, 2022). Entretanto, tal característica é extremamente variável e homoplástica dentro do grupo, com algumas espécies possuindo grande variabilidade intraespecífica de coloração do disco (ex. *Potamotrygon orbignyi* em Silva & Carvalho, 2015) e espécies distintas possuindo colorações semelhantes entre si (ex. *P. limae* e *P. scobina* em Fontenelle, Silva & Carvalho, 2014). Do mesmo modo, são animais conhecidos por possuírem alto grau de hibridização natural (Sanches *et al.*, 2021), o que pode contribuir tanto para a alta variabilidade de coloração no disco, quanto para os dados discrepantes nas filogenias moleculares mencionadas. O fato de alguns animais ocorrerem em rios e bacias de difícil acesso contribuem para a baixa representatividade de espécimes do grupo em coleções científicas comparado aos seus congêneres marinhos, o que dificulta mais ainda o estudo da sistemática do grupo tanto molecularmente quanto morfologicamente.

2.2 Conhecimento da morfologia dentária

O conhecimento sobre a morfologia dentária do grupo das raias de água doce neotropicais é escasso quando comparado a outras estruturas morfológicas, como por exemplo as estruturas que compõem o endoesqueleto (ex. Silva & Carvalho 2011a,b; Loboda & Carvalho 2013; Fontenelle, Silva & Carvalho, 2014; Silva & Carvalho, 2015; Araújo *et al.*, 2024). Seguindo o exemplo do que ocorre com outros grupos de elasmobrânquios (Guinot *et al.*, 2018), a morfologia dentária tem sido consistentemente ignorada em muitos trabalhos (ex. Carvalho, Maisey & Grande, 2004; Deynat, 2006; Carvalho & Lovejoy, 2011). Grande parte do conhecimento atual é derivado de descrições em revisões sistemáticas, descrições de novas espécies (ex. Rosa, 1985; Loboda & Carvalho, 2013), ou de poucos trabalhos mais aprofundados no tema (ex. Cappetta, 2012; Adnet, Gismondi & Antonie, 2014).

Como citado anteriormente, Rosa (1985) foi um dos primeiros a realizar uma revisão sistemática do grupo com ênfase em elementos esqueléticos, incluído a dentição. Em seu trabalho, foram apresentadas ilustrações da placa dentária e de dentes isolados de 15 espécies. Entretanto, as descrições são breves, visto que o trabalho teve como escopo uma revisão sistemática abrangente e que incluiu um número maior de complexos anatômicos. Todas as descrições e revisões posteriores seguiram o padrão de descrição da morfologia dentária de Rosa (1985), sendo alguns trabalhos um pouco mais detalhados (ex. Silva & Carvalho, 2015). Ao contrário de Rosa (1985), boa parte dos trabalhos disponibilizaram apenas imagens ou ilustrações das placas dentárias, mas sem ilustrações individuais dos dentes (Loboda & Carvalho, 2013; Fontenelle, Silva & Carvalho, 2014; Silva & Carvalho, 2015; Carvalho, 2016a; Fontenelle & Carvalho, 2017; Silva & Loboda, 2019; Loboda *et al.*, 2021), enquanto outros apresentaram apenas a descrição morfológica de maneira textual mas sem imagens ou ilustrações (Rosa, Carvalho & Wanderley, 2008; Carvalho & Lovejoy, 2011; Carvalho & Ragno, 2011; Silva & Carvalho, 2011a,b; Carvalho 2016b). Talvez o exemplo mais notório sobre como os dentes foram pouco explorados em representantes de Potamotrygonidae está no trabalho de Deynat (2006). Neste trabalho o autor descreve uma nova espécie mas traz informações superficiais sobre a morfologia dentária: “boca pequena e ligeiramente arqueada com várias fileiras de dentes, pontiaguda nos machos e rombos

nas fêmeas”. Apenas posteriormente, Silva & Carvalho (2015) expandiram a quantidade de informações sobre a morfologia dentária nessa espécie.

Cappetta (2012) foi um dos primeiros a explorar a dentição de algum representante da família Potamotrygonidae utilizando outras metodologias, como por exemplo, a Microscopia Eletrônica de Varredura (MEV). Em sua obra, ele propõe uma nomenclatura anatômica para todos os elasmobrânquios, e estuda detalhadamente uma grande diversidade morfológica de diversos representantes extintos e vivos do grupo. Dentre estes, dois representantes da família Potamotrygonidae foram analisados (*Styracura schmardae*; *Potamotrygon motoro*). Posteriormente, Adnet, Gismondi & Antonie (2014) exploraram potenciais fósseis do gênero *Potamotrygon*, e realizaram uma análise mais detalhada sobre a morfologia dentária do grupo. Neste trabalho, a ilustração da dentição de 16 espécies vivas foi disponibilizada, e os autores realizaram as descrições de acordo com a morfologia dentária compartilhada pelos espécimes. Entretanto, nenhum caráter foi proposto nesse estudo, que carece também de uma análise da evolução morfológica destas estruturas.

2.3 Hábitos alimentares

Seguindo o padrão observado em outras áreas de estudo das raias de água doce neotropicais, o conhecimento sobre a ecologia e os hábitos alimentares da família Potamotrygonidae também é escasso (Shibuya, 2022). Tal conhecimento é restrito a alguns poucos trabalhos com número amostral relevante (ex. Shibuya, Araújo & Zuanon, 2009; Moro, Charvet & Rosa, 2011) ou de alguns poucos indivíduos capturados que tiveram seus conteúdos estomacais analisados (e.g., Lasso *et al.*, 2013b). Informações relevantes sobre os hábitos alimentares de cerca de 20 espécies da subfamília Potamotygoninae estavam previamente distribuídas em aproximadamente 55 diferentes trabalhos e que foram posteriormente compilados nos estudos de Kolmann *et al.* (2022) e Shibuya (2022), com exceção dos trabalhos de Wrigglesworth (2018) e OShea *et al.* (2020). Adicionalmente, baseado em informações de dados alimentares conhecidos para uma grande parte dos elasmobrânquios, Cappetta (2012) correlacionou a morfologia dentária desses animais com o tipo de alimentação. Neste mesmo

contexto, esse autor também reconheceu oito tipos de dentição: “clutching, tearing, type, crushing, grinding, clutching-grinding, cutting-grinding e crushing-grinding”.

3 OBJECTIVES

- Realize a morphological and comparative description of the dental plates in species of Potamotrygonidae;
- Carry out a combined phylogenetic analysis based on the teeth characters proposed in the present study;
- Perform a historical reconstruction of the feeding habits and dental types on the resultant phylogenetic tree to understand the evolution of these characteristics within the family Potamotrygonidae.

4 MATERIALS AND METHODS

Observations were made primarily through dissections of ethanol preserved and stained specimens from the ichthyological collections of Federal University of Paraíba (UFPB) and Zoology Museum of the University of São Paulo (MZUSP). A total of 42 specimens (21 species) were analyzed (see 4.4 Material examined section). Only male and female adult specimens from each species were considered to evaluate sexual heterodonty. The only exception is *Styracura schmardae* in which a sub-adult male and a juvenile female were evaluated because of the lack of available adult specimens from both sexes.

4.1 Dissection and equipment

Both upper and lower dental plates were removed from the specimens with the aid of surgical materials (tweezers and scalpel) and were then measured. Plates were photographed with a SONY DC-ZS70 camera and were posteriorly evaluated through the use a stereoscope, a Micro CT Scanner model Skyscanner 1172 (Bruker) from the

Microscopy and Biological Imaging Laboratory (LAMIB) of UFPB and a Leica M205A Microscope from the Paulo Young Laboratory of Marine Invertebrates (LIPY) from the same institution. The list of specimens analyzed and the equipment used is provided in item 4.4.

For the Micro CT scan, the parameters utilized for the analysis were: rotation step 0.60, frame 4, random movement 10. Medium pixels (2000x1332), no filter, 60kv-167uA. The follow up reconstructions were also made with the following settings: smoothing 4; rings 3; beam-hardening 15. Output: 0.075174-0.258727. The resulting images were reconstructed using Amira (v. 5.3.3.). All resulting images were edited using Photoshop software.

4.2 Morphological description and phylogenetics analysis

For the morphological descriptions the upper and lower plate shapes as well as the functional teeth rows of species were considered. Also, individual teeth were explored across each plate to assess monognathic heterodonty. For teeth description, near symphysis, intermediate and lateral rows from functional files of the right side of the plate were standardized as positions 1, 2 and 3, respectively (Figure 1). The lower plate of the female of *Potamotrygon histrix* was unavailable for analysis and only the upper plate was studied. Nomenclature for dental plates and teeth followed Cappetta (2012), Silva & Carvalho (2015) and Guinot et al. (2018) (Figure 2). Labial and Lingual visor were confusing terms to describe the teeth morphology provided by Cappetta (2012) and that referred to more than one structure. Consequently, they were adapted herein as Labial edge (**Lae**) and Lingual edge (**Lie**). Accessory cusps (**Acus**) refer to smaller cusps present laterally to the main cusp (**Cus**). The second transverse crest (**Strc**) refers to a crest that is unique to *Styracura schmardae*. Although all species have sexual heterodonty, cases in which this feature was incipient were described as absent. All gradual levels of monognathic heterodonty were evaluated from near symphysis towards lateral teeth. The description of the crown of teeth of the functional files were prioritized since it was not possible to analyze all the dental plates of specimens with the Micro CT-Scan. Measurements of the crown were taken from the base of the crown.

A combined analysis was carried out using the dental morphological characters proposed herein that were combined with molecular data (Figures 66 and 67). DNA sequences, mitochondrial (ATPase, CYTB, COI) and nuclear (ITS1), were obtained from GenBank (based on data provided by Fontenelle *et al.*, 2021a). The molecular matrix was constructed with the GB-to-TNT program (Goloboff & Catalano, 2012) and aligned with the Muscle program (Edgar, 2004). Duplicate sequences for the same taxa will be filtered and removed, also with GB-to-TNT. This software uses alignment programs and produces a molecular matrix ready to be analyzed with TNT. The combined matrix was divided into six blocks of characters, two morphological (&[num], &[cont]) and four molecular (&[dna]) (Supporting Information S1).

The phylogenetic analysis was carried out using TNT v.1.6 (Goloboff and Morales, 2023). The root was placed in *Styracura schmardae* as it is currently recovered as closely related to Potamotrygoninae (Lovejoy, 1996, Carvalho, Loboda & Silva, 2016, Fontenelle *et al.*, 2021a, Araújo *et al.* 2024). Interrelationships were inferred through maximum parsimony, with searches for the most parsimonious trees obtained through a traditional heuristic search, with random seed set to zero and a total of 1000 saved trees. As proposed in previous studies (Mirande, 2017; Mirande 2019), the analysis was performed under extended implied-weighting (XIW) to deal with missing information mainly for molecular characters (Goloboff, 2014). Four weighting schemes were employed to explore the most parsimonious trees following Mirande (2019): SEP - each character will be weighted according to its own homoplasy; COD - sequences divided into sets of three contiguous sites (codons) and each character weighted by the average homoplasy of its set; BLK - each character weighted by the average homoplasy of the entire data partition (markers); POS - sites of each codon position of the coding sequences weighted according to the average homoplasy of all characters of the same position in each block. We calculated the average amount of homoplasy (*xpiwe&homoplasy* command; Goloboff, 2014) (Presti *et al.*, 2023) for the matrix under equal-weighting search and determined the values of k at which a character has on average a weight corresponding to 50, 55, 60, 65, 70, 75, 80, 85, 90, 95% (= equal weighting) of the weight of a completely non-homoplastic one (Mirande, 2019). The concavity constant (k) determines how strongly homoplastic characters are weighted based on their fit (Goloboff 1993, Goloboff *et al.* 2008). Fit (f) is currently implemented from TNT v.1.5 with the formula $f = k/(k + e)$, where “ e ” is the number of extra

(homoplastic) steps (Mirande 2009). The searches for each analytical condition were performed using “traditional heuristic search” (Goloboff, 1999).

The trees recovered according to the different weighting schemes (SEP, COD, BLK, POS) and weighing forces (k) were subjected to a sensitivity analysis (following Mirande, 2019), comparing tree topologies using the distortion coefficient (Farris, 1989) (Supporting information S2) of SPR distances (subtree pruning and regrafting; Goloboff, 2008) (Supporting information S3). The distortion coefficient and SPR distances graphs were created with the TNT script “*TreeDistMatrix.run*” (Torres, Goloboff & Catalano, 2022). The evolution of the dental characters were discussed in light of the most parsimonious tree selected by the combined analysis and subsequently subjected to the sensitivity test (Figure 59). The molecular blocks were inactivated and only the morphological characters were optimized under the resultant tree using the TNT script “*WincladTree.run*” (Supporting information S4).

The support for the tree was calculated following two different schemes. The first was through symmetric resampling (1000 replicates, change probability 0.33) following the same parameters as the analytical conditions of the traditional heuristic search. The results are expressed as differences in “Group Present/Contradicted” frequencies (GC values) (Goloboff *et al.*, 2003) (Figure 60). The support values shown in square brackets (e.g., [4]) indicate that the clade has support practically equal to zero. That is, there is almost as much evidence against as in favor of the existence of the clade. The second support scheme was calculated using the Relative Bremer Support. Nearly 38,000 replicates were generated and 10 different values of additional steps were used (1, 3, 5, 7, 9, 11, 13, 15, 17, 19).

4.3 Feeding habits, dental types and historical reconstructions

Feeding habits were compiled from the literature using Google scholar and ResearchGate search portals. Information was also gathered from the review works of Shibuya, (2022) and Kolmann *et al.* (2022). Only works with a substantial sample number were considered. A spreadsheet (Table 1) was built including the species, literature from which information regarding the prey preference was retrieved, prey

consumed, and area of study. Each species was then assigned to one main feeding habit: generalist, piscivorous, carcinophagous, molluscivorous and insectivore.

Adaptative dental types were applied correlating the teeth morphology with classification proposed by Cappetta (2012) (Table 2; Figure 68). Considering that all works surveyed did not indicate food partitioning between sexes, only the morphology of teeth in females was considered for this classification, as the teeth morphology in males, which is cuspidated in most species, is probably related to a reproductive feature (see 6.3 section). A brief description of the adaptative types is provided in results (for full description see Cappetta, 2012), and specimens which had not feeding habits information available were attributed to one according to the morphological comparison to similar dental information available (e.g., *Potamotrygon histrix*, *P. leopoldi*, *P. brachyura*, *P. jabuti*, *P. albimaculata* and *P. limai*). The historical reconstruction of the adaptative dental types and of the feeding habits were carried out using the parsimony and unordered characters options in MESQUITE (version 3.81) using the resulting phylogenetic tree of the present study (Figures 69 and 70).

4.4 Material examined

Styracurinae: *Styracura schmardae* **MZUSP uncat.** (Micro CT, sub-adult male, 550 mm DW) **UFPB 9217** (Leica, juvenile female, 274 mm DW, Camará Beach, Marapanim - PA). Potamotrygoninae: *Heliotrygon rosai* **UFPB 13708** (Micro CT, female, skeleton only); *Heliotrygon rosai* **UFPB uncat.** (Micro CT, male, skeleton only); *Paratrygon aiereba* **MZUSP 104986** (Leica, female, 563 mm DW, Rio Jamari, Amazon basin - AM); *Paratrygon aiereba* **MZUSP 103896** (Micro CT, male, 508 mm DW, Tapajós river - PA); *Plesiotrygon iwamae* **MZUSP 108774** (Leica, female, 563 mm DW, Marajó basin, Tocantins river - PA); *Plesiotrygon iwamae* **UFPB 5656** (Micro CT, male, 499 mm DW, Marajó basin, Colares - PA); *Potamotrygon jabuti* **MZUSP 105019** (Leica, male, 298 mm DW, Jamanxim river, Tapajós river - PA); *Potamotrygon jabuti* **MZUSP 105037** (Micro CT, female, 330 mm DW, Jamanxim river, Tapajós river - PA); *Potamotrygon brachyura* **MZUSP 104990** (Leica, male, 413 mm DW, Uruguai river, Paraná basin - RS); *Potamotrygon brachyura* **MZUSP 104224** (Leica, female, 425 mm DW, Prata basin - MT); *Potamotrygon leopoldi* **MZUSP 104449** (Leica, male,

334 mm DW, Xingú river - PA); *Potamotrygon leopoldi* **MZUSP 104448** (Leica, female, 492 mm DW, Xingú river - PA); *Potamotrygon motoro* **UFPB 6080** (Micro CT, female, skeleton only, Arari Lake, Marajó Island - PA); *Potamotrygon motoro* **UFPB 14988** (Micro CT, male, 340 mm DW, Arroyo Javier, Argentina); *Potamotrygon yepezi* **UFPB 1427** (Micro CT, male, 146 mm DW, Maracaibo Lake, Venezuela); *Potamotrygon yepezi* **UFPB 1427** (Micro CT, female, 142 mm DW, Maracaibo Lake, Venezuela); *Potamotrygon signata* **UFPB 7737** (Leica, female, 295 mm DW, Parnaíba river, City of Uruçuí - PI); *Potamotrygon signata* **UFPB 6508** (Leica, male, 269 mm DW, Poti River, Prata do Piauí – PI); *Potamotrygon marquesi* **MZUSP 117792** (Leica, male, 211 mm DW, Taraucá river - AC); *Potamotrygon marquesi* **UFPB unact.** (Leica, female, 341 mm DW); *Potamotrygon orbignyi* **UFPB 6081** (Micro CT, male, skeleton only, Negro river, Barcelos - AM); *Potamotrygon orbignyi* **UFPB 7778** (Micro CT, female, 188 mm DW, Parnaíba river, City of Uruçuí - PI); *Potamotrygon schroederi* **MZUSP 108453** (Micro CT, female, 410 mm DW, Negro river, Amazon basin - AM); *Potamotrygon schroederi* **UFPB 2845** (Leica, male, 399 mm DW, Alto Negro - AM); *Potamotrygon albimaculata* **MZUSP 129871** (Leica, male, 324 mm DW); *Potamotrygon albimaculata* **MZUSP uncat.** (Micro CT, female, 380 mm DW); *Potamotrygon humerosa* **MZUSP 104641** (Leica, male, 347 mm DW, Abacaxis river, Amazon basin - AM); *Potamotrygon humerosa* **MZUSP 104633** (Leica, female, 226 mm DW, Abacaxis river, Amazon basin - AM); *Potamorygon amandae* **MZUSP 110916** (Leica, female, 274 mm DW, Paraguai river, Prata basin - MT); *Potamorygon amandae* **MZUSP 111912** (Micro CT, male, 237 mm DW, Prata basin - MT); *Potamotrygon wallacei* **UFPB 5217** (Micro CT, female, skeleton only, Itú river, tributary of the Negro river, 70km above Barcelos - AM); *Potamotrygon wallacei* **UFPB 5216** (Leica, male, 340 mm DW, Itú river, tributary of the Negro river, 70km above Barcelos - AM); *Potamotrygon limai* **MZUSP 104033** (Leica, male, 359 mm DW, Samuel dam, Madeira river - RO); *Potamotrygon limai* **MZUSP 104073** (Leica, female, 498 mm DW, Samuel dam, Madeira river - RO); *Potamotrygon scobina* **MZUSP 104268** (Leica, female, 401 mm DW, Tocantins river, Marajo basin - PA); *Potamotrygon scobina* **MZUSP 104244** (Micro CT, male, 377 mm DW, Tocantins river, Marajo basin - PA); *Potamotrygon hystrix* **MZUSP 117243** (Leica, male, 202 mm DW, Salobra river - MT); *Potamotrygon hystrix* **MZUSP 117240** (Leica, female, 210 mm DW, Salobra river - MT); *Potamotrygon falkneri* **MZUSP 014848** (Leica, male, 436

mm DW, Paraguai river - MT); *Potamotrygon falkneri* **MZUSP 106270** (Leica, female, 358 mm DW, Paraná river - MS).

5 RESULTS

5.1 Morphological description of mature Potamotrygonidae dental plates

***Styracura schmardae* (Figures 3 and 4):** Teeth set in quincunx and wider than long in the upper and lower plates of males and females. The upper plate is arched and anteroposteriorly short while the lower plate is trapezoidal and flattened, being longer than the upper plate. Both dental plates are wider than long. The lower plate has a nearly trapezoidal labial margin (position 2). The upper plate is more arched laterally, near symphysis, and less arched in mid-lateral portions. The upper plate is also flattened and antero-posteriorly longer near the symphysis (position 1) than in intermediate and lateral portions (positions 2 and 3). No significant color variation is present between functional labial files and non-functional lingual files. Males have 36/37 tooth rows on upper and lower plates respectively, and females have 36 tooth rows on both plates. Tooth morphology varies gradually in size among the plate in males and females. Despite this, the species has little to no sexual heterodonty, with males and females sharing the same tooth morphology. The species is devoid of dignathic heterodonty.

All teeth from both plates present a trapezoidal-shaped crown in occlusal view. The labia edge (**Lae**) is straight to slightly convex. The surface of the crown presents a transversal crest (**Trc**) located near the lingual edge (**Lae**) that bears an incipient single cusp (**Cus**) that has 1/6 of the crown width. Additionally, the crown presents a second transverse crest (**Strc**) located in the midportion of the crown. Teeth gradually decrease in size from near symphysis (position 1) towards lateral (position 3) portion.

***Heliotrygon rosai* (Figures 5, 6 and 7):** Teeth set in quincunx, wider than long in the upper and lower plates of males and females. The upper plate is arched and shorter in length than the lower plate, while the lower plate is flattened and reniform in shape in occlusal view. The lingual margin of the upper and lower plates is curved. No color variation is present between functional labial files and non-functional lingual files.

Males have 25 tooth rows on both upper and lower plates, and females have 29/32 tooth rows on upper and lower plates, respectively. All teeth vary little between the upper and lower plates, and the species have mild sexual heterodonty compared to most potamotrygonins with slight differences in teeth shape between sexes.

Males and females have a similar tooth morphology. Teeth from both plates have a trapezoid-shaped crown base in occlusal view. Both labial (**Lae**) and lingual edges (**Lie**) are slightly convex. The transverse crest (**Tcr**) and the medial lingual ridge (**Mlr**) develop into a single pointed cusp (**Cus**) with a conical shape. The cusp possesses a convex blunt labial face that ends in a half circle shaped apex (**Apx**). All cusps are oriented towards the lingual portion. The size of the crown and the cusp decrease slightly from near symphysis towards the lateral portions of the plates. Cusps in males are slightly more developed than in females.

***Paratrygon aiereba* (Figures 8, 9 and 10):** Teeth set in quincunx and wider than long in the upper and lower plates of males and females. The upper plate is arched and shorter in length than the lower plate, while the lower plate is flattened and reniform in shape in occlusal view. The lingual margin of the upper and lower plates is curved. No color variation is present between functional labial files and non-functional lingual files. Males have 29/28 tooth rows on upper and lower plates, respectively, and females have 25 tooth rows on both plates. All teeth vary little between the upper and lower plates, and the species has sexual heterodonty, with cusps in males being considerably larger than females.

Males and females have a similar crown morphology. Teeth from both plates have a trapezoid-shaped crown, like in *Heliotrygon rosai*. Both labial (**Lae**) and lingual edges (**Lie**) are convex. The transverse crest (**Tcr**) and the medial lingual ridge (**Mlr**) develop into a single triangular-shaped pointed cusp (**Cus**). The cusp possesses a convex blunt labial face that ends in a pointed apex (**Apx**). All cusps are oriented towards the lingual portion. The crown and cusp size decrease slightly from near symphysis of tooth plates (devoid of monognathic heterodonty), towards lateral portion of plates in males, decreasing considerably in females (gradual monognathic heterodonty).

***Plesiotrygon iwamae* (Figures 11, 12 and 13):** Teeth set in quincunx, wider than long in the upper and lower plates of males and females. The upper plate is arched and shorter than the lower plate, while the lower plate is flattened and reniform in shape. The upper plate portion (position 1) is flattened and antero-posteriorly longer near symphysis than its intermediate and lateral portions (positions 2 and 3). The lingual margin of the upper and lower plates is curved. No color variation is present between functional labial files and non-functional lingual files. Males have 52/49 tooth rows on upper and lower plates, respectively, and females have 44/43, respectively. All teeth vary little between the upper and lower plates and the species presents sexual heterodonty, with males presenting cuspidated teeth (**Cus**) and females being devoid of cusps. Males and females are devoid of dignathic heterodonty and have a gradual level of monognathic heterodonty.

All teeth from upper and lower plates of males are triangular in occlusal view and bear a trapezoid crown, similar to what is observed in males of *Paratrygon aiereba*, although teeth are considerably shorter in size. Both labial (**Lae**) and lingual edges (**Lie**) are convex. The transverse crest (**Tcr**) and the medial lingual ridge (**Mlr**) develop into a single triangular-shaped cusp (**Cus**). The cusp possesses a convex blunt labial face that ends in a pointed apex (**Apx**). All cusps are directed towards the lingual portion. The size of the crown and of the cusp decrease from near symphysis towards the laterals, with lateral teeth (position 3) presenting a cusp smaller than half the width of the crown. Intermediate (position 2) and lateral teeth cups are slightly arched towards the lateral portion of the plate.

All teeth near symphysis (position 1) and intermediate in position (position 2) from upper and lower plates in females have a fan blade shaped crown, being devoid of cusps. Like in males, the labial edge is concave, with its curvature reaching both marginal angles (**Maa**). The lingual edge is divided in two straight labial marginal edges of the crown (**Lme**). Lateral teeth (position 3) are visibly shorter and have an oval-shaped crown, with no distinct marginal angles between lingual and labial edges.

***Potamotrygon jabuti* (Figures 14, 15 and 16):** Teeth set in quincunx, wider than long in the upper and lower plates of males and females. The upper plate is arched and shorter than the lower plate, while the lower plate is flattened and trapezoidal in shape, with 45°

angle in the lingual margin at level of mid-lateral teeth rows (position 2). The upper plate is laterally more arched near symphysis and is less arched in mid-lateral portions. No significant color variation is present between functional labial files and non-functional lingual files. Males have 24/26 tooth rows on upper and lower plates, respectively, and females have 23/22, respectively. All teeth vary depending on the position on the plate and the species has sexual heterodonty, with a few teeth from males having cusps (**Cus**) and all teeth in females completely devoid of cusps.

Males present dignathic heterodonty and a gradual level of monognathic heterodonty in both plates. Teeth near symphysis (position 1) from upper and lower plates of males have a drop-shaped crown, with a convex labial edge (**Lae**). The transverse crest (**Tcr**) and the medial lingual ridge (**MLr**) form a single pointed cusp that is triangular-shaped in occlusal view. Lower intermediate teeth (position 2) have a similar morphology, with cusps slightly less developed than in near symphysis. Upper intermediate teeth have an irregular hexagonal shape, with both lingual (**Lie**) and labial (**Lae**) edges similar in size and resembling a trapeze. The crown is devoid of cusps. Upper and lower lateral teeth (position 3) are also absent of cusps. Lateral upper teeth have an oval shape with no discernible marginal angles (**Maa**). The lateral lower plate also has an irregular hexagonal shape, and the crown length of teeth is shorter than that of upper intermediate teeth.

In females, the upper plate has a disjunct level of monognathic heterodonty, and the lower plate has a gradual level of monognathic heterodonty. The upper teeth near symphysis (position 1) have a pentagon-shaped crown with three sides of the pentagon on the labial edge and the remaining two on the lingual edge. The lower plate teeth near symphysis have an irregular hexagonal shape, being larger than upper teeth near symphysis, and with size similar to intermediate teeth from the upper plate. Upper intermediate teeth (position 2) also have an irregular hexagonal crown shape like near symphysis lower teeth, with both having twice the size of all remaining teeth. Upper lateral teeth (position 3), lower intermediate and lower lateral teeth have a pentagon-shaped crown, which is similar in size to the upper near symphysis crown.

***Potamotrygon brachyura* (Figures 17, 18 and 19):** Teeth set in quincunx, wider than long in the lateral plate portions of males and females. Upper plate is arched and shorter

while the lower plate is trapezoidal in shape and flattened, being longer than the upper plate. Both dental plates are wider than long. The lower plate has a nearly trapezoidal lingual margin (position 2). The upper plate is laterally more arched near symphysis and less arched in mid-lateral portions. The lingual-most portion of the lower plate in the male specimen has a more pronounced lateral angle. No significant color variation is present between functional labial files and non-functional lingual files. Males have 36/34 tooth rows on upper and lower plates, respectively, and females have 31/29, respectively. All teeth vary depending on the position on the plate and the species has sexual heterodonty, with a few male teeth bearing cusps (**Cus**) and all female teeth devoid of cusps.

Males are devoid of dignathic heterodonty and have a gradual level of monognathic heterodonty. Lower teeth near symphysis (position 1) have a drop-shaped crown with both labial (**Lae**) and lingual edges (**Lie**) convex. The lingual edge is longer than the labial edge, with both marginal angles (**Maa**) located more labially. The transverse crest (**Tcr**) and the medial lingual ridge (**Mlr**) are well developed into a single triangular and pointed cusp in occlusal view. Lower intermediate teeth (position 2) have a similar morphology of teeth near symphysis, but with the cusps being considerably shorter in length. Lower lateral teeth (position 3) have a different morphology, bearing an irregular and a somewhat wider than long hexagonal shape, being considerably shorter than teeth from other portions. The crown lacks a transverse crest, a medial lingual ridge and a cusp. Upper teeth near symphysis (position 1) have similar characteristics of lower teeth near symphysis, but with the crown width larger and crown length shorter. The cusps are also narrower than lower teeth near symphysis. Upper intermediate teeth (position 2) have a lozenge-shaped crown in occlusal view. Their cusps are smaller than teeth in all other portions of both plates. Lateral upper teeth (position 3) have an asymmetrical wider than long oval crowns, which are devoid of a transverse crest, a medial lingual ridge and cusps.

The females have a mild level of dignathic heterodonty compared to other potamotrygonine species (e.g., *Potamotrygon motoro*) and a gradual level of monognathic heterodonty. Upper and lower teeth near symphysis (position 1) have a fan blade shaped crown with a small transverse crest (**Trc**) present in the lingual portion of the crown. Upper intermediate (position 2) teeth have a quadrangular shape, being slightly larger than all other teeth from upper and lower plates. They are also devoid of

a transverse crest. Lower intermediate teeth and both upper and lower lateral teeth (position 3) vary from an irregular quadrangular shape with indistinct margins to an oval shaped crown, with a width twice the size of the length in both cases.

***Potamotrygon leopoldi* (Figures 20, 21 and 22):** Teeth set in quincunx, with no great distinctions between crown length and crown width in teeth near symphysis (position 1). Teeth from the upper plate of males and females are wider than long in intermediate and lateral portions (position 2 and 3). In males, near symphysis and intermediate lower plate teeth have similar crown width and length, and lateral teeth are wider than long. Females have similar width and length in all positions. The upper plate is arched and shorter than the lower plate, while the lower plate is flattened and trapezoidal in shape, with marked lateral angles (position 2). The upper plate is more arched near symphysis and less arched on mid-lateral portions. No significant color variation is present between functional labial files and non-functional lingual files. Males have 23 tooth rows on both plates and females have 34 tooth rows on both plates also. All teeth vary depending on the position on the plate with males and females having digenathic heterodonty and a disjunct level of monognathic heterodonty in the upper plate and a gradual level of monognathic heterodonty in the lower plate. The species has a mild level of sexual heterodonty compared to most potamotrygonines with slight differences in tooth shape between sexes. The major difference relies on tooth row counting.

For females, all teeth are flattened, and completely devoid of cusps, transverse crests (**Tcr**) and median lingual ridges (**Mr**). The upper plate near symphysis (position 1) and lateral (position 3) teeth have a crown shape that varies between a lozenge and a trapezoid. The lingual edge (**Lie**) is convex while the labial edge (**Lae**) is subdivided in two straight portions. Upper plate intermediate teeth (position 2) have an irregular hexagonal shaped crown that is bigger than all other teeth, having two marginal angles (**Maa**), two lingual marginal angles (**Lima**) and two labial marginal angles (**Lama**). All lower plate teeth have similar shape and size from upper plate teeth near symphysis.

Upper plate teeth in males have the same crown morphology of that described for females. Lower plate teeth vary in shape between a lozenge and a pentagon near symphysis teeth (position 1), with the three sides of the pentagon on the lingual edge (**Lie**). Intermediate and lateral teeth rows (positions 2 and 3) vary from a lozenge to a

fan-shaped crown. Intermediate teeth crown size is similar to those near the symphysis, while lateral teeth are elliptical, being shorter and wider.

***Potamotrygon motoro* (Figures 23, 24 and 25):** Teeth set in quincunx and wider than long in the upper and lower plates of males and females. The dental plates are somewhat like *P. jabuti*. The upper plate is arched and shorter than the lower plate, while the lower plate is flattened and trapezoidal in shape, with marked lateral angles in the lingual margin (position 2). The upper plate is more arched near symphysis and less arched in mid-lateral portions. The upper plate near symphysis (position 1) is also more flattened and antero-posteriorly longer than intermediate and lateral portions (positions 2 and 3). No significant color variation is present between functional labial files and non-functional lingual files. Males have 30/34 tooth rows on upper and lower plates, respectively, and females have 37/35, respectively. The species has sexual heterodonty, with males and females being devoid of cusps (**Cus**) on functional files (males non functional files near symphysis have one single cusp). Both males and females present dignathic heterodonty, and a disjunct level of monognathic heterodonty in the upper plate, and a gradual level of monognathic heterodonty in the lower plate.

Upper and lower plate teeth near symphysis (position 1) in males have a trapezoidal-shaped crown, with convex labial (**Lae**) and lingual edges (**Lie**) and a convex transversal crest (**Trc**). Upper intermediate teeth (position 2) have a similar morphology of near symphysis teeth. However, they are considerably bigger, having twice the size of teeth in position 1. Lower intermediate teeth have the same overall lozenge-shaped crown of near symphysis teeth, but are wider. The upper and lower lateral (position 3) teeth are similar in shape and have a similar size to upper and lower teeth near symphysis, and lower intermediate teeth. Both present an oval shaped crown, being devoid of cusps.

Females upper and lower plate teeth near symphysis teeth (position 1) have a similar morphology to that of males, but are slightly (one third) bigger in size. Intermediate lower teeth (position 2) follow the same pattern. Upper intermediate teeth have an irregular hexagonal shaped-crown, which is wider than long and has two labial marginal angles (**Lama**) and two lingual marginal angles (**Lima**). The upper intermediate teeth are two to three times the size of near symphysis teeth. Lateral teeth

(position 3) vary from a lozenge to oval-shaped, being devoid of cusps and slightly smaller than intermediate lower teeth.

***Potamotrygon yepesi* (Figures 26, 27 and 28):** Teeth set in quincunx and wider than long in the dental plates of males and females. The upper plate is arched and shorter while the lower plate is flattened and overall trapezoidal in shape. It is also longer than the upper plate. The upper plate near symphysis (position 1) is more flattened and longer than intermediate and lateral portions (positions 2 and 3). The upper and lower plates have the labial margin continuously curved. Females have color variation between functional and non-functional files on both plates while males are devoid of color variation in teeth. Males have 25/23 tooth rows on upper and lower plates, respectively, and females have 28/25, respectively. The species has sexual heterodonty, with males presenting cuspidated teeth (**Cus**) and females being devoid of cusps. Males and females do not have dignathic heterodonty but present a gradual level of monognathic heterodonty.

Upper plate teeth near symphysis (position 1) in males have a fan-shaped crown and lower plate teeth have a drop-shaped crown. The labial edge is convex (**Lae**), and the transverse crest (**Tcr**) and the medial lingual ridge (**Mlr**) combined form a single triangular pointed cusp. Upper plate lower intermediate teeth (position 2) have an overall bell-shaped crown with cusps smaller than near symphysis teeth. Upper intermediate teeth have a similar morphology of near symphysis upper teeth, but the cusps are slightly less developed. In both regions the cusps are slightly curved towards the lateral portion of the plate. Both upper and lower lateral teeth (position 3) have a similar crown morphology in relation to upper plate intermediate teeth.

The upper and lower teeth near symphysis (position 1) in females have a near pentagon-shaped crown with three sides on the labial edge. The labial edge is convex with no distinct lingual marginal angles. Intermediate teeth (position 2) from both plates have a similar morphology to teeth near symphysis. Lateral teeth (position 3) in both plates have a circular-shaped crown with no distinct marginal angles.

***Potamotrygon signata* (Figures 29, 30 and 31):** The teeth are set in a quincunx pattern and wider than long in the plates of both males and females. The upper plate is arched and shorter, while the lower plate is trapezoidal, and longer than the upper plate. The upper plate is continuously curved, more flattened and anteroposteriorly longer near the symphysis compared to its intermediate and lateral portions. The lower plate has a nearly trapezoidal labial margin.

Females exhibit color variation between functional and non-functional files on both plates, whereas males lack such variation, similar to *P. yepezi*. Sexual dimorphism present in the teeth. Males bear a greater number of tooth rows on the upper and lower plates, 34/29, respectively, while females have 32/28. Tooth morphology varies depending on position within the plate, and the species exhibits sexual heterodonty. All teeth in males possess a single visible cusp (**Cus**), while those in females have a smaller primary cusp and two accessory cusps (**Acus**). Neither males nor females exhibit dignathic heterodonty, and they display a gradual level of monognathic heterodonty.

Upper and lower plate teeth near-symphysis in males have an overall triangular shape in occlusal view. The labial edge (**Lae**) is concave, and both the transverse crest (**Tcr**) and the medial lingual ridge (**Mlr**) are well developed into a single pointed cusp. The upper and lower intermediate teeth share a similar morphology but have slightly less developed cusps than near-symphysis teeth, curving slightly toward the lateral portion of the plate. The lower intermediate teeth possess a larger cusp with a more rounded tip than the upper intermediate teeth. Lateral teeth from both plates also have a triangular shape, but their cusps are considerably smaller than those of the near-symphysis and intermediate teeth, having approximately half the crown width. The lingual edge varies from concave to straightened.

Upper and lower plate teeth near-symphysis in females have an overall trapezoidal shape. Teeth from both plates are tricuspidate, with the main cusp being smaller than that of the lateral teeth in males. The accessory cusps are slightly smaller than the main cusp and develop at both labial marginal angles (**Lama**). The labial edge is concave, similar to the near-symphysis and intermediate teeth of males. The intermediate teeth on the upper and lower plates share a similar shape to the near-symphysis teeth. The intermediate teeth on the upper plate are shorter in length than those on the lower plate, and their main cusp is shorter than the accessory cusps. The lower intermediate teeth are nearly identical in length and cusp size to the

near-symphysis teeth. Lateral teeth on the upper and lower plates are similar in shape to the intermediate teeth of the upper plate. The upper lateral teeth have a shorter main cusp than the accessory cusps, whereas the lower lateral teeth have a main cusp that is slightly larger than the accessory cusps.

***Potamotrygon marquesi* (Figures 32 and 33):** Teeth set in quincunx and wider than long in the upper and lower plates of males and females. The upper plate is arched and shorter than the lower plate, while the lower plate is flattened and trapezoidal in shape, with lateral marked angles in the lingual margin (position 2). The upper plate is continually curved in males and is more arched near symphysis and less arched in intermediate portions in females. Females also have the upper plate near symphysis (position 1) flattened and antero-posteriorly longer than intermediate and lateral portions (positions 2 and 3). Males present color variation between functional and non-functional files on both plates, and females do not (however, Silva e Loboda, 2019 also report color variation for females). Males have 31/34 tooth rows on upper and lower plates, respectively, and females have 26/28, respectively. All teeth vary depending on the position on the plate and the species has sexual heterodonty, with a few teeth from males having cusps (**Cus**) and all teeth in females completely devoid of cusps.

Males have dignathic heterodonty and a gradual level of monognathic heterodonty in both plates. Upper and lower plate teeth near symphysis (position 1) have a trapezoid-shaped crown and a convex labial edge (**Lae**). The transverse crest (**Tcr**) and the medial lingual ridge (**Mlr**) form a single pointed cusp in the upper plate, while lower plate teeth have a single main cusp and two accessory cusps (**Acus**). Intermediate teeth (position 2) also have a trapezoid-shaped crown, which are wider and shorter than near symphysis teeth. The upper plate is devoid of cusps, while the lower plate has one main extremely short cusp and two similar in size accessory cusps. Lateral teeth (position 3) have an oval-shaped crown, and are shorter than all other teeth, with no distinct marginal angles between lingual and labial edges.

Females present dignathic heterodonty and a disjunct level of monognathic heterodonty on the upper plate, and a gradual level of monognathic heterodonty on the lower plate. The morphology of all upper and lower teeth are like that observed in the

female *P. motoro*. However, all teeth are slightly shorter, and the differences between teeth from different portions of the plate are less evident.

***Potamotrygon orbignyi* (Figures 34, 35 and 36):** Teeth set in quincunx and wider than long in all upper and lower plates of males and females. The upper plate is arched and shorter than the lower plate, while the lower plate is flattened and nearly reniform-shaped. The lingual margin of both upper and lower plates is continually curved. Both males and females have color variation between functional and non-functional teeth files. Males have 31/29 tooth rows on upper and lower plates, respectively, and females have 34/26, respectively. All teeth vary little between the upper and the lower plates and the species have sexual heterodonty. Males have one main cusp (**Cus**) in lower teeth and two additional accessory cusps (**Acus**) in upper plate teeth. This is consistent with Silva & Carvalho, 2015 which found that mature males can present a dentition that varies from monocuspidated to threecuspidated. Females present one main cusp and two accessory cusps (**Acus**) in all teeth. Males have dignathic heterodonty, while females do not. Both sexes present a gradual level of monognathic heterodonty.

Upper plates near symphysis (position 1) and intermediate teeth (position 2) in males have trapezoidal-shaped crowns, while lower teeth have triangular-shaped crowns. In both cases, the labial edge (**Lae**) is slightly concave. The transverse crest (**Tcr**) and the medial lingual ridge (**Mlr**) form a single pointed cusp in the lower teeth, while the upper teeth have additionally two accessory cups in the transversal crest. The intermediate teeth are slightly smaller in size than near symphysis teeth. Lateral teeth (position 3) vary from a trapezoidal to an oval-shaped crown, which are devoid of cusps. Upper and lower plates near symphysis (position 1), intermediate (position 2) and lateral teeth (position 3) in females have an arrangement like male lower plate teeth.

***Potamotrygon schroederi* (Figures 37, 38 and 39):** Teeth set in quincunx and wider than long in the upper and lower plates of males and females. The upper plate is arched and shorter than the lower plate of both males and females. The lower plate in males is reniform, with a continually curved lingual margin, while in females it is flattened and trapezoidal in shape, with marked mid-lateral angles in the lingual margin (position 2).

The upper plate is curved in both sexes. No color variation is present between functional labial files and non-functional lingual files. Males have 34/35 tooth rows on upper and lower plates, respectively, and females have 56 on both plates. All teeth vary little between the upper and lower plate, and the species have sexual heterodonty. Both sexes present a gradual level of monognathic heterodonty.

Upper and lower plate teeth near symphysis (position 1) in males have a triangular-shaped crown in occlusal view. The labial edge (**Lae**) is concave, and the transverse crest (**Tcr**) and the medial lingual ridge (**MLr**) form a single cusp (**Cus**), with a rounded in the apex (**Apx**) compared to other species of potamotrygonine (e.g., *P. yepzei*). Intermediate teeth (position 2) on both plates have a similar shape to near symphysis teeth, but with a pointed apex. Lateral teeth (position 3) from both plates have a reniform-shaped crown and lack cusps, bearing a concave labial edge, and a convex lingual edge (**Lie**). Lower teeth are wider and shorter than upper teeth.

Upper and lower plate teeth in females have a reniform-shaped crown and lack cusps, being similar to lateral teeth of males. Teeth near symphysis are bigger in size than intermediate and lateral teeth, and they gradually decrease in size towards the lateral side of the plate. Teeth near symphysis are also longer and narrower than intermediate and lateral teeth, and they get gradually shorter and wider towards the lateral side of the plate.

***Potamotrygon albimaculata* (Figures 40 and 41):** Teeth set in quincunx and wider than long in the upper and lower plates of males and females. The upper plate is arched and shorter than the lower plate, while the lower plate is flattened and trapezoidal in shape as a consequence of the marked mid-lateral angles on the labial margin (position 2). The upper plate is continually curved in males and is more arched near symphysis and less arched in intermediate portions in females. The upper plate near symphysis in females (position 1) is more flattened and longer than intermediate and lateral portions (positions 2 and 3). No color variation is present between functional labial files and non-functional lingual files. Males have 33/37 tooth rows on upper and lower plates, respectively, and females have 37/44. All teeth vary little between the upper and lower plates, and the species have sexual heterodonty. Both sexes present a gradual level of

monognathic heterodonty with males presenting a single cusp (**Cus**) in some teeth, and females lacking them completely.

Upper and lower plate teeth near symphysis (position 1) in males have a triangular-shaped crown. The labial edge (**Lae**) is convex, and the transverse crest (**Tcr**) and the medial lingual ridge (**Mlr**) form a single pointed cusp that has the same size of the crown base. Intermediate teeth (position 2) on both plates are nearly similar to near symphysis, with few differences. The cusp is slightly shorter, and the labial edge is slightly concave in the mid-portion of the plates. Lateral teeth (position 3) have an overall trapezoidal shape with the labial edge larger than the lingual edge (**Lie**). The labial edge has also a more marked concave curvature than intermediate teeth, and all teeth lack cusps.

Upper and lower plates near symphysis and lateral teeth (positions 1 and 2) in females have a lozenge-shaped crown. The upper teeth from both positions are slightly wider and shorter than lower teeth. The lateral teeth (position 3) have a trapezoidal-shaped crown, and are similar in shape to the lateral teeth of males, but have a convex lingual edge rather than concave like in males.

***Potamotrygon humerosa* (Figures 42, 43 and 44):** Teeth set in quincunx and wider than long in the upper and lower plates of males and females. The upper plate is arched and shorter than the lower plate, while the lower plate is flattened and trapezoidal in shape. The upper plate is curved. The upper plate is more flattened and longer near symphysis (position 1) than intermediate and lateral portions (positions 2 and 3). No color variation is present between functional labial files and non-functional lingual files. Males have 45 tooth rows on both upper and lower plates, and females have 36/38 tooth rows on upper and lower plates, respectively. All teeth vary little between the upper and lower plate, and the species have sexual heterodonty. Both sexes present a gradual level of monognathic heterodonty with males bearing a single cusp (**Cus**), and females lacking them completely. Male teeth from both plates share a similar morphology to what is observed in males of *P. signata*, while female teeth share an identical to that of females of *P. schroederi*.

***Potamotrygon amandae* (Figures 45, 46 and 47):** Teeth set in quincunx and wider than long in the upper and lower plates of males and females. The upper plate is arched and shorter than the lower plate, while the lower plate is flattened and trapezoidal in shape. The upper plate is curved. The upper plate is more flattened and longer near symphysis (position 1) than intermediate and lateral portions (positions 2 and 3). Both males and females present color variation between functional and non-functional files on both plates. Males have 40/37 tooth rows on upper and lower plates, respectively, and females have 34/29. All teeth vary little between the upper and lower plate, and the species have sexual heterodonty. Both sexes present a gradual level of monognathic heterodonty with males presenting a single cusp (**Cus**) in some teeth, and females bearing a small main cusp and two accessory cusps (**Acus**). Teeth from both plates in males and females share a similar morphology with teeth in *P. signata*, although males have cusps in intermediate and lateral teeth that are slightly curved towards the lateral of the plate.

***Potamotrygon wallacei* (Figures 48 and 49):** Teeth set in quincunx and wider than long in the plates of males and females. The upper plate is arched and shorter than the lower plate, while the lower plate is flattened and reniform in shape. The lingual margin of both the upper and lower plates is continually curved. No color variation is present between functional labial files and non-functional lingual files. Males have 49/45 tooth rows on upper and lower plates, respectively, and females have 52/50. Tooth morphology varies depending on position within the plate, and the species exhibits sexual heterodonty. All teeth in males possess a single visible cusp (**Cus**), while females lack cusps. Males and females do not have dignathic heterodonty and present a gradual level of monognathic heterodonty. The teeth morphology in males are similar to *P. amandae* while that in females are similar to *P. schroederi*.

***Potamotrygon limai* (Figures 50 and 51):** Teeth set in quincunx and wider than long in the dental plates of males and most positions in females. The only exception are the lower plate teeth near symphysis (position 1), which have equal proportions. The upper plate is arched and short while the lower plate is flattened and trapezoidal, being longer than the upper plate. No color variation is present between functional and

non-functional files. Males have 41/42 tooth rows on upper and lower plates, respectively, and females have 47/56, respectively. All teeth vary depending on the position on the plate and exhibit a gradual level of monognathic heterodonty. The species has sexual heterodonty, with most teeth of males bearing cusps (**Cus**) and all teeth in females lacking them.

Males have triangular-shaped crowns in all near symphysis (position 1) and intermediate (position 2) teeth on both plates. The labial edge (**Lae**) is straight, and both the transverse crest (**Trc**) and the medial lingual ridge (**Mlr**) form a single cusp. Intermediate teeth are slightly smaller than near symphysis teeth. Lateral teeth (position 3) are trapezoidal in shape and devoid of cusps.

Lower plate teeth in females from all portions except near symphysis (position 1) have an irregular hexagonal-shaped crown. The size of teeth decreases gradually from near symphysis to lateral (position 3) portion. Lower plate teeth near symphysis have a lozenge-shaped crown and are devoid of cusps.

***Potamotrygon scobina* (Figures 52, 53 and 54):** *P. scobina* has all the features of plate and teeth morphology in males and females like *P. limai*. Males have 39/43 tooth rows on upper and lower plates, respectively, and females have 44/42, respectively. However, males of *P. scobina* have cusps approximately 1/3 smaller than *P. limai*. Females have lower teeth near symphysis (position 1) trapezoidal and wider than long.

***Potamotrygon hystrix* (Figures 55 and 56):** Teeth set in quincunx and wider than long in the plates of males and most positions in females. The only exception are the lower plate teeth near symphysis (position 1), which have equal proportions. The upper plate is arched and shorter while the lower plate is flattened and trapezoidal, being longer than the upper plate. Both males and females present color variation between functional and nonfunctional files. Males have 24/20 tooth rows on upper and lower plates, respectively, and females have 28 tooth rows in the upper plate. All teeth vary depending on the position on the plate and exhibit a gradual level of monognathic heterodonty. The species has sexual heterodonty, with all teeth from males having cusps

(**Cus**) and all teeth in females completely devoid of cusps. Males do not have dignathic heterodonty.

Both plates in males have the crown with a morphology similar to teeth near symphysis (position 1) in *P. signata* males. Teeth decrease in size from near symphysis towards the lateral (position 3) portion of the dental plate. Lateral teeth are three times smaller than teeth near symphysis. Teeth near symphysis are oriented lingually while intermediate (position 2) and lateral teeth are slightly curved towards the lateral of the plate, a condition similar to the observed in *P. amandae*. Upper plate teeth in females have a similar morphology to the upper teeth in females of *P. limai*.

***Potamotrygon falkneri* (Figures 57 and 58):** Both plates of males and females with teeth set in quincunx and with no distinctions between crown width and length near symphysis (position 1) only, but with crowns wider than long in the remaining positions. The upper plate is arched and short while the lower plate is flattened and trapezoidal in shape, being visibly longer than the upper plate. No color variation is present between functional and nonfunctional teeth files. Males have 45/51 tooth rows on upper and lower plates, respectively, and females have 36/39, respectively. Tooth morphology varies gradually among the plate in males and females. Additionally, the species has little to no sexual heterodonty, with males and females sharing the same teeth morphology. However, Silva & Carvalho (2011) describes that part of the male specimens may bear one pointed cusp. The species is also devoid of dignathic heterodonty.

The teeth near symphysis (position 1) have a reniform-shaped crown, with both labial (**Lae**) and lingual (**Lie**) edges being convex and delimited by two lateral marginal angles (**Maa**). The lingual portion of the surface of the crown presents a subtle transverse crest (**Trc**). Intermediate (position 2) and lateral (position 3) teeth also have a reniform-shaped crown, and are progressively wider than long medially.

5.2 Character description

Below are 51 newly proposed characters based on the oral plates and individual teeth morphology of species of Potamotrygonidae. The first four characters are quantitative and the other 47 are qualitative. Since most species of Potamotrygonidae have sexual dimorphism, the majority of character statements are presented for each sex of the same species.

Oral plate morphology

1. Male upper plate; number of teeth rows: minimum = 23; maximum = 52
2. Male lower plate; number of teeth rows: minimum = 20; maximum = 51
3. Female upper plate; number of teeth rows: minimum = 23; maximum = 56
4. Female upper plate; number of teeth rows: minimum = 22; maximum = 56
5. Male dental plates; dark color; occurrence: (0) absent, (1) present.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon leopoldi*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. limai*, *P. falkneri*, *P. scobina*, *P. wallacei*, *P. yepezi*, *P. motoro*, *P. schroederi* and *P. signata*, all male functional and nonfunctional teeth present a cream coloration (0) (Figures 3A,C; 8A,C; 11A,C; 20A,C; 17A,C; 14A,C; 42A,C; 40A,C; 50A,C; 57A,C; 52A,C; 48A,C; 26A,C; 23A,C; 37A,C and 29A,C). In *Potamotrygon marquesi*, *P. hystrix*, *P. amandae* and *P. orbignyi*, all males present a brownish coloration in functional files in contrast to clearer teeth in nonfunctional files (1) (Figures 32A,C; 55A,C; 45A,C and 34A,C).

6. Female dental plates, dark color, occurrence: (0) absent, (1) present.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon leopoldi*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. limai*, *P. falkneri*, *P. scobina*, *P. wallacei*, *P. motoro* and *P. schroederi*, all female functional and non-functional teeth present the same coloration (0) (Figures 3B,D; 5B,D; 8B,D; 20B,D; 11B,D; 17B,D; 14B,D; 42B,D; 40B,D; 50B,D; 57B,D; 52B,D; 48B,D; 23B,D and 37B,D). In *Potamotrygon hystrix*, *P. amandae*, *P. orbignyi*, *P. yepezi* and *P. signata*, all females present a brownish coloration in functional files in contrast to cream colored teeth in nonfunctional files (1) (Figures 55B; 45B,D; 34B,D; 26B,D; and 29B,D). In the present study, *Potamotrygon marquesi* female functional and non-functional teeth showed the same coloration, but specimens analyzed by Silva & Loboda, 2019 had color variation in teeth. Consequently, this character was coded as polymorphic for this species (0,1) (Figure 32B,D).

7. Male dignathic heterodonty; occurrence: (0) absent, (1) present

This character was proposed by Cappetta (2012). In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon hystrix*, *P. brachyura*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. falkneri*, *P. scobina*, *P. wallacei*, *P. yepezi*, *P. schroederi* and *P. signata* the morphology of upper and lower plate teeth in males is similar and lack dignathic heterodonty (0) (Figures 3A,C; 5A,C; 8A,C; 11A,C; 55A,C; 17A,C; 42A,C; 40A,C; 45A,C; 50A,C; 57A,C; 52A,C; 48A,C; 26A,C; 37A,C and 29A,C). In *Potamotrygon marquesi*, *P. leopoldi*, *P. jabuti*, *P. orbignyi* and *P. motoro*, upper and lower plate teeth morphology varies and bears dignathic heterodonty (1) (Figure 32A,C; 20A,C; 14A,C; 34A,C and 23A,C).

8. Female dignathic heterodonty; occurrence: (0) absent, (1) present

This character was proposed by Cappetta (2012). In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. falkneri*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. schroederi* and *P. signata*, the morphology of upper

and lower plate teeth in females is similar and lack dignathic heterodonty (0) (Figures 3B,D; 5B,D; 8B,D; 11B,D; 42B,D; 40B,D; 45B,D; 50B,D; 57B,D; 52B,D; 34B,D; 48B,D; 26B,D; 37B,D and 29B,D). In *Potamotrygon marquesi*, *P. leopoldi*, *P. brachyura*, *P. jabuti*, and *P. motoro* upper and lower teeth morphology varies to some degree and exhibits dignathic heterodonty (1) (Figures 32B,D; 20B,D; 17B,D; 14B,D and 23B,D). Pertinent data in *Potamotrygon hystrix* could not be retrieved, and its condition was coded as missing (?).

9. Sexual heterodonty; occurrence: (0) absent, (1) present

In *Styracura schmardae* (outgroup), *Heliotrygon rosai* and *Potamotrygon leopoldi*, males and females have similar teeth morphology (0) (Figures 3, 5 and 20). In *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. hystrix*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. motoro*, *P. schroederi* and *P. signata* males and females have different teeth morphology and exhibit sexual heterodonty (1) (Figures 8, 11, 32, 55, 17, 14, 42, 40, 45, 50, 52, 34, 48, 26, 23, 37 and 29). In the present study no differences in teeth morphology were observed between males and females of *Potamotrygon falkneri*. However, Silva & Carvalho (2011a) reported differences in morphology between sexes. Consequently, this character was coded as polymorphic for this species (0,1) (Figure 57).

10. Male, upper plate, monognathic heterodonty; morphological variation: (0) gradual, (1) disjunct.

This character was proposed by Cappetta (2012). The gradual variation happens when the teeth morphology gradually changes from near symphysis to lateral rows. The disjunct variation happens when near symphysis, intermediate and lateral teeth abruptly differ in morphology. In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. hystrix*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. falkneri*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. schroederi* and *P. signata* the monognathic heterodonty in males is gradual (0) (Figures 3A, 5A, 8A, 11A, 32A, 55A, 17A, 14A, 42A, 40A, 45A, 50A, 57A, 52A, 34A, 48A, 26A, 37A and 29A). In *Potamotrygon*

leopoldi and *P. motoro* the monognathic heterodonty in males varies significantly and is interpreted as disjunct (1) (Figures 20A and 23A).

**11. Female upper plate; monognathic heterodonty; morphological variation:
(0) gradual, (1) disjunct.**

This character was proposed by Cappetta (2012). The gradual variation happens when the teeth morphology gradually changes from near symphysis to lateral rows. The disjunct variation happens when near symphysis, intermediate and lateral teeth abruptly differ in morphology. In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon hystrix*, *P. brachyura*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. falkneri*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. schroederi* and *P. signata* the monognathic heterodonty in the upper plate of females is gradual (0) (Figures 3B, 5B, 8B, 11B, 55B, 17B, 42B, 40B, 45B, 50B, 57B, 52B, 34B, 48B, 26B, 37B and 29B). In *Potamotrygon marquesi*, *P. leopoldi*, *P. jabuti* and *P. motoro* the monognathic heterodonty in the upper plate of females is evident and interpreted as disjunct (1) (32B, 20B, 14B and 23B).

12. Upper plate; ridge on intermediate portion; occurrence: (0) present, (1) absent.

In *Styracura schmardae* (outgroup), *Potamotrygon marquesi*, *P. leopoldi*, *P. brachyura*, *P. jabuti* and *P. motoro* the upper plate has a ridge in between the symphysis and lateral portions (intermediate) (0) (Figures 3A,B; 32A,B; 20A,B; 17A,B; 14A,B and 23A,B). In *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon hystrix*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. falkneri*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. schroederi* and *P. signata* the upper plate is devoid of a ridge in the intermediate portion of the plate (1) (Figures 5A,B; 8A,B; 11A,B; 42A,B; 40A,B; 45A,B; 50A,B; 57A,B; 52A,B; 34A,B; 48A,B; 26A,B; 37A,B and 29A,B).

13. Lower plate, labial margin; morphology: (0) Near the symphysis straightened, (1) near symphysis curved.

In *Styracura schmardae* (outgroup), *Potamotrygon marquesi*, *P. histrix*, *P. leopoldi*, *P. brachyura*, *P. jabuti*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. scobina*, *P. motoro* and *P. schroederi* the lower plate labial margin near symphysis is straightened (0) (Figures 3C,D; 32C,D; 55C,D; 20C,D; 17C,D; 14C,D; 40C,D; 45C,D; 50C,D; 52C,D; 23C,D and 37C,D). In *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon humerosa*, *P. falkneri*, *P. orbignyi*, *P. wallacei*, *P. yepezi* and *P. signata* the lower plate labial margin near symphysis is curved (1) (Figures 5C,D; 8C,D; 11C,D; 42C,D; 57C,D; 34C,D; 48C,D; 26C,D and 29C,D).

Tooth morphology

14. Male upper plate teeth near symphysis; base of the crown; size: (0) wider than long, (1) as long as wide.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. histrix*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. motoro*, *P. schroederi* and *P. signata* the base of the crown in upper teeth near symphysis in males is wider than long (0) (Figures 4A, 64A, 94A, 12A, 33A, 56A, 18A, 15A, 43A, 41A, 46A, 50A, 53A, 35A, 49A, 27A, 24A, 38A and 30A). In *Potamotrygon leopoldi* and *P. falkneri* the base of the crown has the same proportions in upper teeth near symphysis in males (1) (Figures 21A and 58A).

15. Male lower plate teeth near symphysis; base of the crown; size: (0) wider than long, (1) as long as wide.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. histrix*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. motoro*, *P. schroederi* and *P. signata* the base of the crown in lower teeth near symphysis in males is wider than long (0) (Figures 4D, 64D, 94D, 12D, 33D, 56D, 18D, 15D, 43D, 41D, 46D, 50C, 53C, 35D, 49D, 27D, 24D, 38D and 30D). In *Potamotrygon*

leopoldi and *P. falkneri* the base of the crown has the same proportions in lower teeth near symphysis in males (1) (Figures 21D and 58D).

16. Male lower plate intermediate teeth, base of the crown; size: (0) wider than long, (1) as long as wide.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. hystrix*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. falkneri*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. motoro*, *P. schroederi* and *P. signata* the base of the crown is wider than long in lower intermediate teeth in males (0) (Figures 4E, 64E, 94E, 12E, 33E, 56E, 18E, 15E, 43E, 41E, 46E, 50C, 58E, 53D, 35E, 49E, 27E, 24E, 38E and 30E). In *Potamotrygon leopoldi* the base of the crown has the same proportions in lower intermediate male teeth (1) (Figure 21E).

17. Female upper plate teeth near symphysis; base of the crown; size: (0) wider than long, (1) as long as wide.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. motoro*, *P. schroederi* and *P. signata* the base of the crown in upper teeth near symphysis in females is wider than long (0) (Figures 3B, 7A, 10A, 13A, 32B, 19A, 16A, 44A, 40B, 47A, 51A, 54A, 36A, 48B, 28A, 25A, 29A and 31A). In *Potamotrygon hystrix*, *P. leopoldi* and *P. falkneri* the base of the crown has the same proportions in female's upper teeth near symphysis (1) (Figures 55B, 22A and 57B).

18. Female lower plate teeth near symphysis; base of the crown; size: (0) wider than long, (1) as long as wide.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. motoro*, *P. schroederi* and *P. signata* the base of the crown is wider than long in female's lower teeth near symphysis is (0) (Figures 3D, 7D, 10D, 13D, 32D, 19D, 16D, 44D, 40D,

47D, 54D, 36D, 48D, 28D, 25D, 37D and 31C). In *Potamotrygon leopoldi*, *P. limai* and *P. falkneri* the base of the crown has the same proportions in female's lower teeth near symphysis (1) (Figures 22D, 51D and 57D). Pertinent data of *Potamotrygon histrix* could not be retrieved, and its condition was coded as missing (?).

19. Female lower plate intermediate teeth; base of the crown; size: (0) wider than long, (1) as long as wide.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. falkneri*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. motoro*, *P. schroederi* and *P. signata* the base of the crown in female's lower intermediate teeth is wider than long (0) (Figures 3D, 710E, 10E, 13E, 32D, 19E, 16E, 44E, 40D, 47E, 51E, 57D, 54E, 36E, 48D, 28E, 25E, 37D and 31D). In *Potamotrygon leopoldi* the base of the crown has the same proportions in the female's lower intermediate teeth (1) (Figure 22E). Pertinent data of *Potamotrygon histrix* could not be retrieved, and its condition was coded as missing (?).

20. Female lower plate lateral teeth; base of the crown; size: (0) wider than long, (1) as long as wide.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. falkneri*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. motoro*, *P. schroederi* and *P. signata* the base of the crown is wider than long in lower intermediate teeth in females (0) (Figures 3D, 710F, 10F, 13F, 32D, 19F, 16F, 44F, 40D, 47F, 51F, 57D, 54F, 36F, 48D, 28F, 25F, 37D and 31D). In *Potamotrygon leopoldi* the base of the crown has the same proportions in lower lateral teeth of females (1) (Figure 22F). Pertinent data of *Potamotrygon histrix* could not be retrieved, and its condition was coded as missing (?).

21. Male upper plate; cusps in teeth near symphysis; occurrence: (0) present, (1) absent.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. histrix*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. schroederi* and *P. signata* the upper teeth near symphysis in males have cups (0) (Figures 4A, 6A, 9A, 12A, 33A, 56A, 18A, 15A, 43A, 41A, 46A, 50A, 53A, 35A, 49A, 27A, 24A, 38A and 30A). In *Potamotrygon leopoldi* and *P. motoro* the upper teeth near symphysis in males are devoid of cusps (1) (Figures 21A and 24A). In the present study, the upper teeth near symphysis in *Potamotrygon falkneri* lack cusps but Silva & Carvalho (2011a) reported the presence of cusps in some male individuals. Consequently, this character was coded as polymorphic (0,1) (Figure 58A).

22. Male upper plate; cusps in intermediate teeth; occurrence: (0) present, (1) absent.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon histrix*, *P. brachyura*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. motoro*, *P. schroederi* and *P. signata* the upper intermediate teeth in males have cups (0) (Figures 4B, 6B, 9B, 12B, 56B, 18B, 43B, 41B, 46B, 50A, 53B, 35B, 49B, 27B, 24B, 38B and 30B). In *Potamotrygon marquesi*, *P. leopoldi*, *P. jabuti* and *P. motoro* the upper intermediate teeth in males lack cusps (1) (Figures 33B, 21B, 15B and 24B). In the present study, the upper intermediate teeth of *Potamotrygon falkneri* lack cusps but Silva & Carvalho (2011a) reported the presence of cusp in some male individuals. Consequently, this character was coded as polymorphic (0,1) (Figure 58B).

23. Male upper plate; cusps in lateral teeth; occurrence: (0) present, (1) absent.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon histrix*, *P. humerosa*, *P. amandae*, *P. limai*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. motoro* and *P. signata* the upper lateral teeth in males have cups (0) (Figures 4C, 6C, 9C, 12C, 56C, 43C, 46C, 50A, 52A, 35C,

49C, 27C, 24C, and 30C). In *Potamotrygon marquesi*, *P. leopoldi*, *P. brachyura*, *P. jabuti*, *P. albimaculata*, *P. motoro* and *P. schroederi* the upper lateral teeth in males lack cusps (1) (Figures 33C, 21C, 18C, 15C, 41C, 24C and 38C). In the present study, the upper lateral teeth of *Potamotrygon falkneri* were found as lacking cusps but Silva & Carvalho (2011a) reported the presence of cusp in some male individuals. Consequently, this character was coded as polymorphic (0,1) (Figure 58C).

24. Male lower plate; cusps in teeth near symphysis; occurrence: (0) present, (1) absent.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. hystrix*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. motoro*, *P. schroederi* and *P. signata* the lower teeth near symphysis in males have cusps (0) (Figures 4D, 6D, 9D, 12D, 33D, 56D, 18D, 15D, 43D, 40C, 46D, 50C, 53C, 35D, 49D, 27D, 24D, 38D and 30D). In *Potamotrygon leopoldi* and *P. motoro* the lower teeth near symphysis in males are devoid of cusps (1) (Figures 21D and 24D). In the present study, the lower teeth near symphysis of *Potamotrygon falkneri* were found lacking cusps. Silva & Carvalho (2011a) reported the presence of cusps in some male individuals. Consequently, this character was then coded as polymorphic (0,1) (Figure 58D).

25. Male lower teeth; cusps in intermediate teeth; occurrence: (0) present, (1) absent.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. hystrix*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. motoro*, *P. schroederi* and *P. signata* the lower intermediate teeth in males have cusps (0) (Figures 4E, 6E, 9E, 12E, 33E, 56E, 18E, 15E, 43E, 40C, 46E, 50C, 53D, 35E, 49E, 27E, 24E, 38E and 30E). In *Potamotrygon leopoldi* and *P. motoro* the lower intermediate teeth in males are devoid of cusps (1) (Figures 21E and 24E). In the present study, the intermediate teeth of *Potamotrygon falkneri* were found lacking cusps

but Silva & Carvalho (2011a) reported the presence of cusps in some male individuals. Consequently, this character was coded as polymorphic (0,1) (Figure 58E).

26. Male lower teeth; cusps in lateral teeth; occurrence: (0) present, (1) absent.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon histrix*, *P. humerosa*, *P. amandae*, *P. limai*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, and *P. signata* the lower lateral teeth in males have cups (0) (Figures 4F, 6F, 9F, 12F, 56F, 43F, 46F, 50C, 53E, 35F, 49F, 27F and 30F). In *Potamotrygon marquesi*, *P. leopoldi*, *P. brachyura*, *P. jabuti*, *P. albimaculata*, *P. motoro* and *P. schroederi* the lower lateral teeth in males are devoid of cusps (1) (Figures 33F, 21F, 18F, 15F, 40C, 24F, and 38F). In the present study, the lower lateral teeth of *Potamotrygon falkneri* were found lacking cusps, but Silva & Carvalho (2011a) reported the presence of cusps in some male individuals. Consequently, this character was coded as polymorphic (0,1) (Figure 58F).

27. Female upper plate; cusps; occurrence: (0) present, (1) absent.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Potamotrygon amandae*, *P. orbignyi* and *P. signata* all upper teeth in females have cups (0) (Figures 3B; 7A,B,C; 10A,B,C; 47A,B,C; 36A,B,C and 29B). In *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. histrix*, *P. leopoldi*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. limai*, *P. falkneri*, *P. scobina*, *P. wallacei*, *P. yepezi*, *P. motoro* and *P. schroederi* all upper teeth in females are devoid of cusps (Figures 13A,B,C; 32B; 55B; 22A,B,C; 19A,B,C; 16A,B,C; 44A,B,C; 40B; 51A,B,C; 57B; 54A,B,C; 48B; 28A,B,C; 25A,B,C and 39A,B,C).

28. Female lower plate; cusps; occurrence: (0) present, (1) absent.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Potamotrygon amandae*, *P. orbignyi* and *P. signata* all lower teeth in females have cups (0) (Figures 3D; 7D,E,F; 10D,E,F; 47D,E,F; 36D,E,F and 29D). In *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. leopoldi*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P.*

albimaculata, *P. limai*, *P. falkneri*, *P. scobina*, *P. wallacei*, *P. yepezi*, *P. motoro* and *P. schroederi* all lower teeth in females are devoid of cusps (Figures 13D,E,F; 32D; 22D,E,F; 19D,E,F; 16D,E,F; 44D,E,F; 40D; 51D,E,F; 57B; 54D,E,F; 48B; 28D,E,F; 25D,E,F and 39D,E,F). Pertinent data of *Potamotrygon histrix* could not be retrieved, and its condition was coded as missing (?).

29. Male upper plate; accessory cusps in teeth near symphysis; occurrence: (0) absent, (1) present.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. histrix*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. falkneri*, *P. scobina*, *P. wallacei*, *P. yepezi*, *P. schroederi*, *P. signata*, *P. leopoldi* and *P. motoro* the upper teeth near symphysis in males lack accessory cusps (0) (Figures 4A, 6A, 9A, 12A, 33A, 56A, 18A, 15A, 43A, 41A, 46A, 50A, 58A, 53A, 35A, 49A, 27A, 24A, 38A, 30A, and 24A). In the present study the upper teeth near symphysis in males of *Potamotrygon orbignyi* lacked cusps, but Silva & Carvalho (2015) reported accessory cusps for males. Consequently, this character was coded as polymorphic (0,1) (Figure 21A).

30. Male upper plate, accessory cusps in intermediate teeth; occurrence: (0) absent, (1) present.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon histrix*, *P. brachyura*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. falkneri*, *P. scobina*, *P. wallacei*, *P. yepezi*, *P. schroederi*, *P. signata*, *P. marquesi*, *P. leopoldi*, *P. jabuti* and *P. motoro* the upper intermediate teeth in males are devoid of accessory cusps (0) (Figures 4B, 6B, 9B, 12B, 33B, 56B, 18B, 15B, 43B, 41B, 46B, 50A, 58B, 53B, 35B, 49B, 27B, 24B, 38B, 30B, and 24B). In the present study, the upper intermediate teeth in males of *Potamotrygon orbignyi* also lacked cusps, but Silva & Carvalho (2015) reported males as having accessory cusps. Consequently, this character was coded as polymorphic (0,1) (Figure 21B).

31. Male upper plate; accessory cusps in lateral teeth; occurrence: (0) absent, (1) present.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon hystrix*, *P. humerosa*, *P. amandae*, *P. limai*, *P. falkneri*, *P. scobina*, *P. wallacei*, *P. yepezi*, *P. signata*, *P. marquesi*, *P. leopoldi*, *P. brachyura*, *P. jabuti*, *P. albimaculata*, *P. motoro* and *P. schroederi* the upper lateral teeth in males lack accessory cusps (0) (Figures 4C, 6C, 9C, 12C, 33C, 56C, 18C, 15C, 43C, 41C, 46C, 50A, 58C, 52A, 35C, 49C, 27C, 24C, 38C, 30C, and 24C). In the present study the upper lateral teeth in males of *Potamotrygon orbignyi* also lacked cusps. Silva & Carvalho (2015) reported males as having accessory cusps. Consequently, this character was coded as polymorphic (0,1) (Figure 21C).

32. Male lower plate, accessory cusps in teeth near symphysis; occurrence: (0) absent, (1) present.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon hystrix*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. falkneri*, *P. scobina*, *P. wallacei*, *P. yepezi*, *P. schroederi*, *P. signata*, *P. leopoldi* and *P. motoro* the lower teeth near symphysis in males are devoid of accessory cusps (0) (Figures 4D, 6D, 9D, 12D, 56D, 18D, 15D, 43D, 40C, 46D, 50C, 58D, 53C, 35D, 49D, 27D, 24D, 38D, 30D, and 24D). The lower teeth near symphysis in males of *Potamotrygon marquesi* have accessory cusps (1) (Figure 33D). In the present study the lower teeth near symphysis of *Potamotrygon orbignyi* lacked cusps, but Silva & Carvalho (2015) reported males as having accessory cusps. Consequently, this character was then coded as polymorphic (0,1) (Figure 21D).

33. Male lower plate; accessory cusps in intermediate teeth; occurrence: (0) absent, (1) present.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon hystrix*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. falkneri*, *P. scobina*, *P. wallacei*, *P. yepezi*, *P. schroederi*, *P. signata*, *P. leopoldi* and *P. motoro* the lower intermediate teeth in males

are devoid of accessory cusps (0) (Figures 4E, 6E, 9E, 12E, 56E, 18E, 15E, 43E, 40C, 46E, 50C, 58E, 53C, 35E, 49E, 27E, 24E, 38E, 30E, and 24E). In *Potamotrygon marquesi* the lower intermediate teeth have accessory cusps (1) (Figure 33E). In the present study the lower intermediate teeth in males of *Potamotrygon orbignyi* lacked cusps. Silva & Carvalho (2015) reported males as having accessory cusps. Consequently, this character was coded as polymorphic (0,1) (Figure 21E).

34. Male lower plate; accessory cusps in lateral teeth; occurrence: (0) absent, (1) present.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon hystrix*, *P. humerosa*, *P. amandae*, *P. limai*, *P. falkneri*, *P. scobina*, *P. wallacei*, *P. yepzei*, *P. signata*, *P. marquesi*, *P. leopoldi*, *P. brachyura*, *P. jabuti*, *P. albimaculata*, *P. motoro* and *P. schroederi* the lateral lower teeth in males are devoid of accessory cusps (0) (Figures 4F, 6F, 9F, 12F, 33F, 56F, 18F, 15F, 43F, 40C, 46F, 50C, 58F, 53C, 35F, 49F, 27F, 24F, 38F, 30F, and 24F). In the present study the lateral lower teeth in males of *Potamotrygon orbignyi* were also devoid of cusps. Silva & Carvalho (2015) reported males as having accessory cusps. Consequently, this character was coded as polymorphic (0,1) (Figure 21F).

35. Female upper plate; accessory cusps; occurrence: (0) absent, (1) present.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. hystrix*, *P. leopoldi*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. limai*, *P. falkneri*, *P. scobina*, *P. wallacei*, *P. yepzei*, *P. motoro* and *P. schroederi* all upper teeth in females are devoid of accessory cusps (0) (Figures 3B; 7A,B,C; 10A,B,C; 13A,B,C; 32B; 56A,B,C; 22A,B,C; 19A,B,C; 16A,B,C; 44A,B,C; 40B; 51A,B,C; 57B; 54A,B,C; 48B; 28A,B,C; 25A,B,C and 39A,B,C). In *Potamotrygon amandae*, *P. orbignyi* and *P. signata* all upper teeth in females have two accessory cusps flanking the main cusp (1) (Figures 47A,B,C; 36A,B,C and 29B).

36. Female lower plate; accessory cusps; occurrence: (0) absent, (1) present.

In *Styracura schmardae* (outgroup), *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. leopoldi*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. limai*, *P. falkneri*, *P. scobina*, *P. wallacei*, *P. yepezi*, *P. motoro* and *P. schroederi* all female lower teeth are devoid of accessory cusps (0) (Figure 3D; 7D,E,F; 10D,E,F; 13D,E,F; 32D; 22D,E,F; 19D,E,F; 16D,E,F; 44D,E,F; 40D; 51D,E,F; 57D; 54D,E,F; 48D; 28D,E,F; 25D,E,F and 37D). In *Potamotrygon amandae*, *P. orbignyi* and *P. signata* all lower teeth in females have two accessory cusps flanking the main cusp (1) (Figures 47D,E,F; 36D,E,F and 31D,E,F). Pertinent data of *Potamotrygon histrix* could not be retrieved, and its condition was coded as missing (?).

37. Male upper plate; labial edge near symphysis; shape: (0) straight, (1) convex, (2) concave.

In *Styracura schmardae* (outgroup) and *Potamotrygon scobina* the upper labial edge near symphysis is straight in males (0) (Figures 4A and 53A). In *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. leopoldi*, *P. brachyura*, *P. jabuti*, *P. falkneri*, *P. yepezi* and *P. motoro* the upper labial edge near symphysis in males is convex (1) (Figures 6A, 9A, 12A, 33A, 21A, 18A, 15A, 58A, 27A and 24A). In *Potamotrygon histrix*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. orbignyi*, *P. wallacei*, *P. schroederi* and *P. signata* the upper labial edge near symphysis in males is concave (2) (Figures 56A, 43A, 41A, 46A, 35A, 49A, 38A and 30A).

38. Male upper plate; intermediate portion of labial edge; shape: (0) straight, (1) convex, (2) concave.

In *Styracura schmardae* (outgroup), *Potamotrygon jabuti* and *P. scobina* the upper intermediate labial edge is straight (0) (Figures 4B, 15B and 53B). In *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. leopoldi*, *P. brachyura*, *P. albimaculata*, *P. falkneri*, *P. yepezi* and *P. motoro* the upper intermediate labial edge is convex in males (1) (Figures 6B, 9B, 12B, 33B, 21B, 18B, 41B, 58B, 27B and 24B). In *Potamotrygon histrix*, *P. humerosa*, *P. amandae*, *P. orbignyi*, *P. wallacei*, *P.*

schroederi and *P. signata* the upper intermediate labial edge is concave in males (2) (Figures 56B, 43B, 46B, 35B, 49B, 38B and 30B).

39. Male upper plate; lateral labial edge; shape: (0) straight, (1) convex, (2) concave.

In *Styracura schmardae* (outgroup) and *Potamotrygon scobina* the upper lateral labial edge is straight in males (0) (Figures 4C and 52A). In *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. leopoldi*, *P. brachyura*, *P. jabuti*, *P. albimaculata*, *P. falkneri*, *P. yepezi* and *P. motoro* the upper lateral labial edge is convex in males (1) (Figures 6C, 9C, 12C, 33C, 21C, 18C, 15C, 41C, 58C, 27C and 24C). In *Potamotrygon hystrix*, *P. humerosa*, *P. amandae*, *P. orbignyi*, *P. wallacei*, *P. schroederi* and *P. signata* the upper lateral labial edge is concave in males (2) (Figures 56C, 43C, 46C, 35C, 49C, 38C and 30C).

40. Male lower plate; labial edge near symphysis; shape: (0) straight, (1) convex, (2) concave.

In *Styracura schmardae* (outgroup) and *Potamotrygon scobina* the lower near symphysis labial edge is straight in males (0) (Figures 4D and 53C). In *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. leopoldi*, *P. brachyura*, *P. jabuti*, *P. falkneri*, *P. yepezi* and *P. motoro* the lower labial edge near symphysis is convex in males (1) (Figures 6D, 9D, 12D, 33D, 21D, 18D, 15D, 58D, 27D and 24D). In *Potamotrygon hystrix*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. orbignyi*, *P. wallacei*, *P. schroederi* and *P. signata* the lower labial edge near symphysis is concave in males (2) (Figures 56D, 43D, 40C, 46D, 35D, 49D, 38D and 30D).

41. Male lower plate; intermediate labial edge; shape: (0) straight, (1) convex, (2) concave.

In *Styracura schmardae* (outgroup) and *Potamotrygon scobina* the lower intermediate is straight in males (0) (Figures 4E and 53D). In *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. leopoldi*, *P.*

brachyura, *P. jabuti*, *P. albimaculata*, *P. falkneri*, *P. yepezi* and *P. motoro* the lower intermediate labial edge is convex in males (1) (Figures 6E, 9E, 12E, 33E, 21E, 18E, 15E, 40C, 58E, 27E and 24E). In *Potamotrygon histrix*, *P. humerosa*, *P. amandae*, *P. orbignyi*, *P. wallacei*, *P. schroederi* and *P. signata* the lower intermediate labial edge is concave in males (2) (Figures 56E, 43E, 46E, 35E, 49E, 38E and 30E).

42. Male lower plate; lateral labial edge; shape: (0) straight, (1) convex, (2) concave.

In *Styracura schmardae* (outgroup), *Potamotrygon brachyura*, *P. jabuti*, and *P. scobina* the lower lateral labial edge is straight in males (0) (Figures 4F, 18F, 15F, and 53E). In *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. leopoldi*, *P. albimaculata*, *P. falkneri*, *P. yepezi* and *P. motoro* the lower lateral labial edge is convex in males (1) (Figures 6F, 9F, 12F, 33F, 21F, 40C, 58F, 27F and 24F). In *Potamotrygon histrix*, *P. humerosa*, *P. amandae*, *P. orbignyi*, *P. wallacei*, *P. schroederi* and *P. signata* the lower lateral labial edge is concave in males (2) (Figures 56F, 43F, 46F, 35F, 49F, 38F and 30F).

43. Female upper plate; labial edge near symphysis; shape: (0) straight, (1) convex, (2) concave.

In *Styracura schmardae* (outgroup), *Potamotrygon histrix*, *P. jabuti*, and *P. scobina* the upper labial edge near symphysis is straight in females (0) (Figures 3B, 55B, 16A and 54A). In *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. leopoldi*, *P. brachyura*, *P. albimaculata*, *P. falkneri*, *P. yepezi* and *P. motoro* the upper labial edge near symphysis is convex in females (1) (Figures 7A, 10A, 13A, 32B, 22A, 19A, 40B, 57B, 28A and 25A). In *Potamotrygon humerosa*, *P. amandae*, *P. orbignyi*, *P. wallacei*, *P. schroederi* and *P. signata* the upper labial edge near symphysis is concave in females (2) (Figures 44A, 47A, 36A, 48B, 39A and 31A).

44. Female upper plate; intermediate labial edge; shape: (0) straight, (1) convex, (2) concave.

In *Styracura schmardae* (outgroup), *Potamotrygon marquesi*, *P. histrix*, *P. leopoldi*, *P. jabuti*, *P. scobina* and *P. motoro* the upper intermediate labial edge is straight in females (0) (Figures 3B, 32B, 55B, 22B, 16B, 54B and 25B). In *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon brachyura*, *P. albimaculata*, *P. falkneri* and *P. yepezi* the upper intermediate labial edge is convex in females (1) (Figures 10B, 13B, 19B, 40B, 57B and 28B). In *Potamotrygon humerosa*, *P. amandae*, *P. orbignyi*, *P. wallacei*, *P. schroederi* and *P. signata* the upper intermediate labial edge is concave in females (2) (Figures 44B, 47B, 36B, 48B, 39B and 31B).

45. Female upper plate; lateral labial edge; shape: (0) straight, (1) convex, (2) concave.

In *Styracura schmardae* (outgroup), *Potamotrygon histrix*, *P. jabuti*, and *P. scobina* the upper lateral is straight in females (0) (Figures 3B, 55B, 16C and 54C). In *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. leopoldi*, *P. brachyura*, *P. albimaculata*, *P. falkneri*, *P. yepezi* and *P. motoro* the upper lateral labial edge is convex in females (1) (Figures 7C, 10C, 13C, 32B, 22C, 19C, 40B, 57B, 28C and 25C). In *Potamotrygon humerosa*, *P. amandae*, *P. orbignyi*, *P. wallacei*, *P. schroederi* and *P. signata* the upper lateral labial edge is concave in females (2) (Figures 44C, 47C, 36C, 48C, 39C and 29B).

46. Female lower plate; labial edge; shape: (0) straight, (1) convex, (2) concave.

In *Styracura schmardae* (outgroup), *Potamotrygon jabuti*, and *P. scobina* the lower labial edge is straight in females (0) (Figures 3D, 16D,E,F and 54D,E,F). In *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. leopoldi*, *P. brachyura*, *P. albimaculata*, *P. falkneri*, *P. yepezi* and *P. motoro* the lower labial edge is convex in females (1) (Figures 7DE,F; 10DE,F; 13DE,F; 32B, 22DE,F; 19DE,F; 40D, 57D, 28DE,F and 25DE,F). In *Potamotrygon humerosa*, *P. amandae*, *P. orbignyi*, *P. wallacei*, *P. schroederi* and *P. signata* the lower labial edge is concave in

females (2) (Figures 44DE,F; 47DE,F; 36DE,F; 48D, 37D and 31C). Pertinent data of *Potamotrygon histrix* could not be retrieved, and its condition was coded as missing (?).

47. Upper and lower plates; base of the crown; second transversal crest; occurrence: (0) present, (1) absent.

In *Styracura schmardae* (outgroup) a second transversal crest is present on the crown surface underneath the transversal crest (0) (Figure 3). In *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. histrix*, *P. leopoldi*, *P. brachyura*, *P. jabuti*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. falkneri*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. motoro*, *P. schroederi* and *P. signata* a second transversal crest is absent (1).

48. Male upper plate; curvature of cusps in intermediate teeth; occurrence: (0) present, (1) absent.

In *Styracura schmardae* (outgroup), *Potamotrygon histrix*, *P. humerosa*, *P. amandae*, *P. wallacei*, *P. yepezi*, *P. signata*, *P. marquesi*, *P. leopoldi*, *P. jabuti* and *P. motoro* the upper intermediate teeth in males have laterally curved cusps (0) (Figures 4B, 55A, 43B, 46B, 48B, 27B, 30B, 21B, 15B and 24B). In *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon brachyura*, *P. albimaculata*, *P. limai*, *P. falkneri*, *P. scobina*, *P. orbignyi*, and *P. schroederi* the upper intermediate teeth in males lack laterally curved cusps, which are oriented lingually (1) (Figures 6B, 9B, 12B, 18B, 41B, 50A, 58B, 53B, 35B and 38B).

49. Male upper plate; curvature of cusps in lateral teeth; occurrence: (0) present, (1) absent.

In *Styracura schmardae* (outgroup), *Potamotrygon histrix*, *P. humerosa*, *P. amandae*, *P. wallacei*, *P. yepezi*, *P. signata*, *P. marquesi*, *P. leopoldi*, *P. brachyura*, *P. jabuti*, *P. albimaculata*, *P. motoro*, and *P. schroederi* the upper lateral teeth in males have laterally curved cusps (0) (Figures 4C, 55A, 43C, 46C, 48C, 27C, 30C, 32C, 21C, 18C, 15C, 41C, 24C and 38C). In *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *P. limai*, *P. falkneri*, *P. scobina*, *P. orbignyi* and *P. schroederi*, upper lateral

teeth in males lack laterally curved cusps, which are oriented lingually (1) (Figures 7C, 10C, 13C, 50A, 58C, 52A, 35C and 38C).

50. Male lower plate; curvature of cusps in intermediate teeth; occurrence: (0) present, (1) absent.

In *Styracura schmardae* (outgroup), *Potamotrygon histrix*, *P. humerosa*, *P. amandae*, *P. wallacei*, *P. yepezi*, *P. signata*, *P. leopoldi*, *P. jabuti* and *P. motoro* the lower intermediate teeth in males have laterally curved cusps (0) (Figures 4E, 55C, 43E, 46E, 48E, 27E, 30E, 15E and 24E). In *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *Potamotrygon marquesi*, *P. brachyura*, *P. albimaculata*, *P. limai*, *P. falkneri*, *P. scobina*, *P. orbignyi* and *P. schroederi* the lower intermediate teeth in males lack laterally curved cusps, being oriented lingually (1) (Figures 6E, 9E, 12E, 21E, 18E, 40C, 50C, 58E, 53D, 35E and 38E).

51. Male lower plate; curvature of cusps in lateral teeth; occurrence: (0) present, (1) absent.

In *Styracura schmardae* (outgroup), *Potamotrygon histrix*, *P. humerosa*, *P. amandae*, *P. wallacei*, *P. yepezi*, *P. signata*, *P. marquesi*, *P. leopoldi*, *P. brachyura*, *P. jabuti*, *P. albimaculata*, *P. motoro*, and *P. schroederi* the lower lateral teeth in males have laterally curved cusps (0) (Figures 4F, 55C, 43F, 46F, 48F, 27F, 30F, 32F, 21F, 18F, 15F, 40C, 24F and 38F). In *Heliotrygon rosai*, *Paratrygon aiereba*, *Plesiotrygon iwamae*, *P. limai*, *P. falkneri*, *P. scobina*, *P. orbignyi* and *P. schroederi*, the lower lateral teeth in males lack laterally curved cusps, being oriented lingually (1) (Figures 7F, 10F, 13F, 50C, 58F, 52E, 35F and 38F).

5.3 Phylogenetic analysis

The phylogenetic analysis of Potamotrygoninae yielded a single most parsimonious tree using POS (extended implied-weighting, XIW) and a *k* value of 4.61909. The tree has 1799,862 steps of length and fit equal to 157,82434 (Figures 59

and 60). The family Potamotrygoninae is divided into two main clades: one formed by *Heliotrygon rosai* and *Paratrygon aiereba*, (clade B), which were recovered as sister taxon (GC = 84; RBS = 17) to the clade including *Plesiotrygon iwamae* and all species of *Potamotrygon* (clade C) (GC = 97; RBS = 24).

Plesiotrygon iwamae was recovered nested within the genus *Potamotrygon*, indicating *Potamotrygon* as paraphyletic, a result similar to previous works exploring freshwater stingrays (Fontenelle *et al.*, 2021a,b; Araújo, 2024). Within clade C, *Potamotrygon brachyura* is recovered as the sister group of *Plesiotrygon iwamae* and all remaining species of *Potamotrygon* (clade D; GC = 75; RBS = 22). *Potamotrygon yepezi*, *P. wallacei*, *P. orbignyi* and *P. signata* are recovered as consecutive sisters species (GC = 21; RBS = 9 / GC = 77; RBS = 23 / GC = 100; RBS = 38 / GC = 99; RBS = 18 respectively) to clade I, that includes the other 12 remaining species of *Potamotrygon* (GC = [4]; RBS = 3).

The species of *Potamotrygon* in clade I are divided into two sister clades (J and L). In clade J, *Potamotrygon amandae* is recovered as sister (GC = 67; RBS = 36) to *P. hystrix* and *P. fakneri* (clade K; GC = 100; RBS = 81). The clade L is branched in two main sister clades (clades M and P; GC = [36]; RBS = 12). The clade M has two lineages (GC = [18]; RBS = 12) with *P. limai* + *P. scobina* (clade N; GC = 81; RBS = 6) forming the sister taxon of *P. humerosa* + *P. schroederi* (clade O; GC = 75; RBS = 10). The clade P (GC = [33]; RBS = 3) includes *P. leopodi* + *P. motoro* (branch Q; GC = 23; RBS = 42) as sister to (*P. marquesi* + (*P. jabuti* + *P. albimaculata*)) (clade R; GC = [22]; RBS = 3).

5.4 Bibliographic survey of feeding habits

The survey of the feeding habits covered 27 publications for 18 of the species sampled in this study (Table 1). For the genus *Paratrygon*, feeding information was available only for *Paratrygon orinocensis* Loboda, Lasso, Rosa & Carvalho, 2021. Since the other species of *Paratrygon* are usually associated with the same prey type (fish) (Loboda *et al.*, 2021), this feeding habit is also assumed for *P. aiereba*.

Eleven prey types were identified and categorized into four general feeding strategies: piscivory, carcinophagy, insectivore, and generalist. Most of the species of Potamotrygonidae were assigned to a specific feeding trait. However, in *Styracura schmardae*, *Potamotrygon motoro*, *P. wallacei*, *P. schroederi*, and *P. amandae* multiple feeding traits were identified. Consequently, they were classified as generalists. Additionally, in all generalists, a preference for a particular prey type could be detected in individuals from the same locality (e.g., *P. motoro* from the Parazinho Reserve was predominantly carcinophagous, whereas *P. motoro* from the Paraná River was mainly insectivorous), except for *P. wallacei* and *P. schroederi*, for which specimens were available from only one location.

All works dealing with feeding habits that were sampled here, except Wrigglesworth, 2018 and OShea *et al.*, 2020, were also evaluated by Shibuya, 2022 and Kolmann *et al.*, 2022, among other species that weren't considered in the present study. All works found little to no significant differences in prey feeding habits between males and females which points to a lack of prey partitioning between sexes.

5.5 Adaptative dental types

Following the adaptative dental types proposed by Cappetta (2012), three of the eight types of dentitions in chondrichthyans can be assigned to potamotrygonids: clutching type, crushing type and crushing-grinding type (Figure 61).

● Clutching type

The clutching type is defined by Cappetta (2012) as possessing “slight dignathic heterodonty and a gradual monognathic heterodonty.” Teeth are also set in “several functional rows” with “lateral cusplets” (treated as accessory cusps in the present study). Most potamotrygonids lack the latter feature; however, since no other adaptive type fits better the morphology of some potamotrygonids and considering that Cappetta (2012) also states that most batoids possess this condition, this adaptive type is therefore applied. In the present study, this adaptative dental type is associated with *Heliotrygon rosai* and *Paratrygon aiereba*. Despite the presence of cusps and accessory cusps in

Potamotrygon amandae, *P. orbignyi*, and *P. signata*, these species are classified as having the crushing type, considering that their cusps are considerably smaller.

- **Crushing type**

The crushing type is defined by Cappetta (2012) as possessing “narrowly imbricated” teeth with numerous functional rows, “with often a transverse kneel (=transversal crest)”. Some species may also be strongly ornamented. Herein, species with subtle cusps are also being considered (see clutching type section). Most of the potamotrygonid species are in this category, such as *Styracura schmardae*, *Plesiotrygon iwamae*, *Potamotrygon hystrix*, *P. brachyura*, *P. humerosa*, *P. albimaculata*, *P. amandae*, *P. limai*, *P. falkneri*, *P. scobina*, *P. orbignyi*, *P. wallacei*, *P. yepezi*, *P. schroederi* and *P. signata*.

- **Crushing-grinding type**

The crushing–grinding type is defined by Cappetta (2012) as a combination of crushing and grinding types. Species bearing this condition exhibit “well-marked monognathic heterodonty.” Most teeth are of the crushing type, while a few intermediate teeth display a hexagonal grinding morphology. In the present study, *Potamotrygon jabuti*, *P. motoro*, *P. leopoldi*, and *P. marquesi* are classified under this category.

5.6 Historical reconstruction of adaptative dental types and feeding habits.

The historical reconstruction of adaptive dental types in our phylogenetic tree (Figure 62) showed a predominance of the crushing type in Potamotrygonidae. The family’s common ancestor, and most of the internal nodes, share this feature in our analysis. At the base of the phylogeny, the clade comprising *Heliotrygon* and *Paratrygon* is the only one specialized in clutching-type dentition. The only other clade to specialize in a different dentition ((*Potamotrygon marquesi* + (*P. jabuti* + *P. albimaculata*)) + (*P. leopoldi* + *P. motoro*)) has a common ancestor reconstructed as

having a crushing–grinding dentition, a trait retained by all species within this clade, except *P. albimaculata*, which has a reversal to the crushing-type dentition.

The historical reconstruction of feeding habits showed a more diverse evolutionary scenario (Figure 63). Potamotrygonids would have evolved from a generalist ancestor, following what was proposed by Kolmann *et al.* (2022) (classified as “omnivore” in their paper). Both *Styracura* and *Potamotrygon brachyura* retained this characteristic. *Heliotrygon* and *Paratrygon* evolved to a piscivorous habit, being the only lineage in the family to specialize in this type of prey. *Plesiotrygon* specialized in a carcinophagous habit, but it is unclear from the historical reconstruction which would have been the predominant feeding habit of the common ancestor (with equal probabilities of having generalist, insectivore or carcinophagous habits). Most of the subsequent lineages were recovered as sharing successive insectivore common ancestors, with *Potamotrygon yepezi*, *P. orbignyi*, *P. hystrix* and *P. falkneri* retaining this feeding preference. The other species would have developed different feeding specializations.

P. wallacei developed a generalized soft-prey specialization from an insectivorous common ancestor. Less inclusively in the phylogeny, the clade comprising (((*Potamotrygon marquesi* + (*P. jabuti* + *P. albimaculata*)) + (*P. leopoldi* + *P. motoro*)) + ((*P. humerosa* + *P. schroederi*) + (*P. limai* + *P. scobina*))) inherited three different feeding specializations from a common ancestor that was either insectivorous or carcinophagous. Within the clade ((*P. marquesi* + (*P. jabuti* + *P. albimaculata*)) + (*P. leopoldi* + *P. motoro*)), *P. leopoldi* and *P. motoro* developed a preference for hard prey from a generalist (hard-prey), carcinophagous, or insectivorous ancestor. Its sister clade, including *P. marquesi* and *P. albimaculata*, specialized in carcinophagy, while *P. jabuti* maintained or developed a preference for hard prey. In the clade ((*P. humerosa* + *P. schroederi*) + (*P. limai* + *P. scobina*)), *P. limai* and *P. scobina* maintained or developed carcinophagous specializations, *P. humerosa* maintained or developed insectivore, and *P. schroederi* developed independently a preference for general soft prey. Lastly, *P. amandae* has a reversal to a generalist feeding habit, while *P. hystrix* and *P. falkneri* have maintained an insectivorous feeding preference.

6 DISCUSSION

6.1 Teeth morphology in Potamotrygonidae

Although previous authors have investigated the dental morphology in elasmobranchs, the variation on teeth morphology in extant potamotrygonids remains poorly explored (see the Theoretical Reference section). Most of the knowledge of potamotrygonid teeth is limited to brief descriptions in taxonomic reviews and descriptions of new species (e.g., Rosa 1985; Rosa, Castello & Thorson, 1987; Deynat 2006; Rosa, Carvalho & Wanderley, 2011; Carvalho & Lovejoy 2011; Carvalho & Ragno 2011; Carvalho, Sabaj-Pérez & Lovejoy 2011; Silva & Carvalho 2011a, 2011b; Loboda & Carvalho 2013; Fontenelle, Silva & Carvalho 2014; Silva & Carvalho 2015; Fontenelle & Carvalho 2017; Carvalho 2016a, 2016b; Carvalho, Rosa & Araújo 2016; Carvalho, Loboda & Silva 2016; Silva & Loboda 2019; Loboda *et al.*, 2021), with only few works focusing exclusively on the morphological variation of teeth (Cappetta, 2012; Adnet, Gismondi & Antonie, 2014). Additionally, so far, no study has attempted to evaluate dental variation in a phylogenetic context within the family Potamotrygonidae.

Our morphological evaluation of teeth corroborates most of the generic descriptions in previous taxonomic studies, although some significant differences were observed. For instance, Rosa (1985) reported tri-cuspidate teeth in both males and females of *Potamotrygon hystrix*. However, specimens of *P. hystrix* analyzed herein exhibited a single prominent cusp in males, which were lacking in females (Figures 55 and 56). Carvalho and Lovejoy (2011) described adult males of *Heliotrygon* spp. as having “sharp, pointed cusps,” while the specimens of *Heliotrygon rosai* analyzed herein displayed teeth with a convex, blunt labial face (Figures 5, 6 and 7). Carvalho, (2016b) described *Potamotrygon albimaculata*, as having males with “very small cusps”, yet the present study, which investigated the same specimens, found males with prominent main cusps, with size equivalent to twice the length of crown (Figures 40 and 41).

In regard to the species *Potamotrygon marquesi*, Silva & Loboda (2019) reported functional teeth with brownish coloration in both sexes. In contrast, the present study identified brownish coloration in teeth of males only (characters 5 and 6; Figures 32 and 33). It is important to highlight that the males analyzed in this study are from the same locality of the holotype (Tarauacá River), whereas the females were collected from Marajó Island, suggesting that the variation observed may reflect geographical variation. Consequently, the occurrence of a dark color in females (character 6) has been interpreted as polymorphic. Silva & Carvalho, (2011a) reported cusps as either present or absent in adult males of *Potamotrygon falkneri* (characters 21 to 26 in the present study). In the present study, all the analyzed males lacked cusps (Figures 57 and 58), and the presence of cusps was consequently interpreted as polymorphic. Likewise, *Potamotrygon orbignyi* presented variation in relation to the presence or absence of accessory cusps in adult males in the work of Silva & Carvalho (2015) (characters 29 to 34 in the present study). The authors reported adult males bearing only a main cusp and sometimes two additional accessory cusps. The adult male specimens analyzed herein lacked accessory cusps (Figures 36 and 37), and this character was also interpreted coded as polymorphic.

Potamotrygon motoro presented the greatest variation in teeth morphology compared to previous studies. For instance, Rosa (1985) and Loboda & Carvalho (2013) reported that adult males exhibit functional monocuspidate teeth near-symphysis, while intermediate and lateral teeth have a trapezoidal crown shape and lack cusps. The specimens evaluated in the study presented a similar crown morphology for both males and females but lacked cusps on all functional teeth (Figures 23, 24 and 25). Nevertheless, monocuspidate teeth were present in nonfunctional lingual teeth near symphysis. Adnet, Gismondi & Antoine (2014) later described two other types of dentition for *P. motoro*: the first type would include tricuspidate, triangular teeth in lingual view, while the second type would be similar to the teeth morphology observed herein. It is likely that this morphological variation, similar to the condition observed for *P. marquesi*, may reflect the great range of geographic distribution of *P. motoro* throughout South America. Variation in teeth morphology may also reflect differences in prey preference across the range of distribution of the species (see 6.3 section).

The morphological variations in *P. motoro* may also indicate distinct, putative cryptic species, as suggested by Adnet, Gismondi & Antoine (2014). Recent works like

Kolmann *et al.*, 2022 have recovered different morphometric results of the dental arch among specimens of distinct locations of *P. mororo*. Loboda, 2010 also exhibits specimens with distinct neurocranium morphology, despite all being considered as variations of the same species. Fontenelle *et al.* (2021a) also recovers *P. motoro* as paraphyletic in molecular analysis. All indicatives may be a sign of the existence of more undescribed cryptic species. This was the case for species already described with similar coloration previously linked to *P. motoro* (*Potamotrygon amandae*, *P. pantanensis*, *P. marquesi* and *P. boesemani*). Furthermore, *P. motoro* should be given attention in further studies regarding morphological and molecular traits.

Adnet, Gismondi & Antoine (2014) also proposed different teeth morphology for *Paratrygon aiereba* and *Potamotrygon leopoldi* from that observed herein: Regarding *Paratrygon aiereba*, they described specimens as having “small teeth” with a “flat labial side” (which is termed as “lingual edge” in the present work). In this study, both male and female specimens exhibited large teeth with prominent cusps (with twice the crown length) and convex labial edges (Figures 8, 9 and 10), according to what was proposed by Loboda *et al.* (2021) for this species. It is possible that the specimens analyzed by Adnet, Gismondi & Antoine, 2014 were juveniles, since their description matches the morphology of the teeth of young specimens of *Paratrygon aiereba* (Lima *et al.*, in prep.). Additionally their specimens were considerably smaller (300 mm DW). Adnet, Gismondi & Antoine (2014) have also reported the occurrence of cuspidated teeth in males of *Potamotrygon leopoldi*, while the males specimens analyzed in this study lacked cusps (Figures 20 and 21). This difference may indicate that the authors may have examined specimens of a morphologically similar species, *P. henlei*, or that cusps develop in males only during the reproductive period, as observed for *Hypanus sabinus* (Lesueur, 1824) (Kajiura & Tricas, 1996). The presence of cusps in some males of *P. falkneri* as indicated by Silva & Carvalho, 2011 could also reflect male specimens that would be under the reproductive period (see 6.3 section for further discussion).

All these differences underscore the diversity of dental morphology in Potamotrygonidae and their phylogenetic significance as explored in the following section.

6.2 Phylogenetic implications

As previously stated, the family Potamotrygonidae is consistently recovered as monophyletic, even though the interrelationships of its members is problematic (see section 2.1). Although the number of morphological studies have increased, few were the studies that tried to explore the family's intergeneric relationships (Rosa, 1985; Lovejoy, 1996; Carvalho & Lovejoy, 2011, Araújo *et al.*, 2024) and fewer were the ones exploring species-level interrelationships (Fontenelle *et al.*, 2021a, 2021b; Araújo 2024). Additionally, the dispute of which marine group would be closely related to potamotrygonines (Brooks, Thorson & Mayes, 1981; Rosa, 1985; Hoberg *et al.*, 1998; Carvalho Maisey & Grande, 2004, has been settled recently, with most studies supporting the sister relationship of freshwater stingrays to the subfamily *Styracurinae* (Lovejoy, 1996; Marques, 2000; Carvalho, Loboda & Silva, 2016; Fontenelle *et al.*, 2021a, 2021b; Araújo 2024; Araújo *et al.*, 2024).

There are three main hypotheses of relationships for potamotrygonines: *Heliotrygon* as sister to the clade (*Paratrygon* + (*Plesiotrygon* + *Potamotrygon*)) (García, Lasso & Villanil, 2013; García *et al.*, 2016), one proposing *Potamotrygon* as sister to the clade(*Plesiotrygon* + (*Heliotrygon* + *Paratrygon*)) and one considering the clade *Heliotrygon* + *Paratrygon* as sister to *Plesiotrygon* + *Potamotrygon* (Carvalho & Lovejoy, 2011; Fontenelle *et al.*, 2021a, 2021b; Araújo, 2024). The present study is in accordance with the last scenario.

The majority of dental characters proposed herein were recovered as homoplastic, and the resultant combined analysis is largely in line with the phylogenetic hypotheses of Fontenelle *et al.* (2021a) and Araújo (2024). Although no dental character supports the subfamily Potamotrygoninae, several other characters support less inclusive clades, such as the sister relationship of *Heliotrygon rosai* and *Paratrygon aiereba*. This clade is supported by three tooth row counting characters (1 to 3), and by the presence of a curvature in the lateral teeth in both plates of males (characters 49:1 and 51:1) while the clade *Potamotrygon* + *Plesiotrygon* (clade C) is supported by the absence cusps on the teeth of females (characters 27:1 and 28:1).

Like previous hypotheses (Toffoli *et al.*, 2008; Fontenelle *et al.*, 2021a; Araújo, 2024) the phylogenetic analysis conducted herein also recovered *Potamotrygon* as

paraphyletic. Toffoli *et al.* (2008) proposed *Plesiotrygon* as sister to *Potamotrygon schroederi*, and this grouping would be nested in a larger clade including other species of *Potamotrygon*. Fontenelle *et al.* (2021a), suggested *Plesiotrygon* as closely related to *Potamotrygon brachyura*, and this clade as sister to all remaining species of *Potamotrygon*. Araújo recovered a different relationship, with *Potamotrygon brachyura* as a successive sister taxon of *Plesiotrygon* and all the other species of *Potamotrygon*. This relationship would be supported by two characters of the neurocranium: the preorbital process laterally projected, and an epiphyseal bar 1/3 longer than the length of the supraorbital process (characters 10:1 and 15:2 in Araújo, 2024). In all cases, *Potamotrygon* is recovered as a paraphyletic without the inclusion of *Plesiotrygon*. Our analysis also recovered *Potamotrygon* as paraphyletic, with *Plesiotrygon* nested inside *Potamotrygon* in an arrangement similar to that proposed by Araújo, 2024. However, there were no dental characters supporting this relationship. This may indicate that molecular data had more influence on recovering this topology than morphological characters.

The other interrelationships within *Potamotrygon* are also similar to Araújo, 2024, contrasting what was proposed by Fontenelle *et al.* (2021a) that suggested that most of the species of *Potamotrygon* were paraphyletic. Like in Araújo (2024) *Potamotrygon yepezi*, *P. wallacei*, *P. orbignyi* and *P. signata* were recovered as consecutive sister taxa to a clade including *P. wallacei* and the remaining species of *Potamotrygon* (clade F), a relationship supported by ten synapomorphies related to the presence of a concave labial edge in all male teeth (characters 37:2 to 42:2), in all upper female teeth (characters 43:2 to 45:2) and in near symphysis lower female teeth (character 46:2).

Other relationships within *Potamotrygon* diverge from Araújo (2024). Araújo (2024) proposed *Potamotrygon motoro* as sister to the remaining species of *Potamotrygon* (his Core *Potamotrygon* Clade; CPC). However, our analysis recovered *P. motoro* nested within a less inclusive clade including ((*Potamotrygon marquesi* + (*P. jabuti* + *P. albimaculata*)) + (*P. leopoldi* + *P. motoro*)). Araújo (2024) also recovered *P. amandae* as sister to a more inclusive clade including *P. henley*, *P. leopoldi*, *P. limai*, *P. scobina*, *P. humerosa*, *P. schroederi*, *P. marquesi*, *P. jabuti* and *P. albimaculata* (his CPCB clade), while our analysis recovered this species as sister to *P. histrix* + *P. falkneri*. Nevertheless, this relationship lacks morphological support in the combined

analysis conducted herein. The differences of the combined analysis of Araujo (2024) and the one conducted herein may be explained by the divergent phylogenetic signals derived from the neurocranium and teeth. While in Araújo (2024) *P. motoro* displayed eight autapomorphies and only shared three neurocranium characters with all remaining species of *Potamotrygon* (characters 15:1, 43:0 and 53:1 in Araújo, 2024), in our analysis *P. motoro* shares seventeen evolutionary novelties with *P. leopoldi*, *P. marquesi*, *P. jabuti* and *P. albimaculata* (characters 1, 7:1, 8:1, 11:1, 22:1, 23:1, 26:1, 37:1 to 43:1, 45:1, 46:1 [homoplastic]; 12:0 [reversal]), sharing other five morphological characters exclusively with *P. leopoldi* (characters 1, 10:1, 21:1, 24:1 and 25:1). On the other hand, in Araújo (2024) *P. amandae* shares two characters of the neurocranium with CPCB (characters 16:1 and 48:1), while in the present study there were no dental characters supporting the sister relationship of *P. amandae* and *P. hystrix* + *P. falkneri* and this clade is supported by molecular data only.

6.3 Teeth morphology and its relation to feeding habits

The bibliographical survey showed a great diversity of feeding habits within Potamotrygonidae. This was also corroborated by Kolmann *et al.* (2022) and the historical reconstruction conducted herein, which demonstrates several cases of independent specializations among the species. Kolmann *et al.* (2022) performed a historical reconstruction of feeding habits using a stochastic model over a tree derived from a molecular analysis. However, some differences are noted when compared to our historical reconstruction since they were based on different phylogenetic and reconstruction methodologies, and the taxa explored were to some extent also different. Interpretation of the feeding habits are also different in Kolmann *et al.* (2022), considering that their "omnivore" is interpreted herein as "generalist". Additionally, they indicated some species as molluscivore and crustaceivore, but they were preferably classified herein as "hard prey" and "soft prey generalist" since these species were interpreted as having a wider prey preference. Further differences in interpretation regards *Potamotrygon hystrix* and *P. falkneri*, as Kolmann *et al.* (2022) considered these species as "omnivores", while they were interpreted herein predominantly as insectivore.

The historical reconstruction performed herein suggests that the common ancestor of Potamotrygonidae was a generalist, a condition also proposed by Kolmann *et al.* (2022). At the base of the phylogeny, the clade composed by *Heliotrygon* and *Paratrygon* specialized in fish prey, a feature exclusive for this clade inside the family. All other potamotrygonines have independently acquired the generalist, soft and hard generalist, carcinophagous and insectivore feeding specializations. However, the hard generalist feeding habit seems to be restricted to *P. jabuti* and *P. leopoldi* + *P. motoro* in the less inclusive clade including ((*Potamotrygon marquesi* + (*P. jabuti* + *P. albimaculata*)) + (*P. leopoldi* + *P. motoro*)).

The historical reconstruction of adaptative dental types showed some interesting insights. It suggests that the ancestral condition in Potamotrygonidae is the crushing type. This is an interesting result considering that there is comparatively a greater variety of feeding habits within the family compared to its dental types. However, two dental types occur exclusively in two less inclusive clades in different portions of the tree. For instance, the clutching type evolved exclusively in the clade including *Heliotrygon* and *Paratrygon* and may be associated with their piscivorous feeding habit. The crushing-grinding dental type is restricted to the clade including (*Potamotrygon marquesi* + (*P. jabuti* + *P. albimaculata*)) + (*P. leopoldi* + *P. motoro*)), except for *P. albimaculata*, that has a reversal to the crushing type. The crushing-grinding dentition seems to be associated with feeding on hard prey. However, it is important to highlight that the dental type does not necessarily agree with feeding habits. For instance, even though the dental type in *P. marquesi* and *P. albimaculata* are different, their feeding habits are the same (carcinophagous, consisting mainly of shrimps [Table 1]).

Of all species analyzed, the one that presented the most diverse feeding habits was *Potamotrygon motoro* (Table 1), a condition also indicated by Shibuya (2022). This may be correlated with the wide geographical distribution of the species depicting different prey preferences according to the river considered. This may also suggest the high morphological intraspecific variability of *P. motoro* or that this species may represent a species-complex (Loboda & Carvalho, 2013 [see section 6.1 for further discussion]). Additionally, *P. motoro* could be interpreted as an opportunistic species, feeding on the most abundant prey available. Another interpretation is that *P. motoro*

may partition prey resources with other potamotrygonins depending on prey availability, a scenario that may occur across seasonal fluctuations (Shibuya, 2022).

Although most of the species of Potamotrygonidae were correlated with the “crushing” dental type, only the teeth morphology of females was used for this analysis. If males were included, they would inevitably fall within the clutching type dentition as a consequence of the presence of cusps on their teeth. This was also pointed out by Cappetta (2012), which reports that most batoid species have males with “clutching” dental type while most females have the “crushing” type. This variation is theorized by a few authors as an adaptation to prey partitioning between males and females to decrease intraspecific competition, as may happen to some species of Rajidae (Feduccia & Slaughter, 1974; Cappetta, 2012). Other authors relate the sexual heterodonty found in batoids as exclusively related to mating purposes, as males are known to hold females with the mouth during reproduction, with females having a thicker tegument as an adaptation to this reproductive behavior (McEachran, 1977; Cappetta, 2012; Paig-Tran *et al.*, 2022). In this context, most of the works explored in the bibliographical survey indicated few to no prey partitioning between males and females. Consequently, the sexual heterodonty observed in potamotrygonids may be related only to reproductive purposes. Taking the above into account, it was interpreted that only female dental morphology may better reflect adaptative functional traits as males have a similar overall morphology in teeth to females before sexual maturation (Lima *et al.*, in prep). Dental morphology may also differentiate in some species of Potamotrygonidae between the mating periods. Kajiura & Tricas (1996) reported that the dentition of the adult male *Hypanus sabinus* (Lesueur, 1824) may be similar to the non-cuspidated female dentition, changing to cuspidated teeth only during the mating season. The absence of cuspidated teeth in adult males reported in the present study for *Potamotrygon falkneri*, *P. leopoldi* and *P. motoro* in comparison to the presence of cuspidated teeth in these species reported by previous authors (Rosa, 1985; Loboda & Carvalho, 2013; Silva & Carvalho, 2011a; Adnet, Gismondi & Antoine, 2014) may indicate that they may have been collected outside the reproductive period, reflecting the putative absence of cusps, a condition that may be widespread within potamotrygonids.

7 CONSIDERAÇÕES FINAIS

A partir dos dados levantados no presente estudo, pôde-se observar a importância que estudos anatômicos baseados na morfologia dentária possuem para a sistemática das raias de água doce. Ao todo, foram propostos 51 novos caracteres para 21 espécies. Esses caracteres demonstraram de maneira geral um alto grau de homoplasia, demonstrando a complexidade evolutiva dessas estruturas na família Potamotrygonidae. Isto se reflete também na adaptação evolutiva das placas dentárias em relação aos hábitos alimentares que demonstram uma complexidade igualmente semelhante no grupo. De modo geral, a presente análise filogenética também recupera dois clados principais em Potamotrygonidae, incluindo *Heliotrygon* + *Paratrygon* como grupo irmão de *Plesiotrygon* + *Potamotrygon*. Do mesmo modo, *Plesiotrygon* foi recuperado como aninhado dentro do gênero *Potamotrygon*, o que sinaliza que *Potamotrygon* é parafilético sem a inclusão de *Plesiotrygon*. Indo na contramão a trabalhos publicados previamente, a espécie *Potamotrygon motoro* foi recuperada como mais proximamente relacionada a *P. leopoldi*, *P. jabuti*, *P. marquesi* e *P. albimaculata*, indo de encontro a hipóteses de estudos taxonômicos prévios que já sugeriam uma possível relação de parentesco próxima entre estas espécies. Por fim, as relações de parentesco propostas neste estudo para os potamotrygonídeos reforçam a necessidade de mais estudos filogenéticos com a família, incluindo outros complexos anatômicos que ajudem a compreender melhor a evolução deste grupo igualmente incrível, e complexo.

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TABELAS

Table 1. The relation of feeding habits, bibliographical survey, and area of study to the species explored in this study.

Species	Feeding habit	References	Area of study
<i>Stryracura schmardae</i>	Generalist		
	Mainly Decapoda and Anelida	Wrigglesworth, 2018; OShea et al., 2020	Caribbean
<i>Heliotrygon gomesi</i>	Piscivorus		
	Fish	Kolmann et al., 2022	x
<i>Paratrygon orinocensis</i>	Piscivorus		
	Fish	Lasso & Lasso-Alcalá, 1996; Barbarino & Lasso, 2005	Orinoco river
<i>Paratrygon</i> sp. 1	Piscivorus		
	Fish	Filho, 2006	Paraná river
<i>Paratrygon</i> sp. 2	Piscivorus		
	Fish	Shibuya, Araújo & Zuanon, 2009	Negro river
<i>Paratrygon</i> sp. 3	Piscivorus		
	Fish	Charvet-Almeida, 2001	Amazon river (Marajó Island)
<i>Plesiotrygon iwamae</i>	Carcinophagous		
	Shrimp and soft crab	Charvet-Almeida, 2001	Amazon river (Marajó Island)
	Shrimp	Filho, 2006	Negro river
<i>Potamotrygon orbignyi</i>	Predominantly Insectivore		
	Mainly Diptera and Ephemeroptera	Lasso & Lasso-Alcalá, 1996; Filho, 2006; Moro, 2010; Moro, Charvet & Rosa, 2011	Orinoco, Paraná, Parnaíba and Parnaíba rivers
	Ephemeroptera and Odonata	Charvet-Almeida, 2001	Amazon river (Marajó Island)
	Ephemeroptera larvae and Odonata	Shibuya, 2009; Shibuya, Araújo & Zuanon, 2009	Negro river
	Mainly Decapoda (Shrimp), Orthoptera and Anelidae	Gama, 2013; Gama & Rosa, 2015	Amazon river (Parazinho Reserve)
<i>Potamotrygon marquesi</i>	Carcinophagous		

	Mainly Shrimp	Gama & Rosa, 2015	Amazon river (Parazinho Reserve)
<i>Potamotrygon motoro</i>	Generalist		
	Mainly Perciforme and Decapoda (Shrimp)	Shibuya, 2009; Shibuya, Araújo & Zuanon, 2009	Negro river
	Decapoda (shrimp and crab)	Gama & Rosa, 2015	Amazon river (Parazinho Reserve)
	Mainly Decapoda and Siluriformes	Almeida et al., 2010	Amazon river (Marajó Island)
	Mainly Siluriformes, Decapoda (shrimp) and Gastropoda	Vasconcelos & Oliveira, 2011	Amazon river (Curiaú River)
	Mainly Ephemeroptera, Trichoptera and Gastropoda	Garrone-Neto et al., 2016	Paraná river
<i>Potamotrygon wallacei</i>	Generalist		
	Mainly Decapoda (Shrimp) and Odonata	Shibuya, 2009; Shibuya, Araújo & Zuanon, 2009	Negro river
<i>Potamotrygon yepezi</i>	Insectivore		
	Diptera	Lasso et al., 2013b	Catatumbo river
<i>Potamotrygon schroederi</i>	Generalist		
	Mainly worms and Odonata larvae	Shibuya, Zuanon & Carvalho, 2020	Negro river
<i>Potamotrygon brachyura</i>	Generalist		
	Unidentified fish and invertebrates	López-Rodríguez et al., 2019	Uruguay river
<i>Potamotrygon amandae</i>	Generalist		
	Mainly Diptera and Ephemeroptera	Silva & Uieda, 2007	Paraná river
	Mainly Gastropoda, Trichoptera and Odonata	Lonardoni et al., 2006	Paraná river
	Odonata, Trichoptera and Ephemeroptera	Lonardoni, 2009	Paraná river
	Mainly Fish	Pagliarini et al., 2020	Paraná river
<i>Potamotrygon signata</i>	Insectivore		
	Mainly Diptera larvae and Ephemeroptera nymphs	Moro, 2010; Moro, Charvet & Rosa, 2012	Parnaíba river
<i>Potamotrygon falkneri</i>	Predominantly Insectivore		

<i>Potamotrygon humerosa</i> <i>Potamotrygon scobina</i>	Mainly Fish, Gastropoda and Trichoptera	Lonardoni et al., 2006	Paraná river
	Mainly Fish, Trichoptera and Ephemeroptera	Lonardoni, 2009	Paraná river
	Mainly Trichoptera and Hemiptera	Silva & Uieda, 2007	Paraná river
	Mainly Leptoceridae and Baetidae	Garrone-Neto et al., 2016	Paraná river
	Mainly Fish and Trichoptera	Pagliarini et al., 2020	Paraná river
	Insectivore		
	Diptera	Shibuya et al., 2016	Tapajós river
	Carcinophagous		
	Shrimp	Gama & Rosa, 2015	Amazon River (Bailique Island)

Table 2. Relation between adaptive dental type and feeding habits to the species explored in this study. Species with feeding habits marked with an asterisk lack reports of prey preference in the literature; inferences were made through direct morphological comparison with similar dental morphologies of known species.

Species	Adaptive dental type	Feeding habit
<i>Styracura schmardae</i>	Crushing	Generalist
<i>Heliotrygon rosai</i>	Clutching	Piscivorous
<i>Paratrygon aiereba</i>	Clutching	Piscivorous
<i>Plesiotrygon iwamae</i>	Crushing	Carcinophagous (soft decapoda)
<i>Potamotrygon marquesi</i>	Crushing-grinding	Carcinophagous (soft decapoda)
<i>Potamotrygon histrix</i>	Crushing	Insectivore*
<i>Potamotrygon leopoldi</i>	Crushing-grinding	Generalist (hard prey)*
<i>Potamotrygon brachyura</i>	Crushing	Generalist*
<i>Potamotrygon jabuti</i>	Crushing-grinding	Generalist (hard prey)*
<i>Potamotrygon humerosa</i>	Crushing	Insectivore
<i>Potamotrygon albimaculata</i>	Crushing	Carcinophagous (soft decapoda)*
<i>Potamotrygon amandae</i>	Crushing	Generalist
<i>Potamotrygon limai</i>	Crushing	Carcinophagous (soft decapoda)*
<i>Potamotrygon falkneri</i>	Crushing	Insectivore
<i>Potamotrygon scobina</i>	Crushing	Carcinophagous (soft decapoda)
<i>Potamotrygon orbignyi</i>	Crushing	Insectivore

<i>Potamotrygon wallacei</i>	Crushing	Generalist (soft decapoda and insects)
<i>Potamotrygon yepezi</i>	Crushing	Insectivore
<i>Potamotrygon motoro</i>	Crushing-grinding	Generalist (mainly shrimp and crab)
<i>Potamotrygon schroederi</i>	Crushing	Generalist (soft prey)
<i>Potamotrygon signata</i>	Crushing	Insectivore

FIGURAS

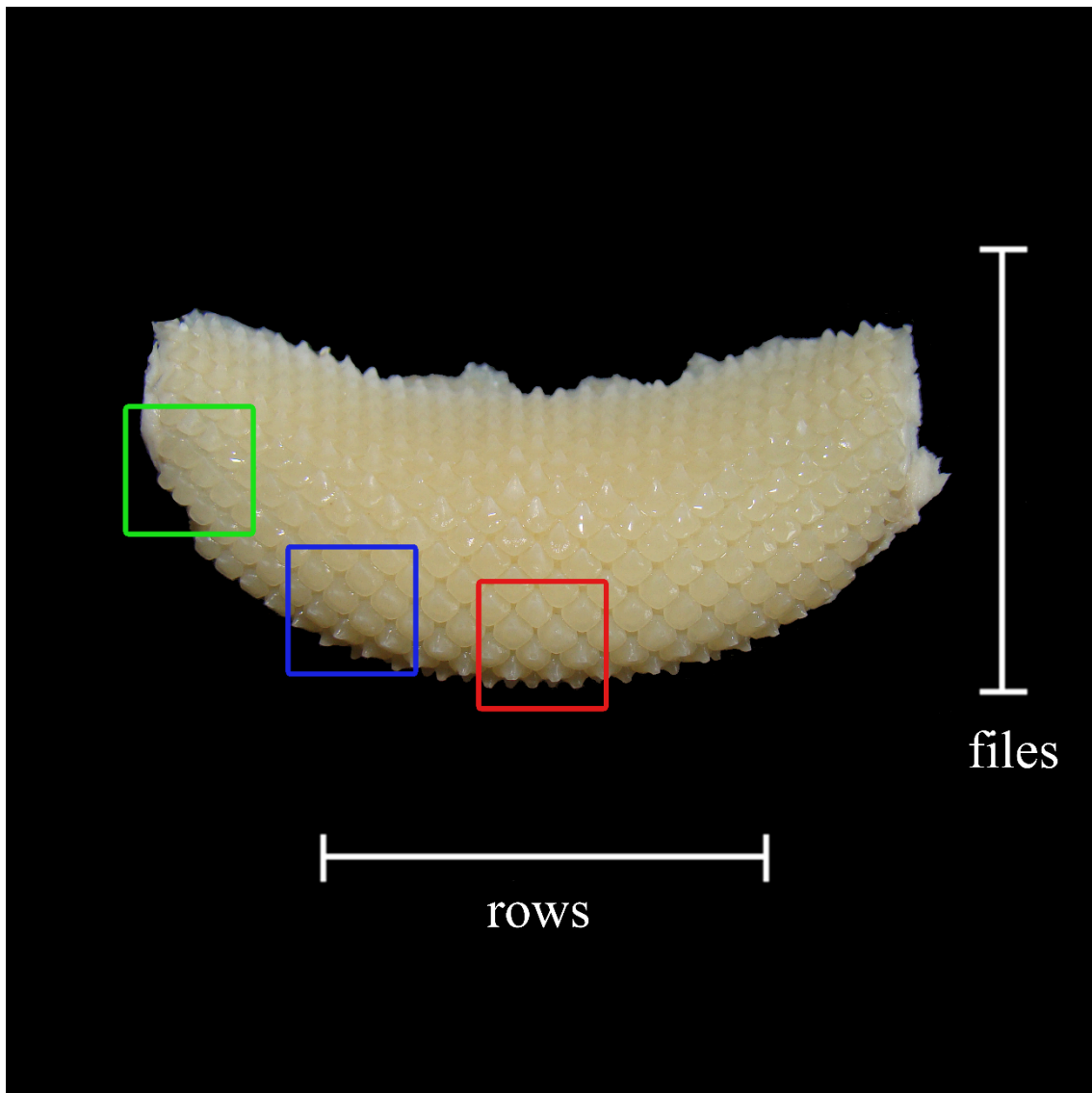


Figure 1. Plate partitioning methodology. Red square refers to near symphysis teeth (position 1), blue square refers to intermediate teeth (position 2), and green square refers to lateral teeth (position 3). Lingual to top and labial to bottom.

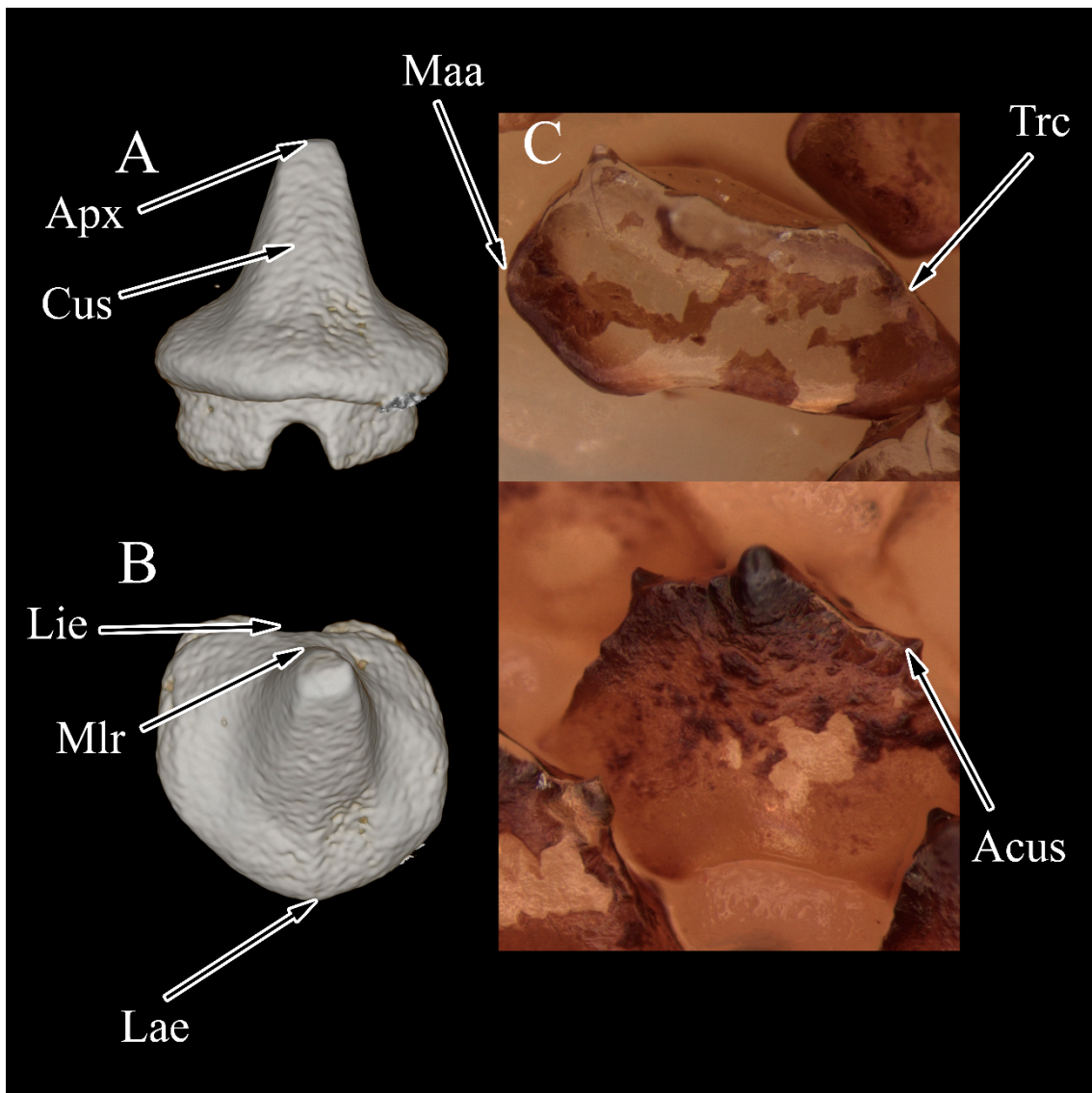


Figure 2. Morphological terminology of teeth. A - lingual view of tooth in *Heliotrygon rosai*. B – occlusal view of tooth in *Heliotrygon rosai*. C – occlusal view of tooth in *Potamotrygon marquesi*. In A labial to front; In B and C labial to bottom. Anatomical abbreviations: Apx, apex; cus, cusp; Lae, labial edge; Lie, lingual edge; Maa, marginal edge; Mlr, mesial lingual ridge; Acus, accessory cusp; Trc, transversal crest.

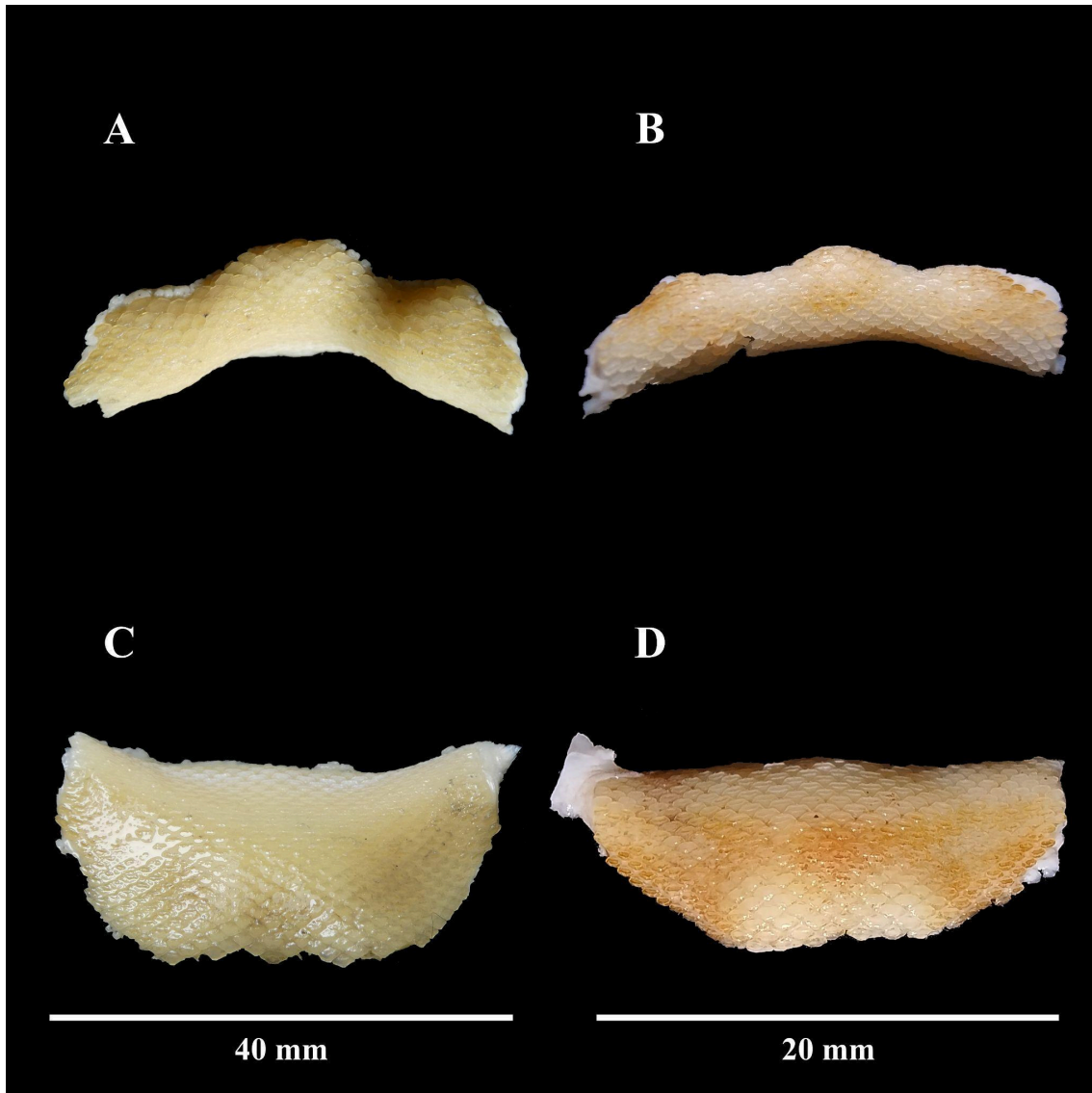


Figure 3. Occlusal view of the upper and lower plates of *Styracura schmardae* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

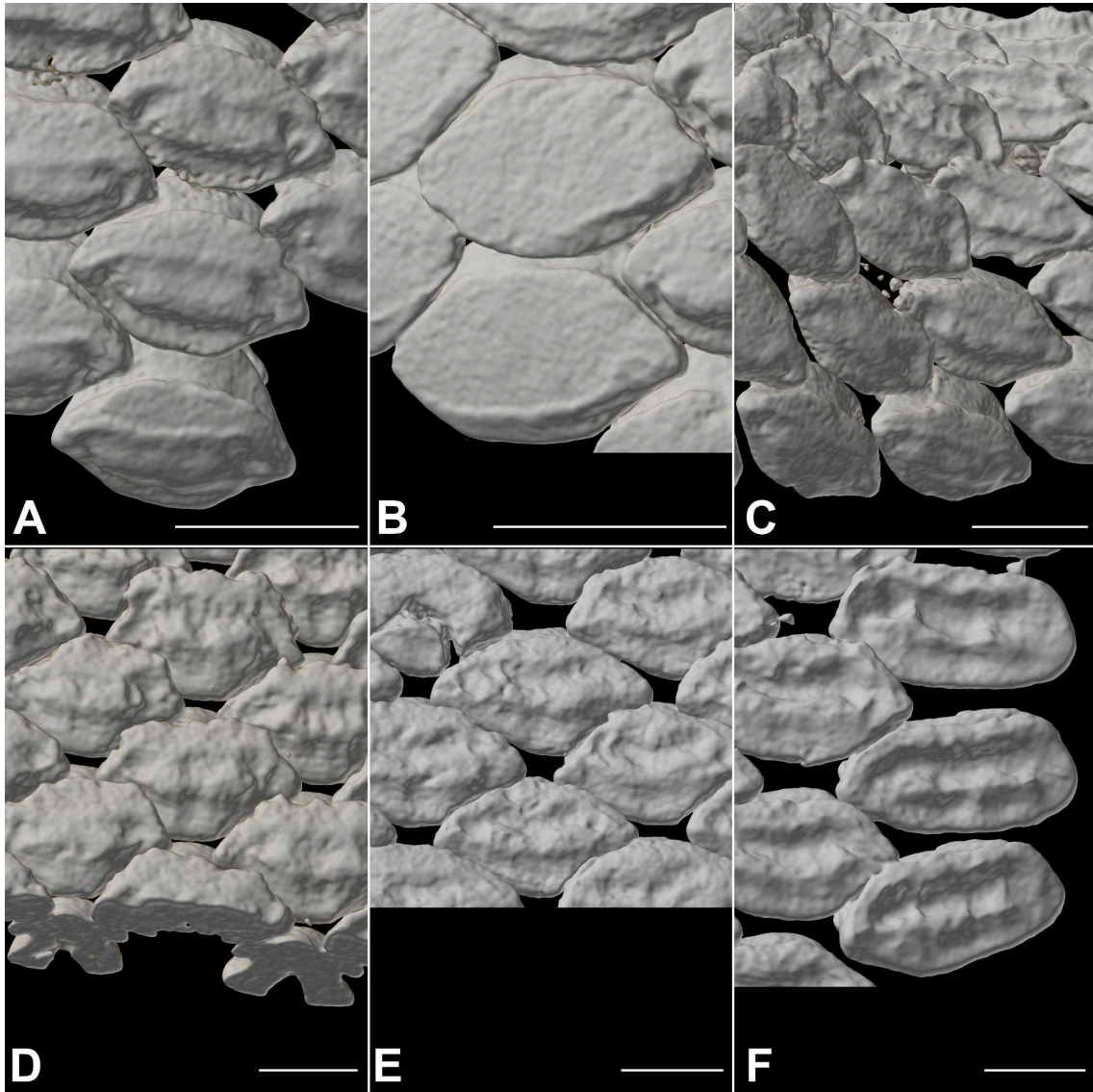


Figure 4. Occlusal view of teeth in a male of *Styracura schmardae*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

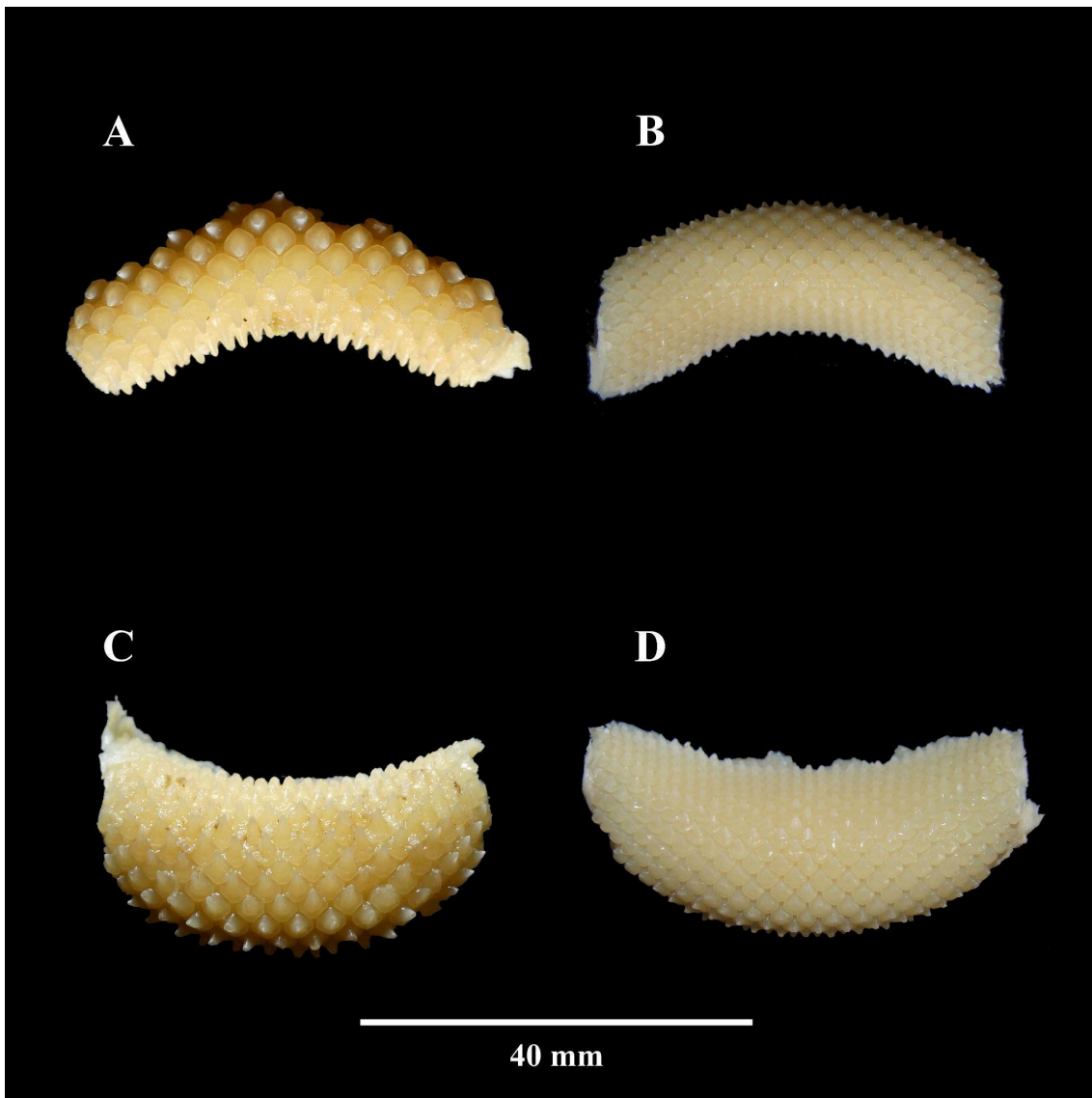


Figure 5. Occlusal view of the upper and lower plates of *Heliotrygon rosai* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

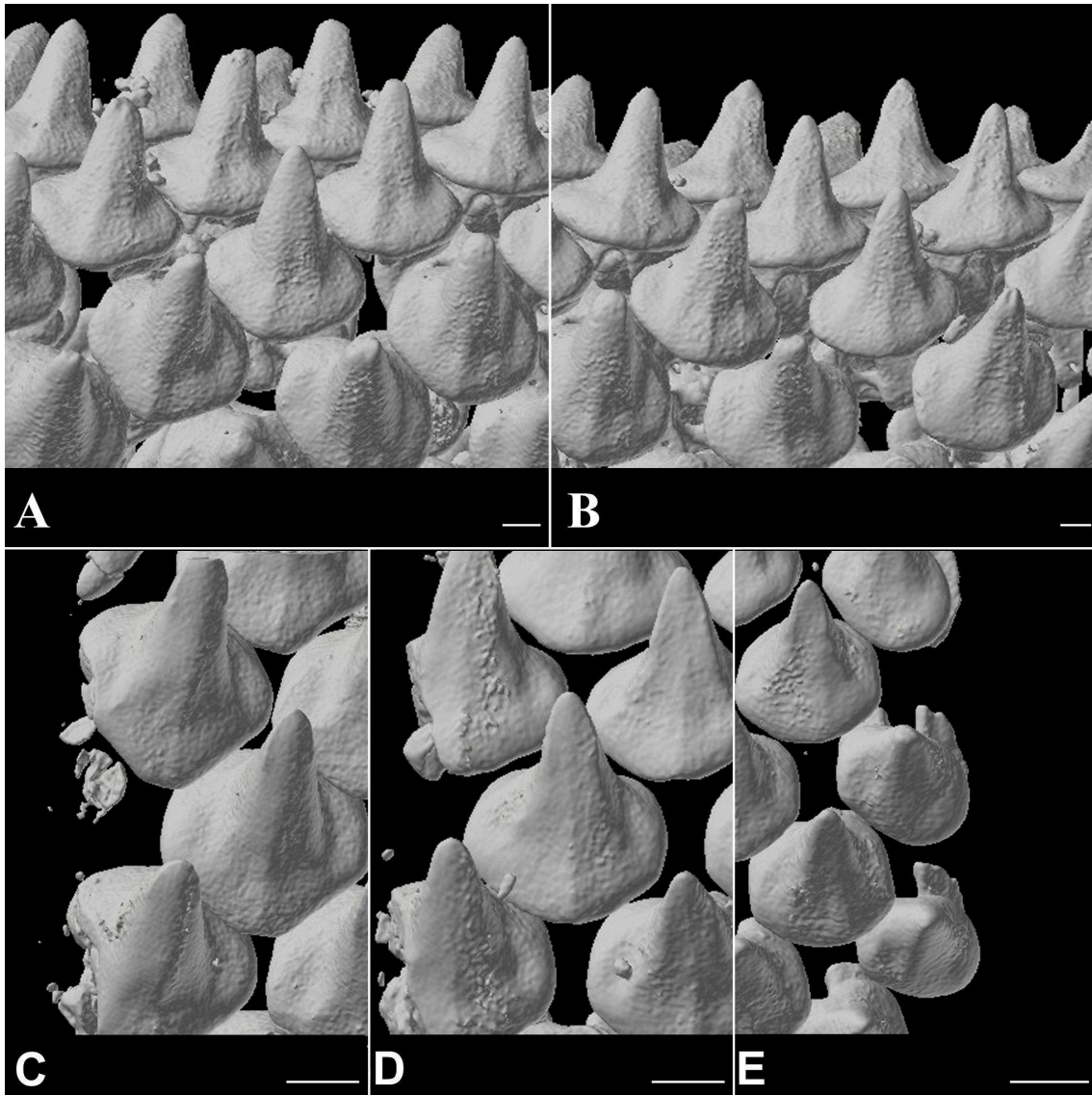


Figure 6. Occlusal view of teeth in a male of *Heliotrygon rosai*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Lower teeth near symphysis (position 1). D - Lower intermediate teeth (position 2). E - Lower lateral teeth (position 3). In A-E labial to bottom. Scale bar = 0.5 mm.

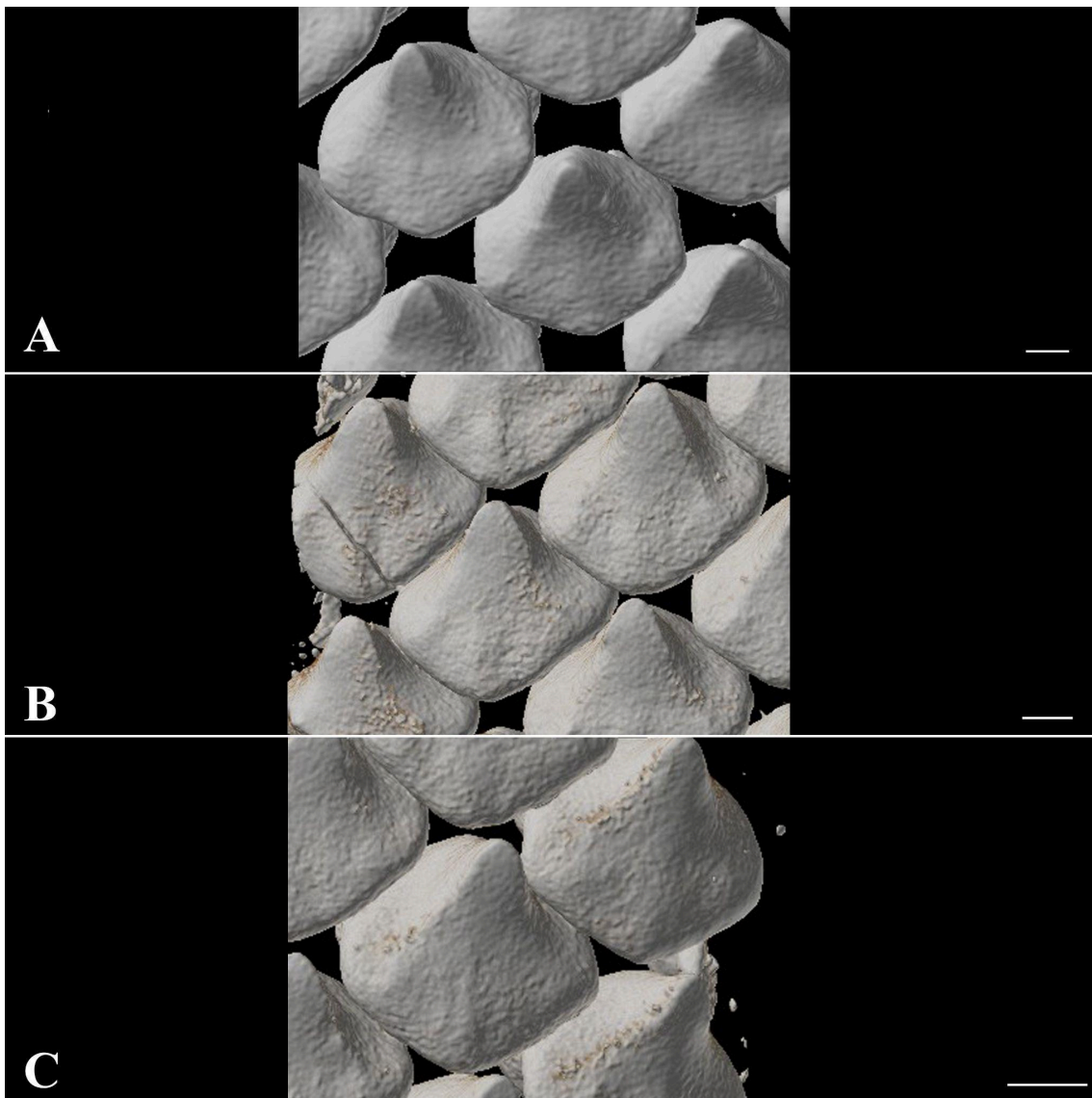


Figure 7. Occlusal view of teeth in a female of *Heliotrygon rosai*. A - Lower teeth near symphysis (position 1). B - Lower intermediate teeth (position 2). C - Lower lateral teeth (position 3). In A-C labial to bottom. Scale bar = 0.5 mm.

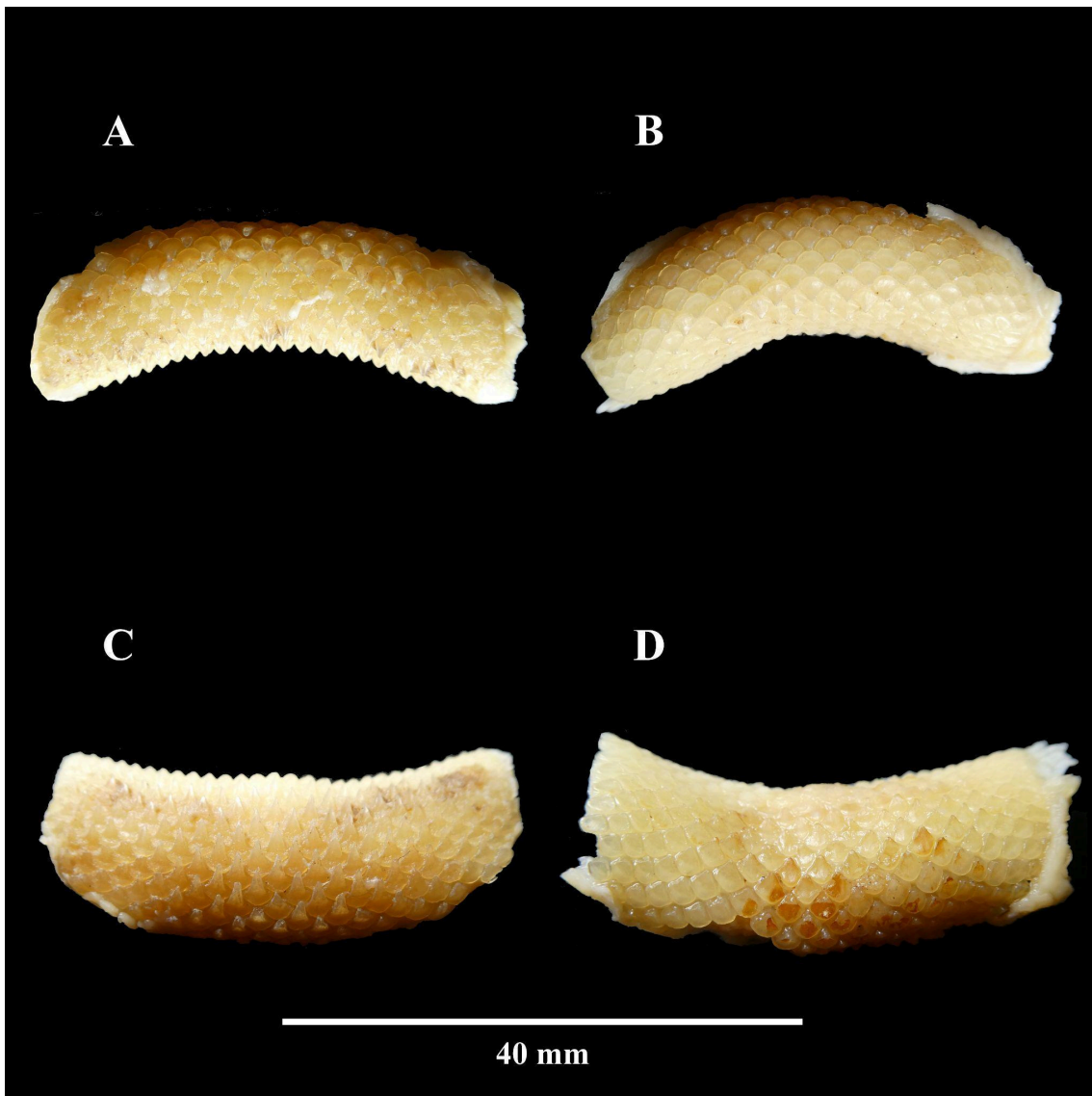


Figure 8. Occlusal view of the upper and lower plates of *Paratrygon aiereba* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

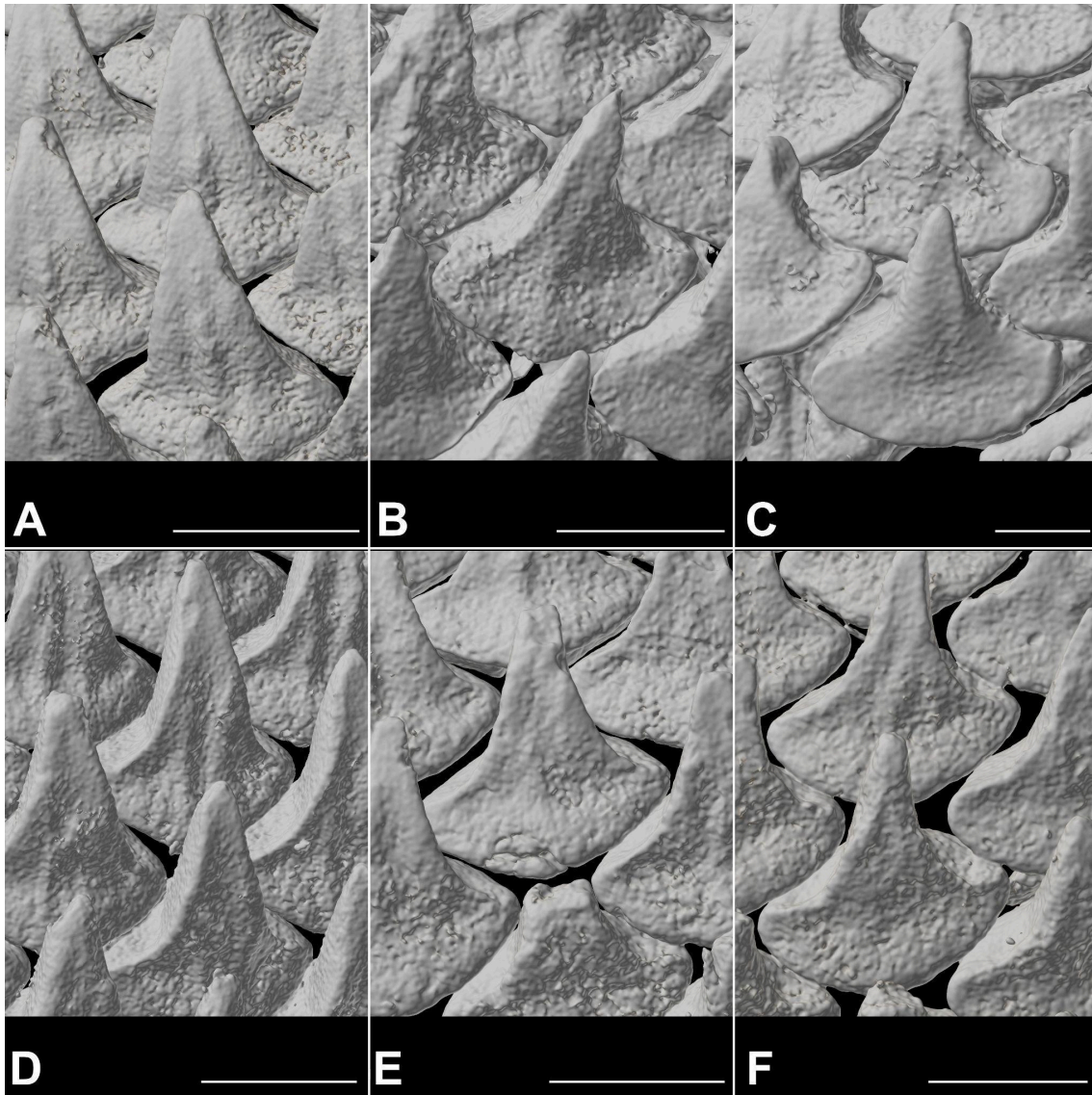


Figure 9. Occlusal view of teeth in a male of *Paratrygon aiereba*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

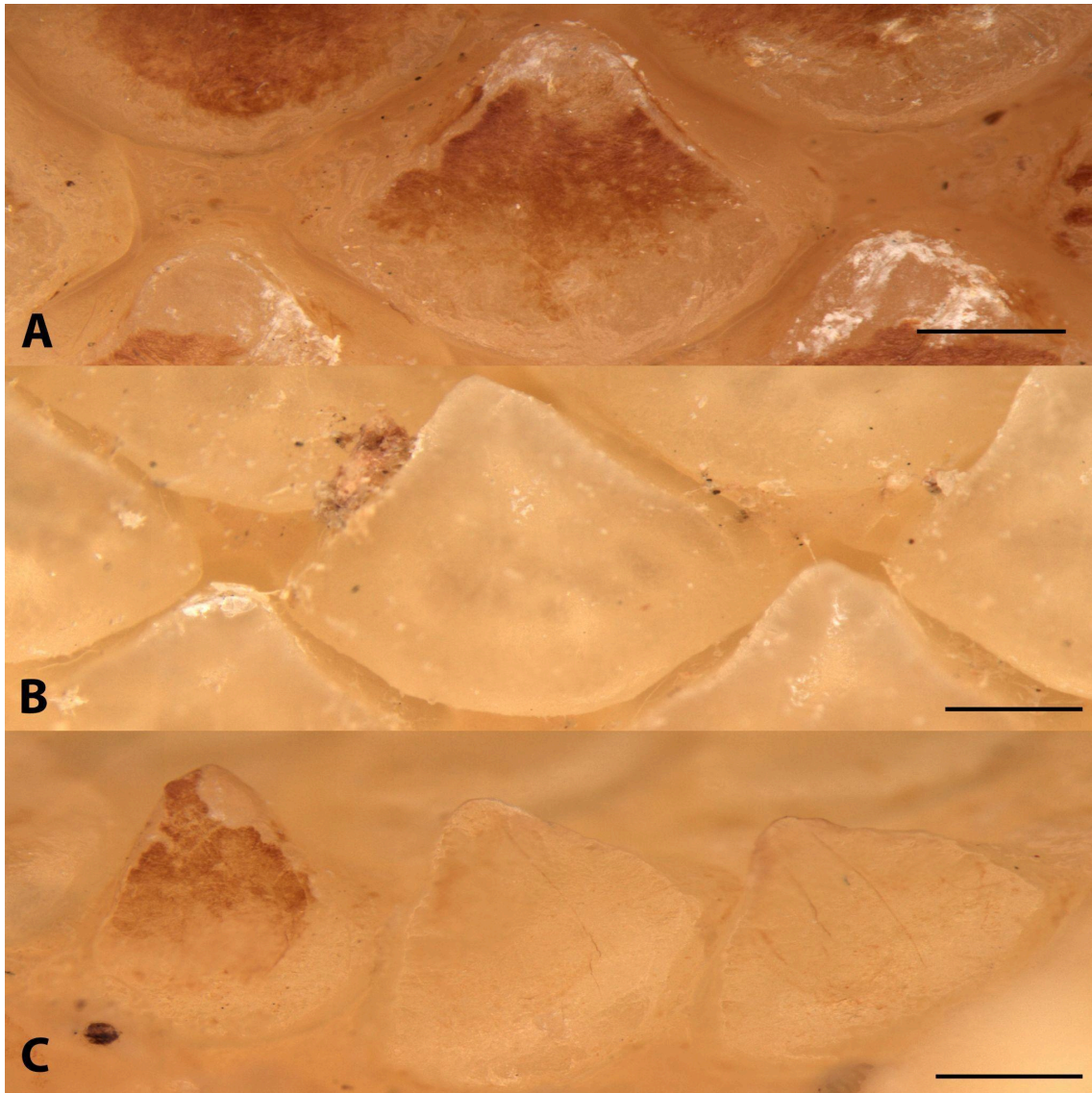


Figure 10. Occlusal view of teeth in a female of *Paratrygon aiereba*. A - Lower teeth near symphysis (position 1). B - Lower intermediate teeth (position 2). C - Lower lateral teeth (position 3). In A-C labial to bottom. Scale bar = 0.5 mm.

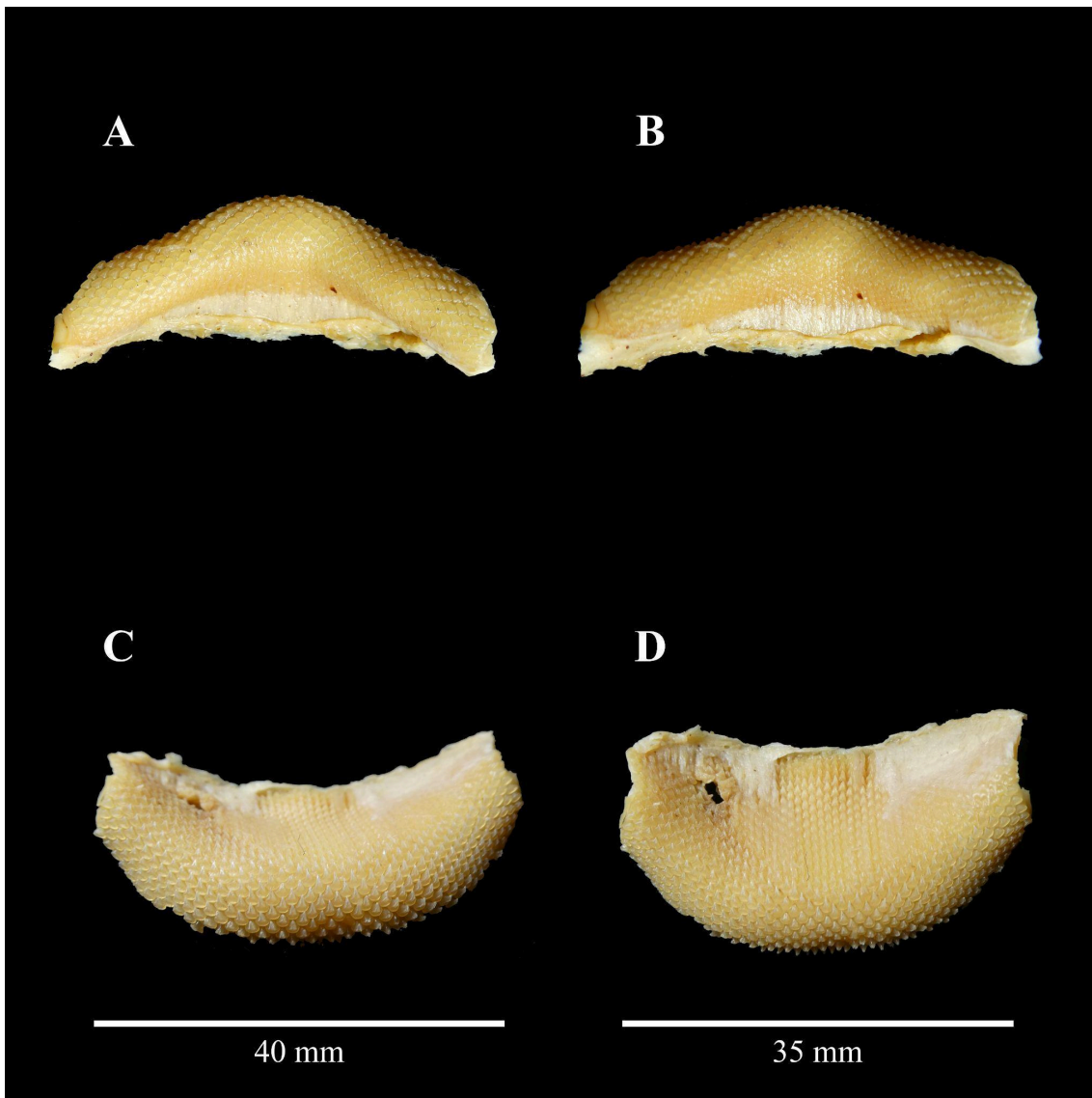


Figure 11. Occlusal view of the upper and lower plates of *Plesiotrygon iwamae* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

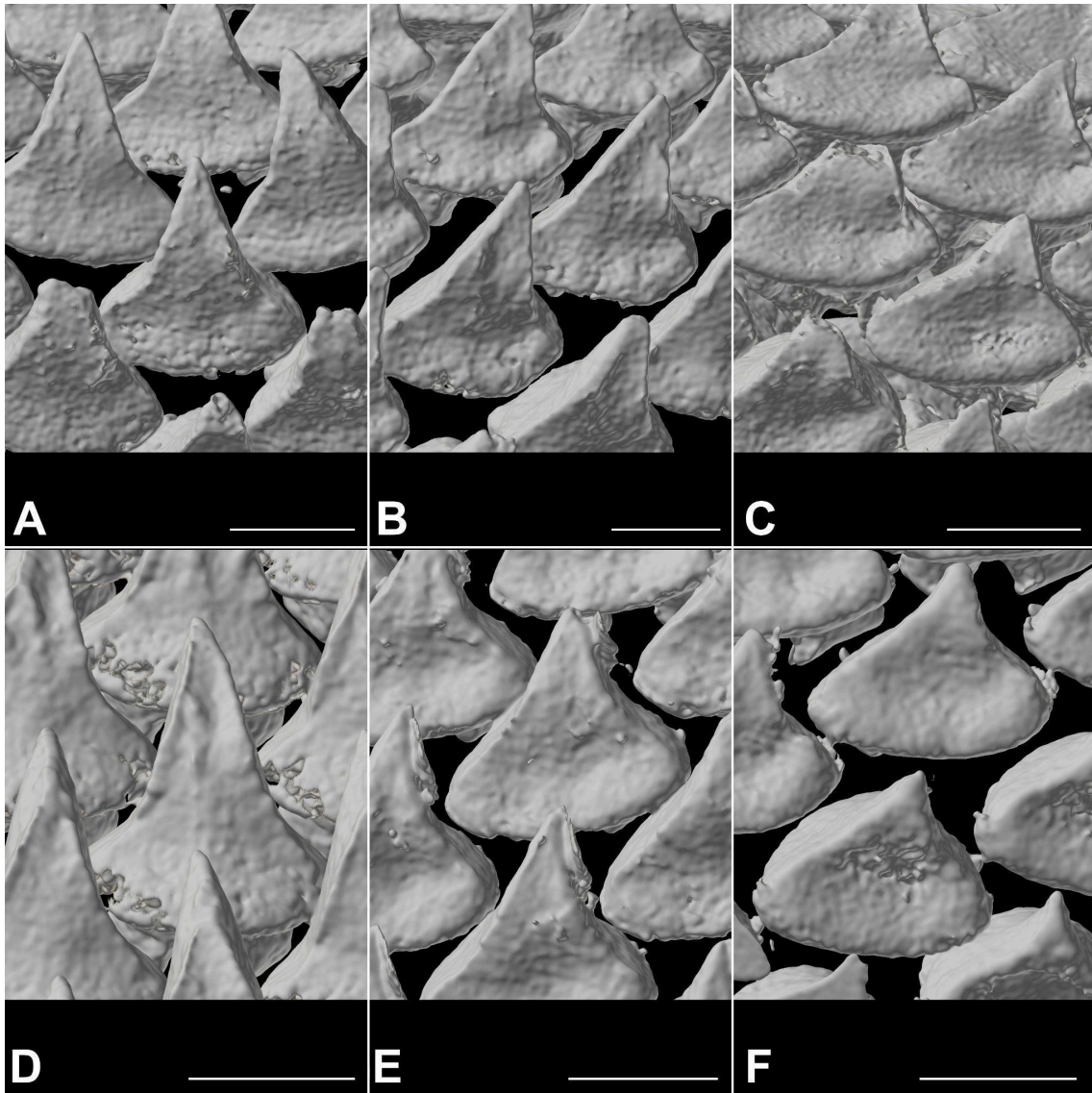


Figure 12. Occlusal view of teeth in a male of *Plesiotrygon iwamae*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

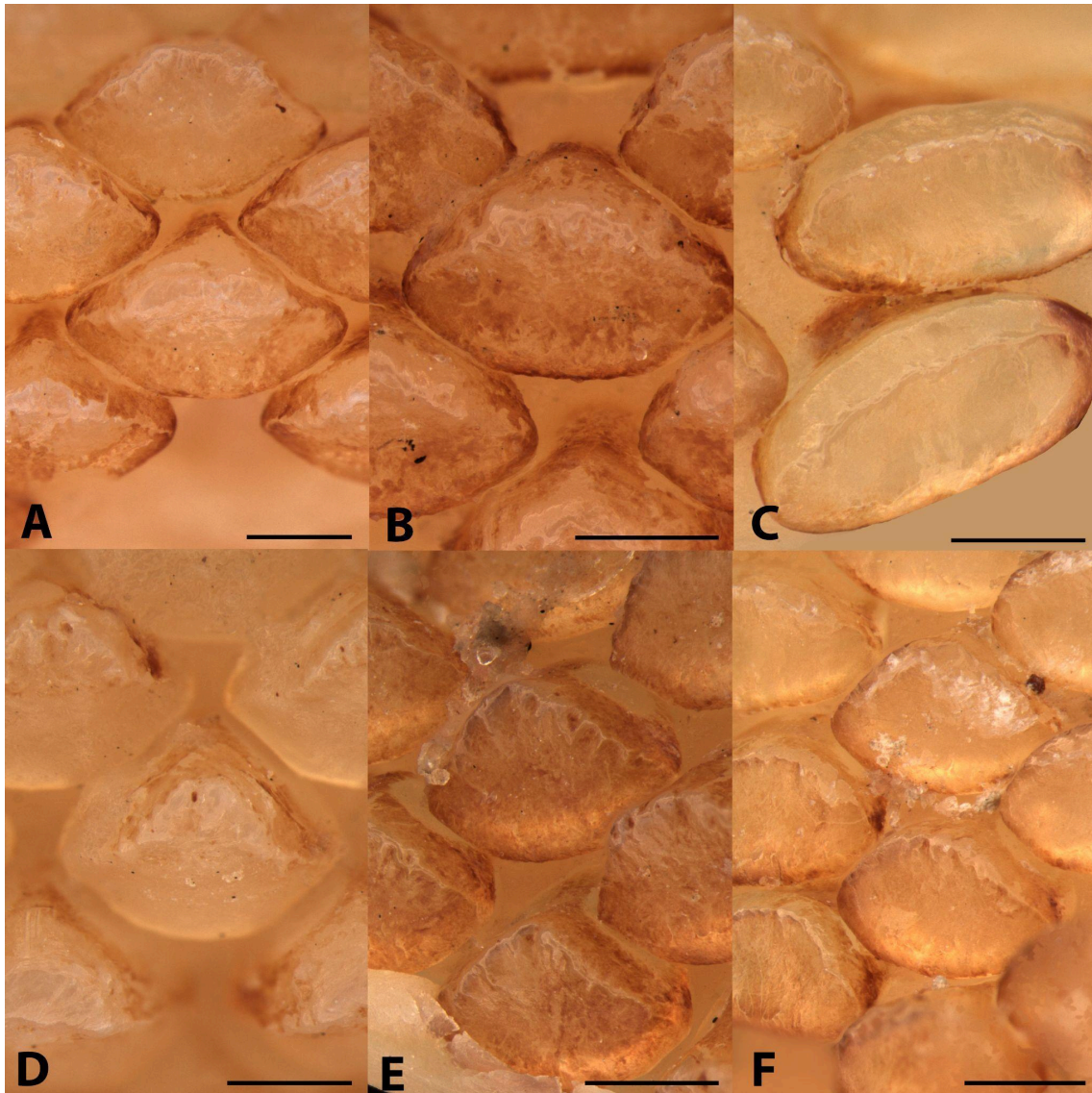


Figure 13. Occlusal view of teeth in a female of *Plesiotrygon iwamae*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

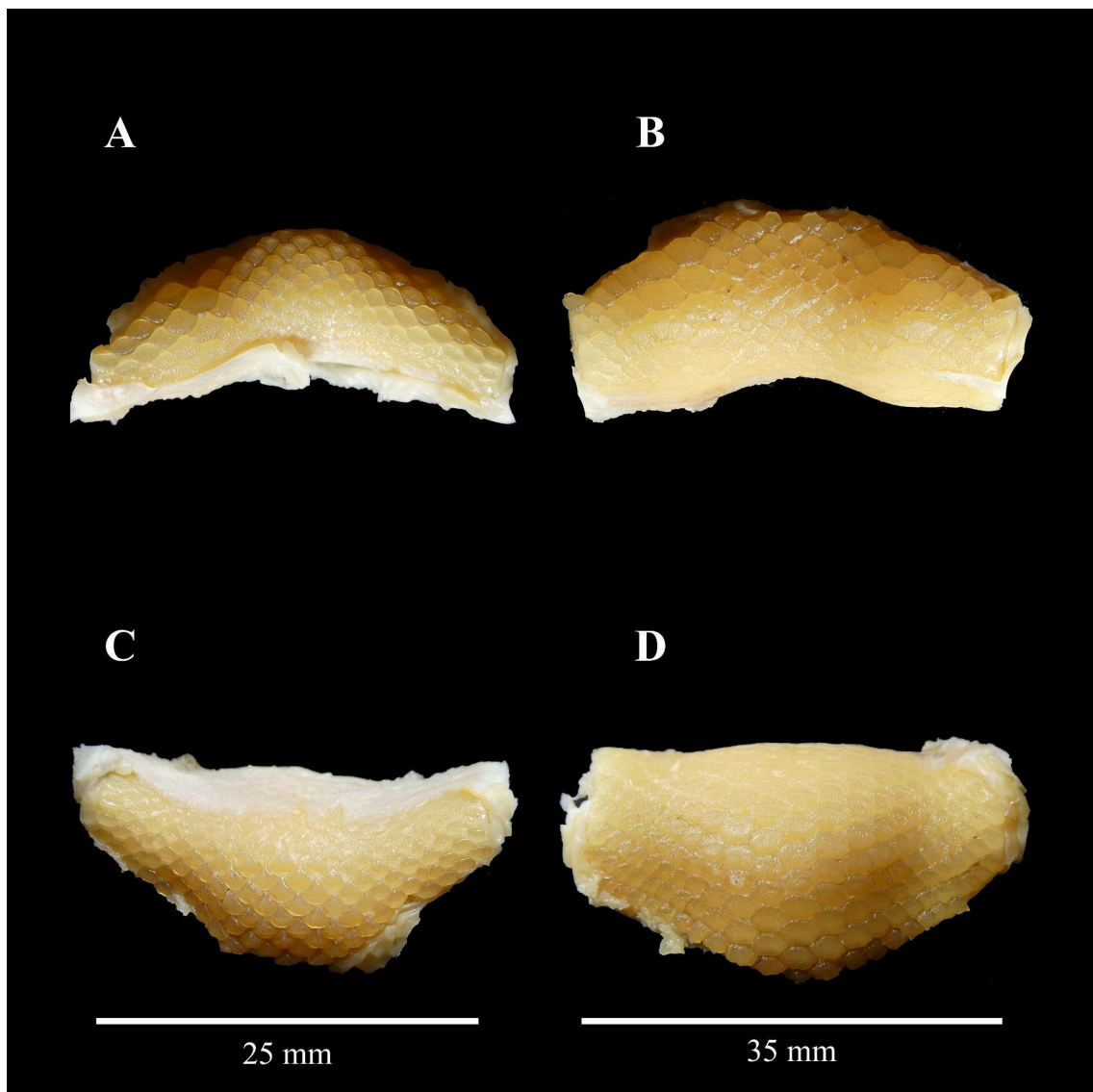


Figure 14. Occlusal view of the upper and lower plates of *Potamotrygon jabuti* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

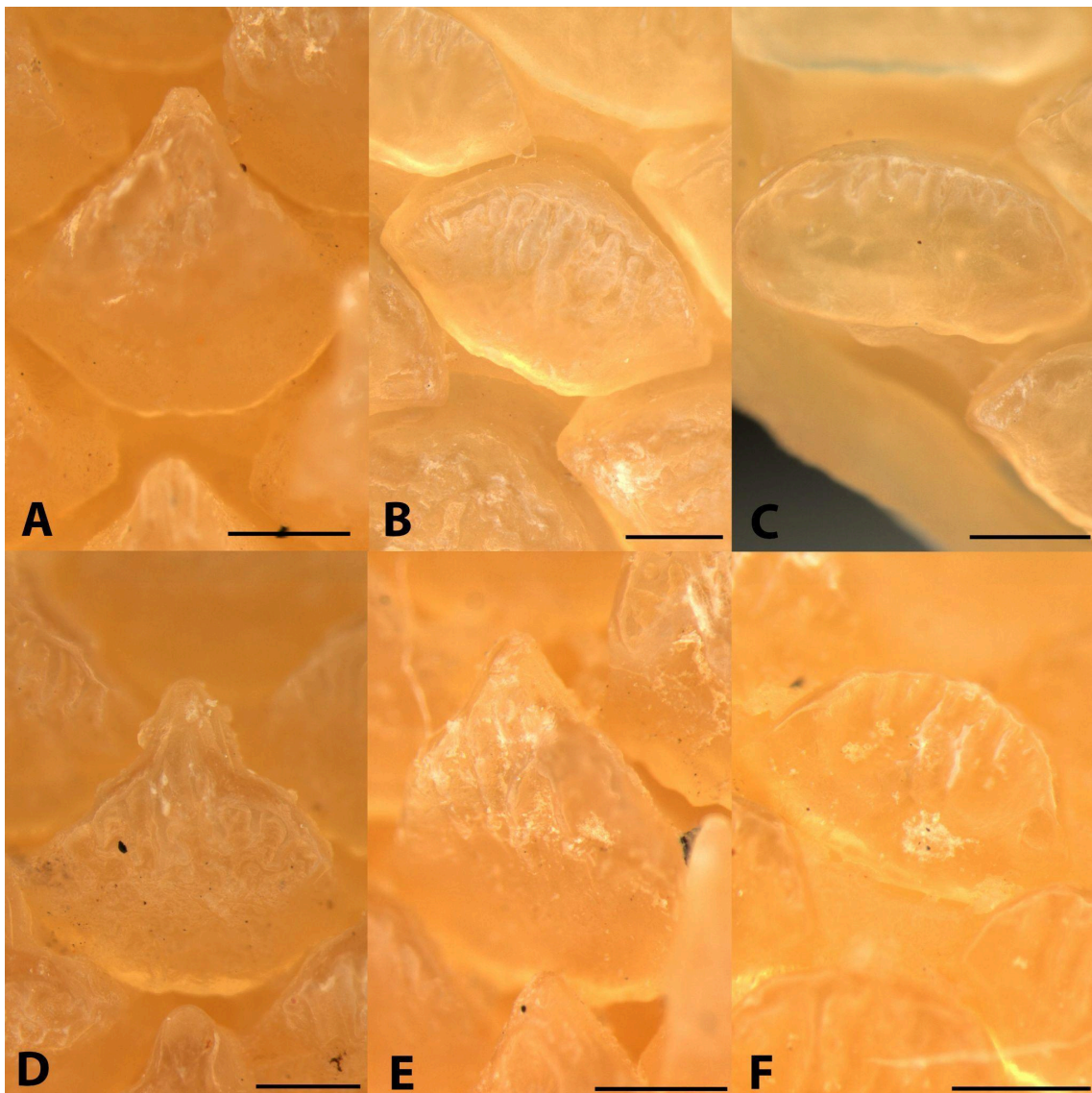


Figure 15. Occlusal view of teeth in a male of *Potamotrygon jabuti*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

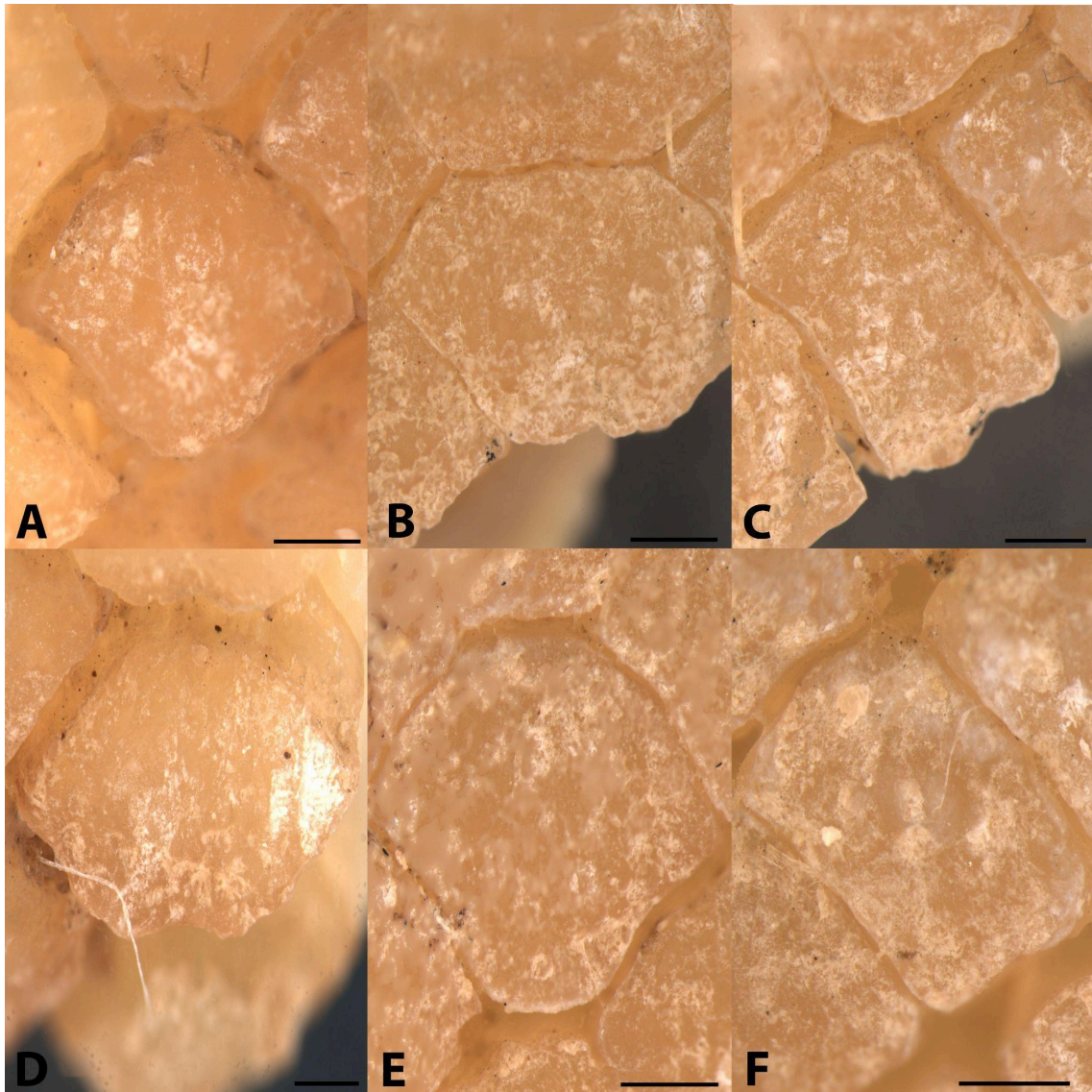


Figure 16. Occlusal view of teeth in a female of *Potamotrygon jabuti*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.



Figure 17. Occlusal view of the upper and lower plates of *Potamotrygon brachyura* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

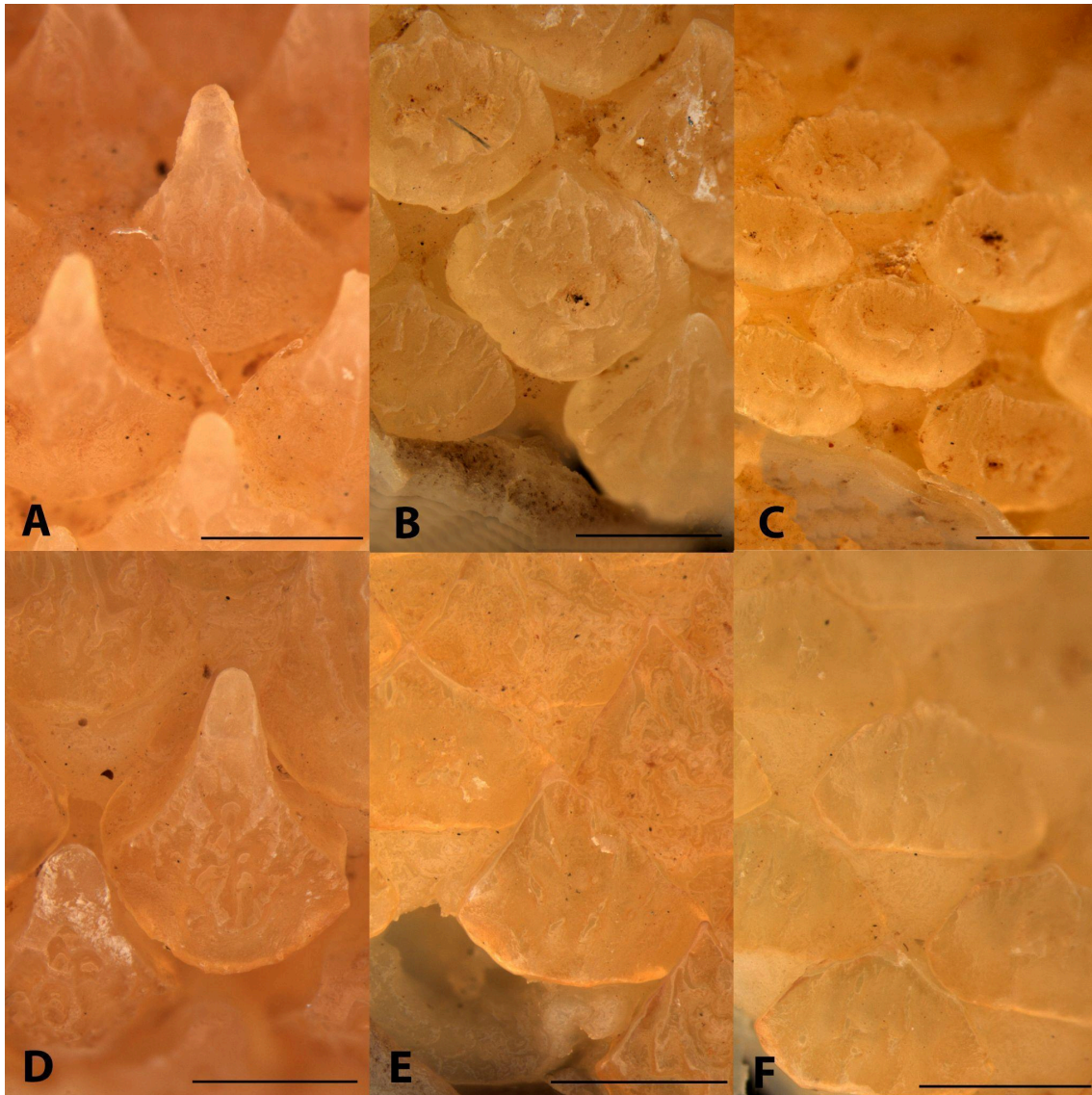


Figure 18. Occlusal view of teeth in a male of *Potamotrygon brachyura*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

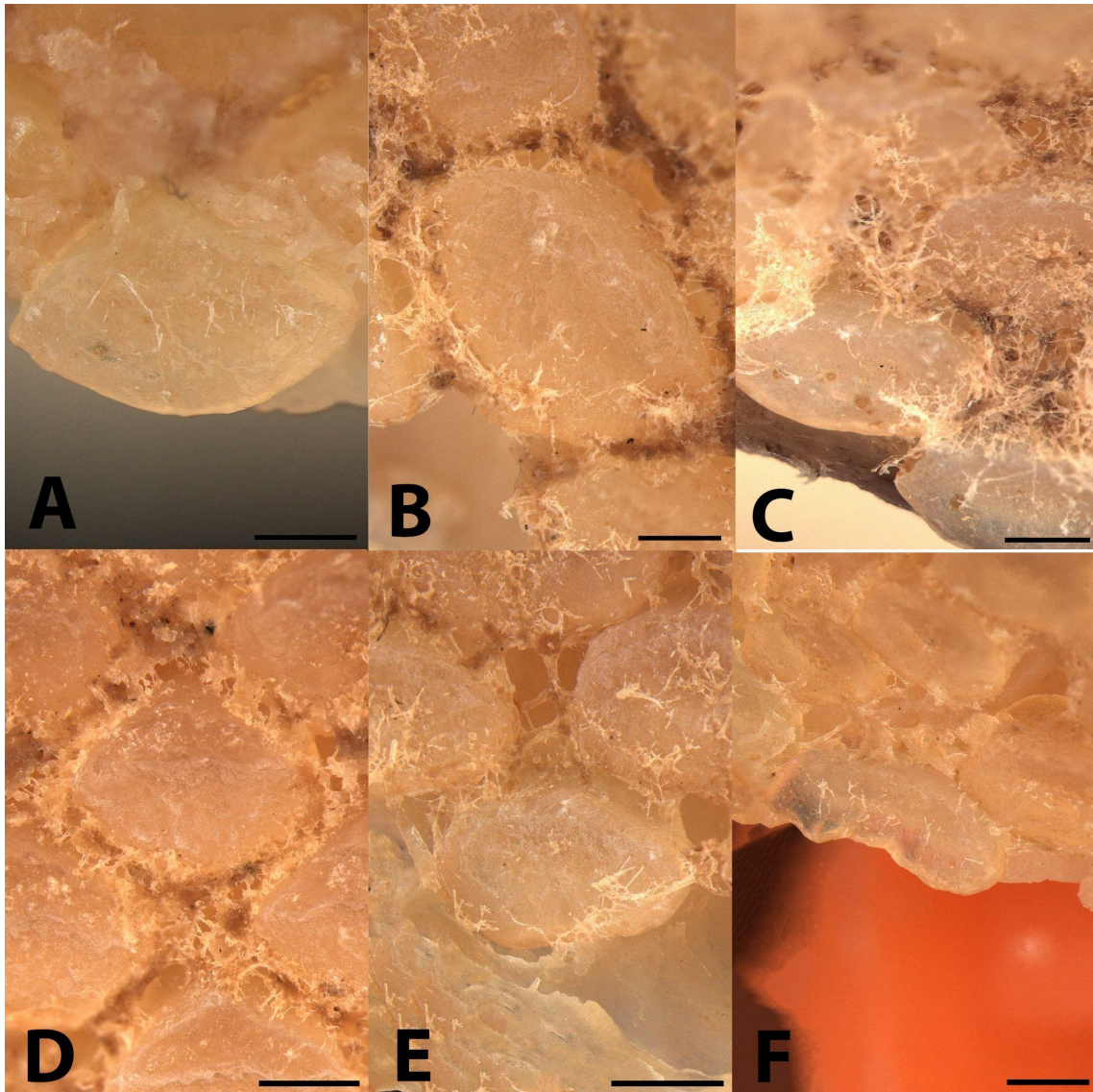


Figure 19. Occlusal view of teeth in a female of *Potamotrygon brachyura*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

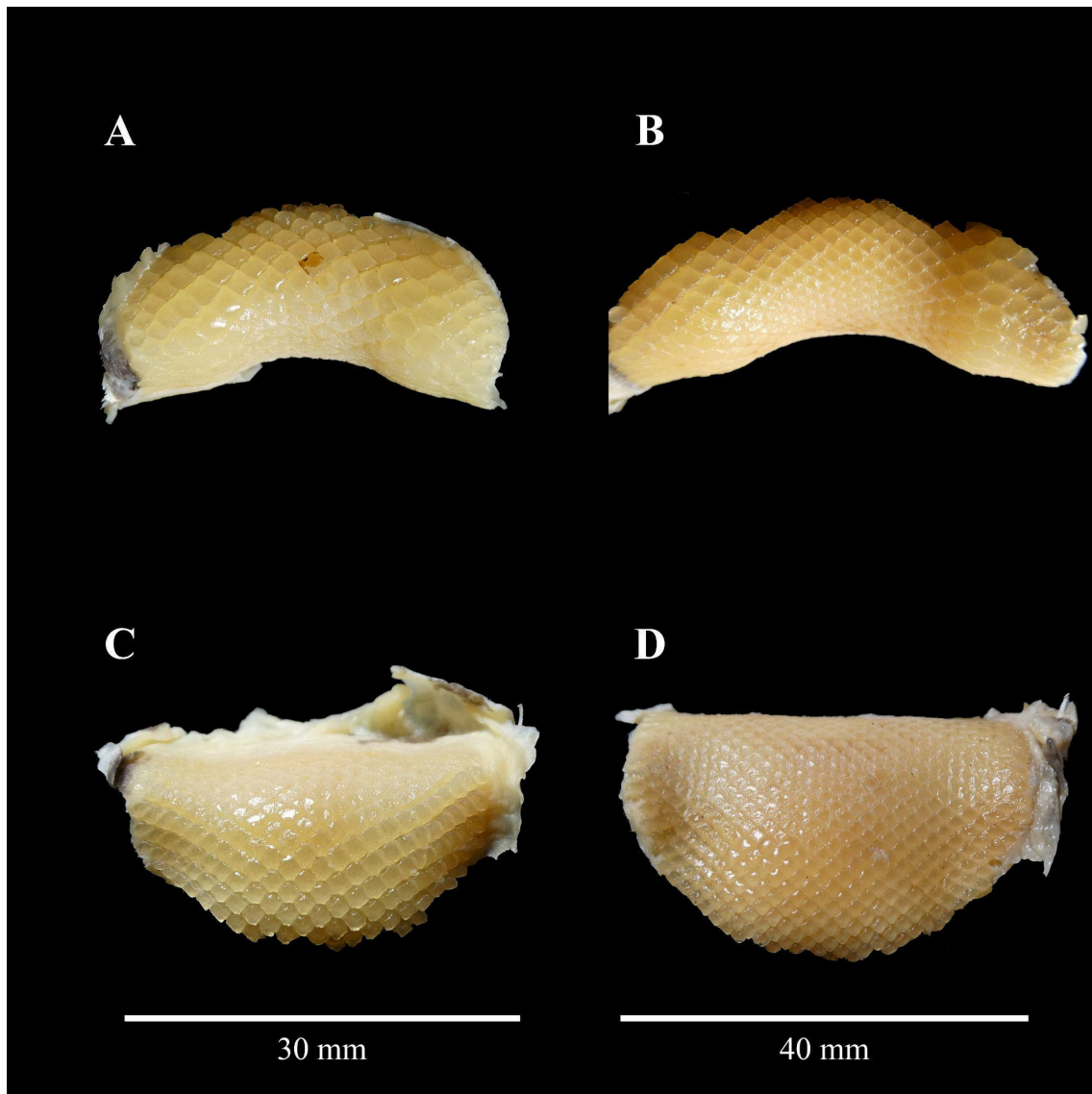


Figure 20. Occlusal view of the upper and lower plates of *Potamotrygon leopoldi* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

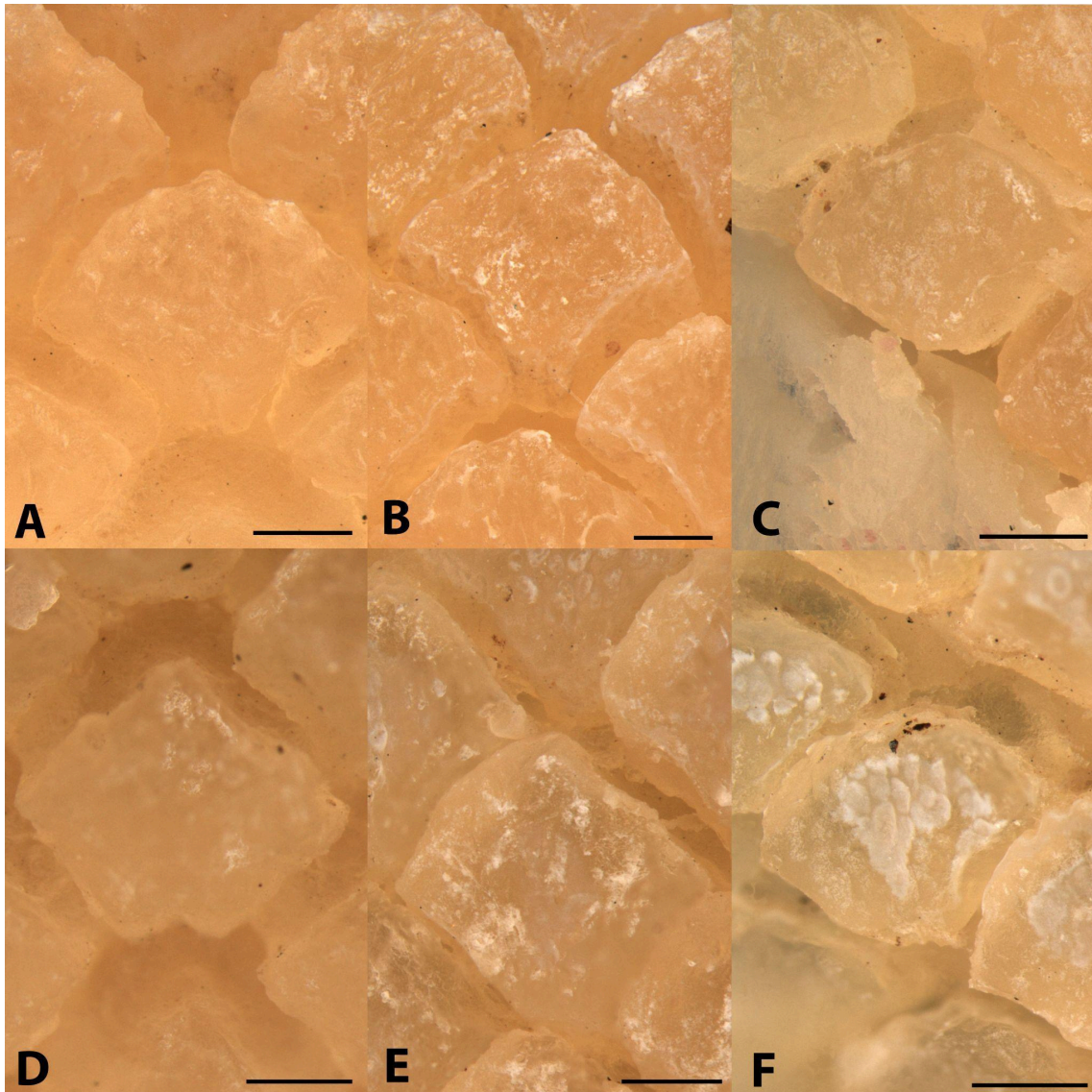


Figure 21. Occlusal view of teeth in a male of *Potamotrygon leopoldi*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

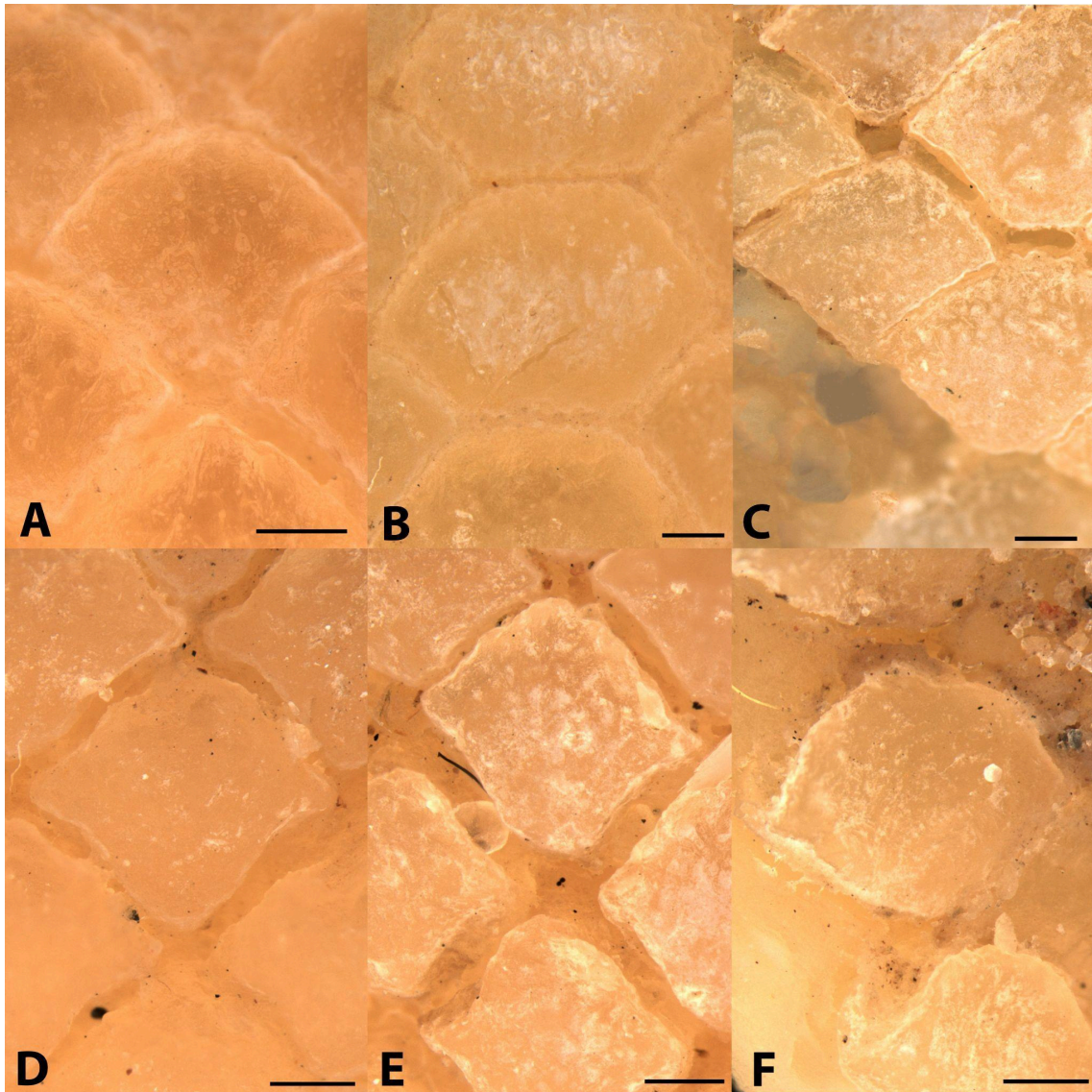


Figure 22. Occlusal view of teeth in a female of *Potamotrygon leopoldi*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

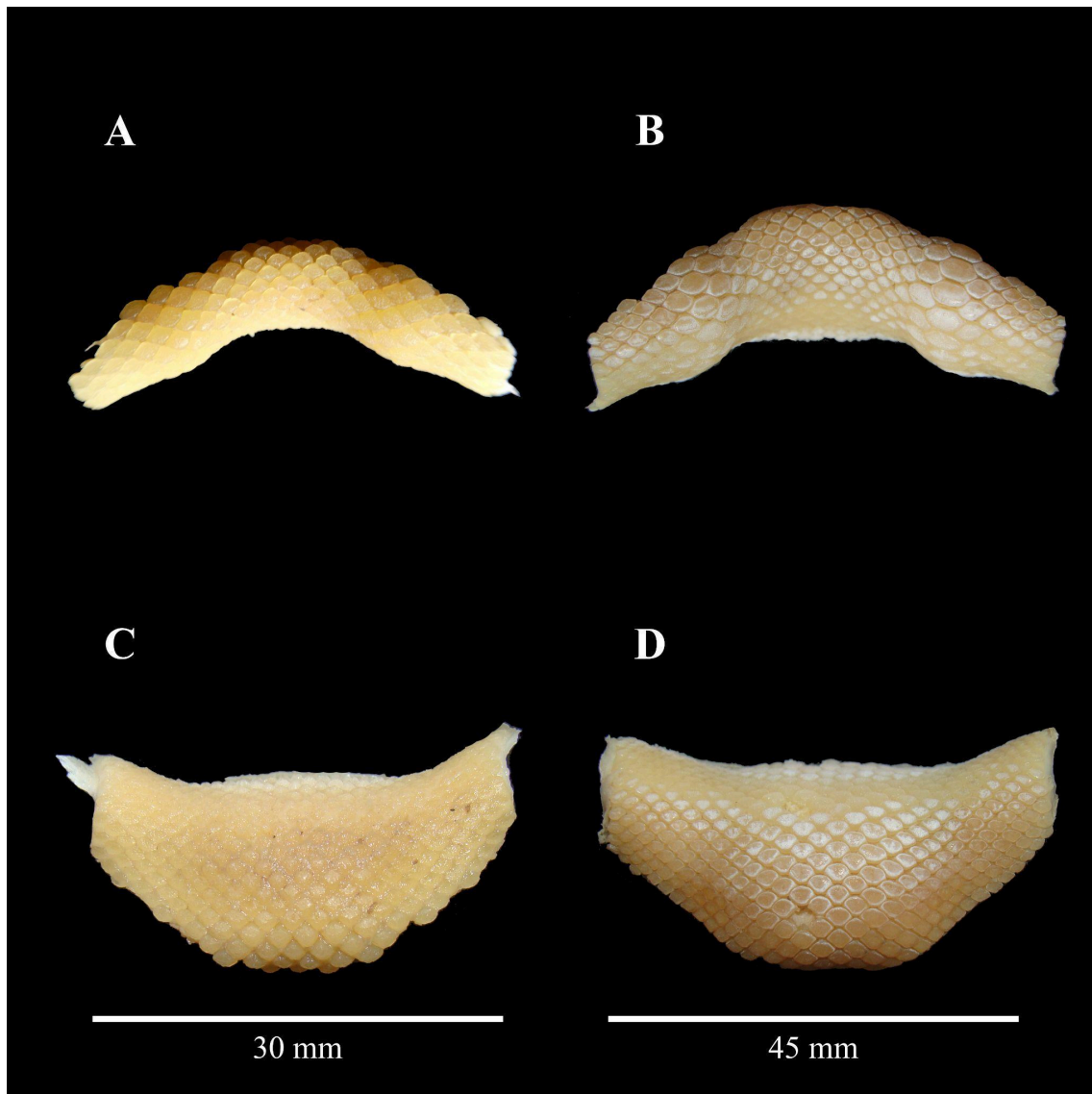


Figure 23. Occlusal view of the upper and lower plates of *Potamotrygon motoro* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

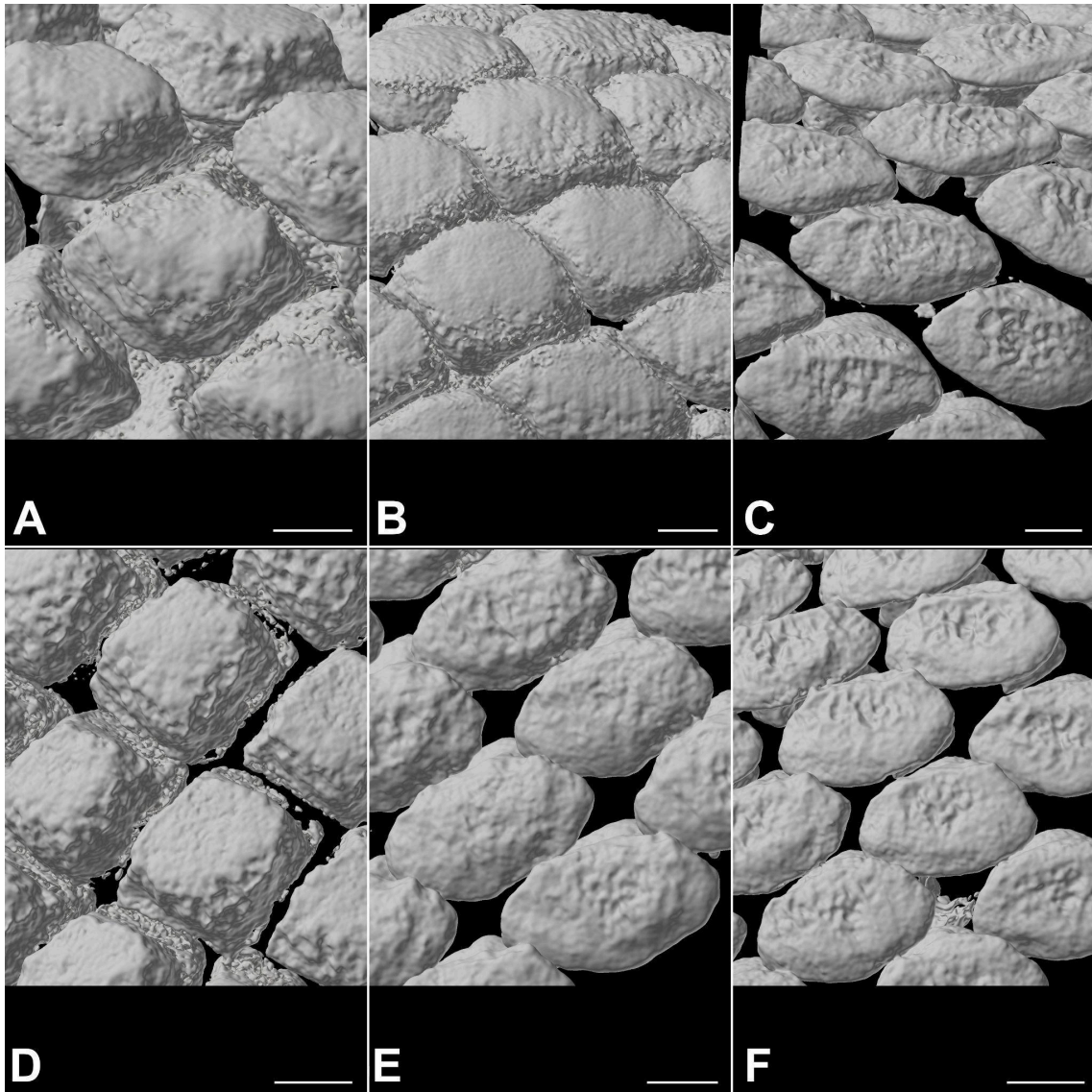


Figure 24. Occlusal view of teeth in a male of *Potamotrygon motoro*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

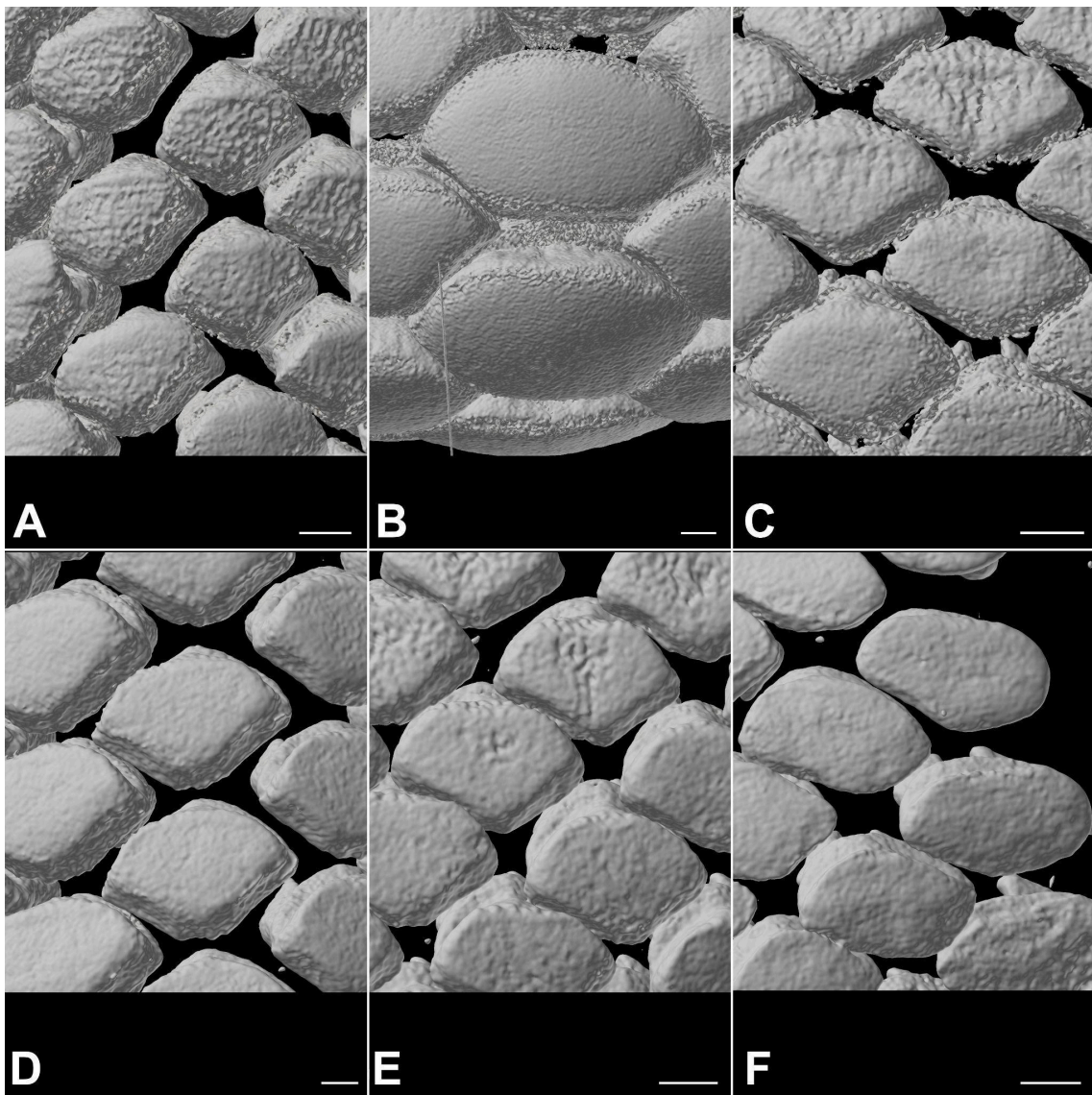


Figure 25. Occlusal view of teeth in a female of *Potamotrygon motoro*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

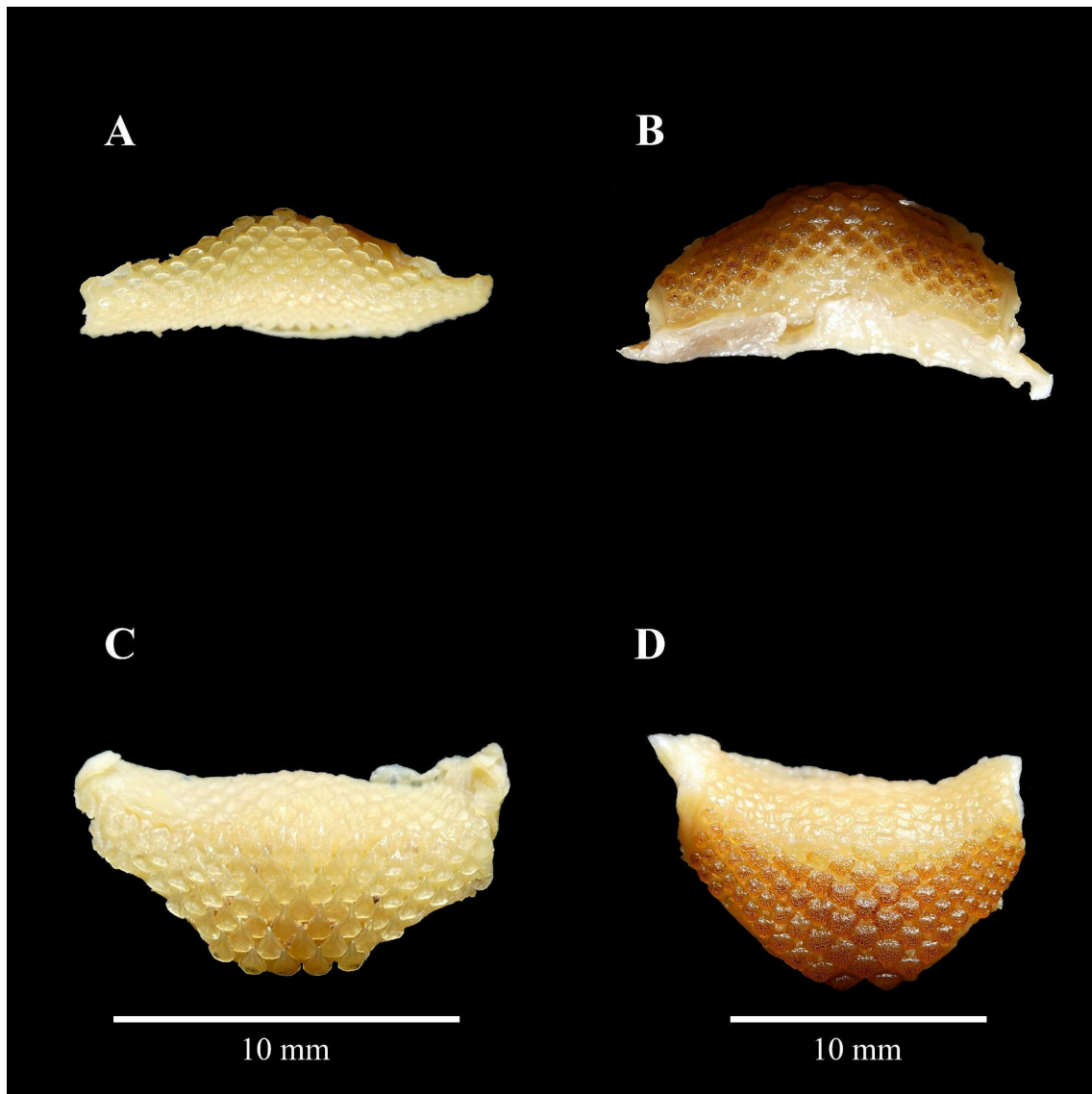


Figure 26. Occlusal view of the upper and lower plates of *Potamotrygon yepezi* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

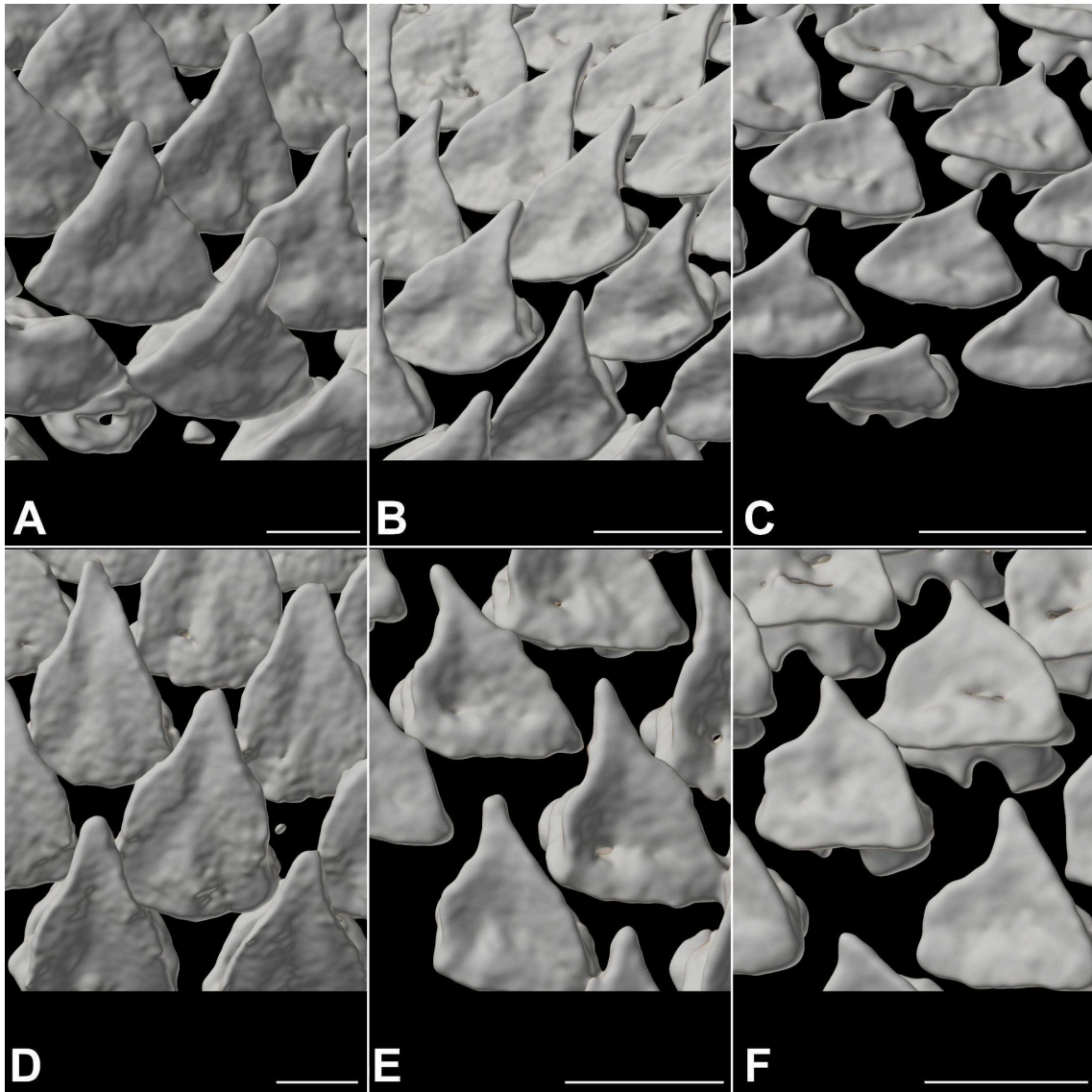


Figure 27. Occlusal view of teeth in a male of *Potamotrygon yepezi*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

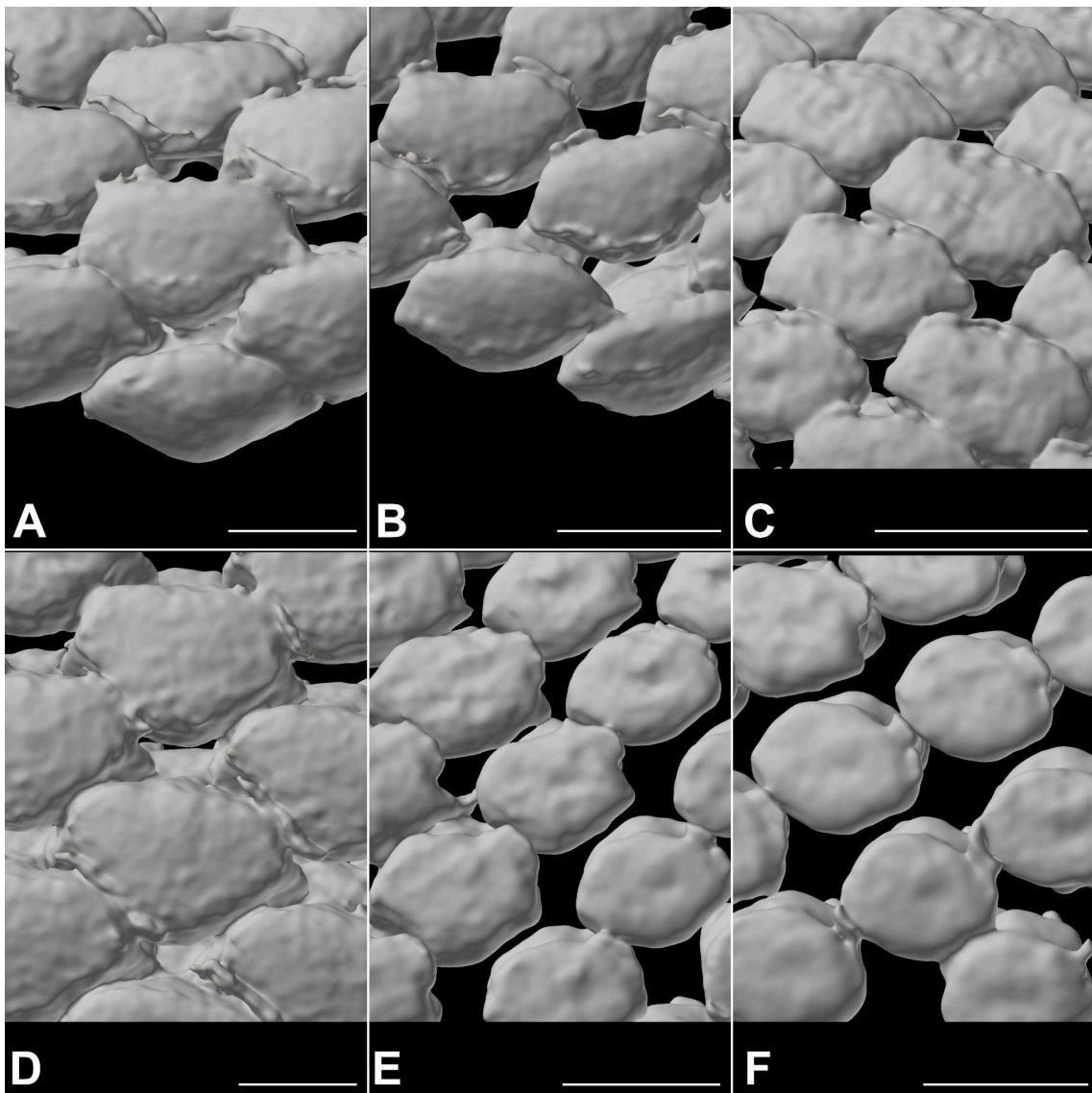


Figure 28. Occlusal view of teeth in a female of *Potamotrygon yepezi*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

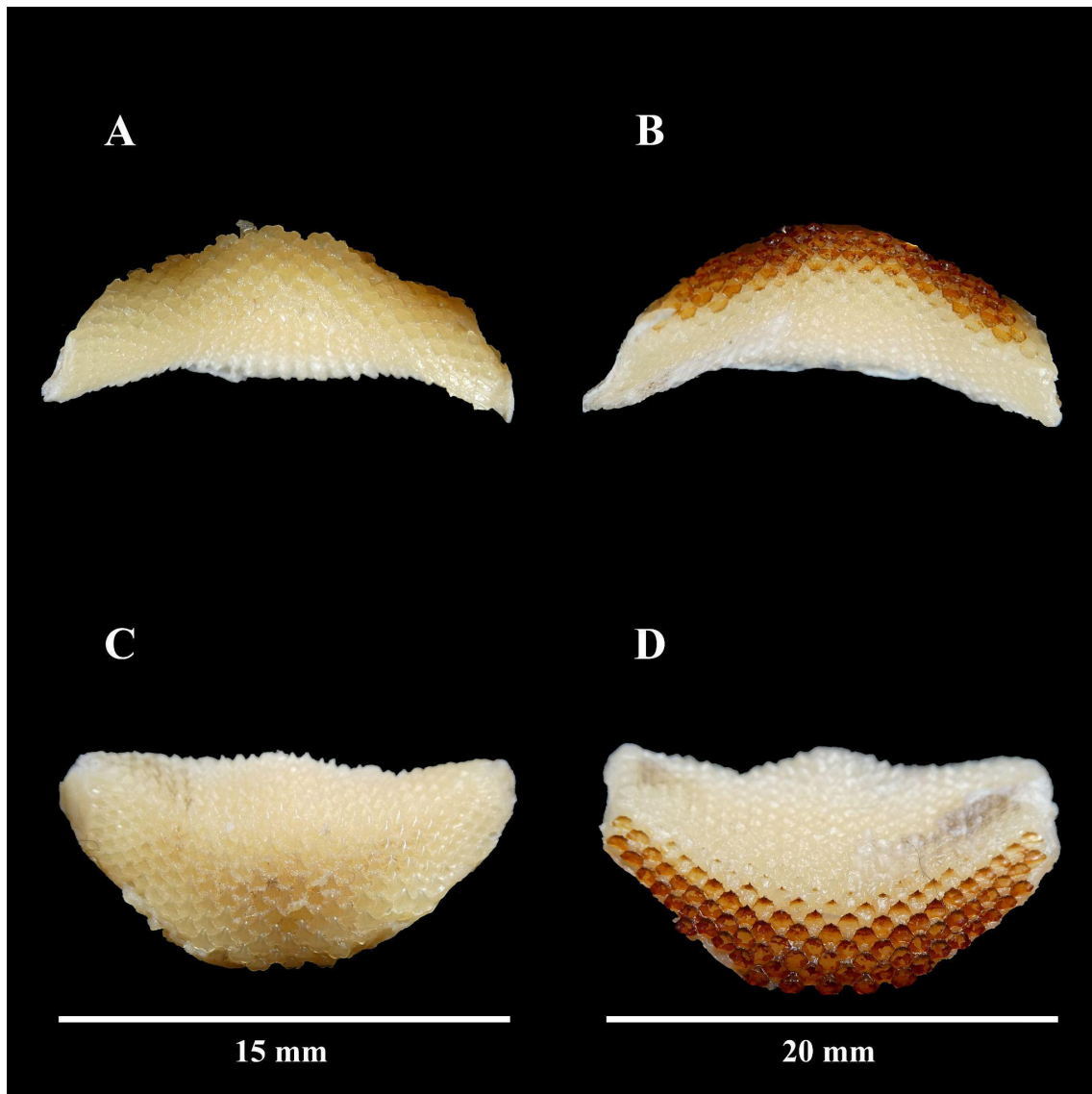


Figure 29. Occlusal view of the upper and lower plates of *Potamotrygon signata* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

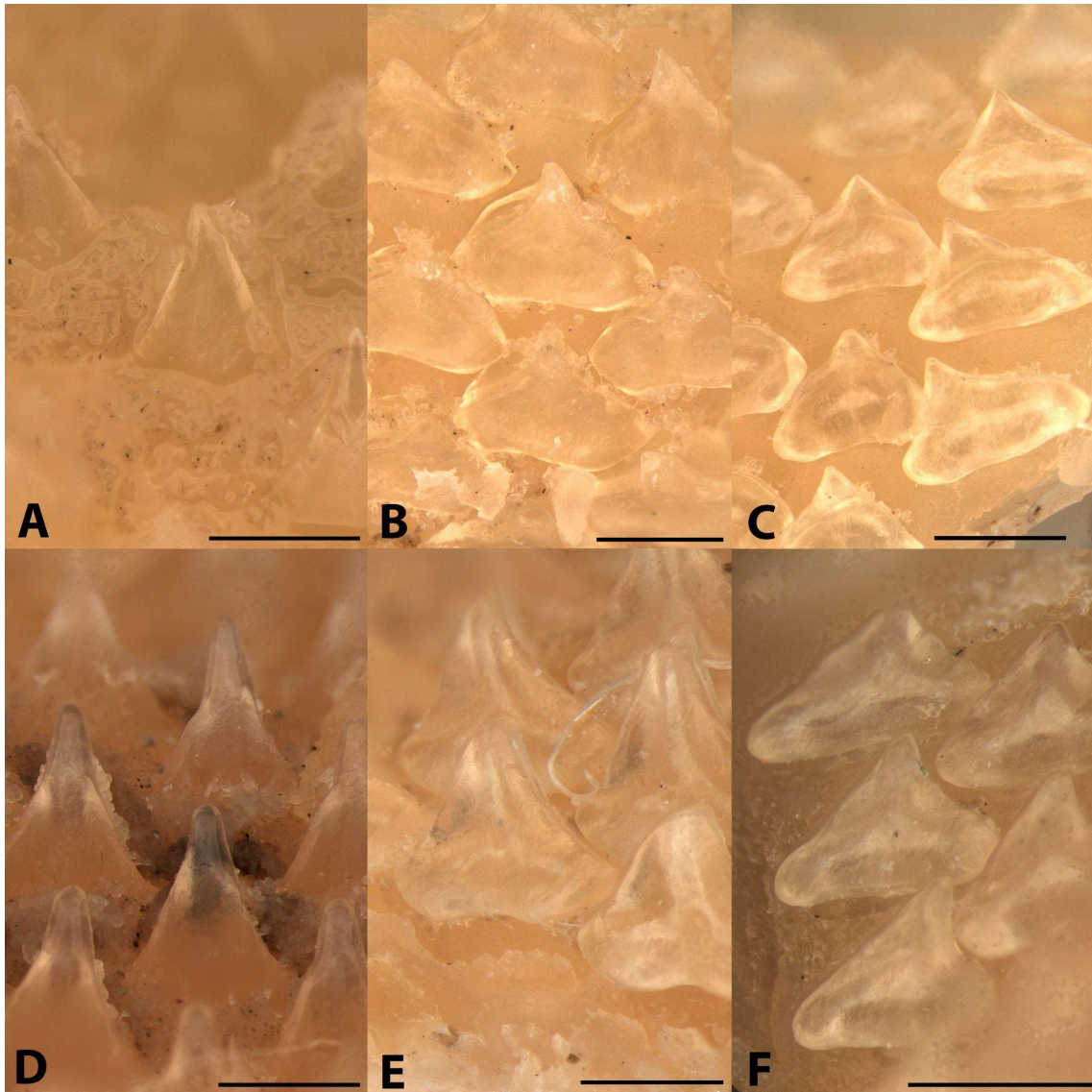


Figure 30. Occlusal view of teeth in a male of *Potamotrygon signata*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

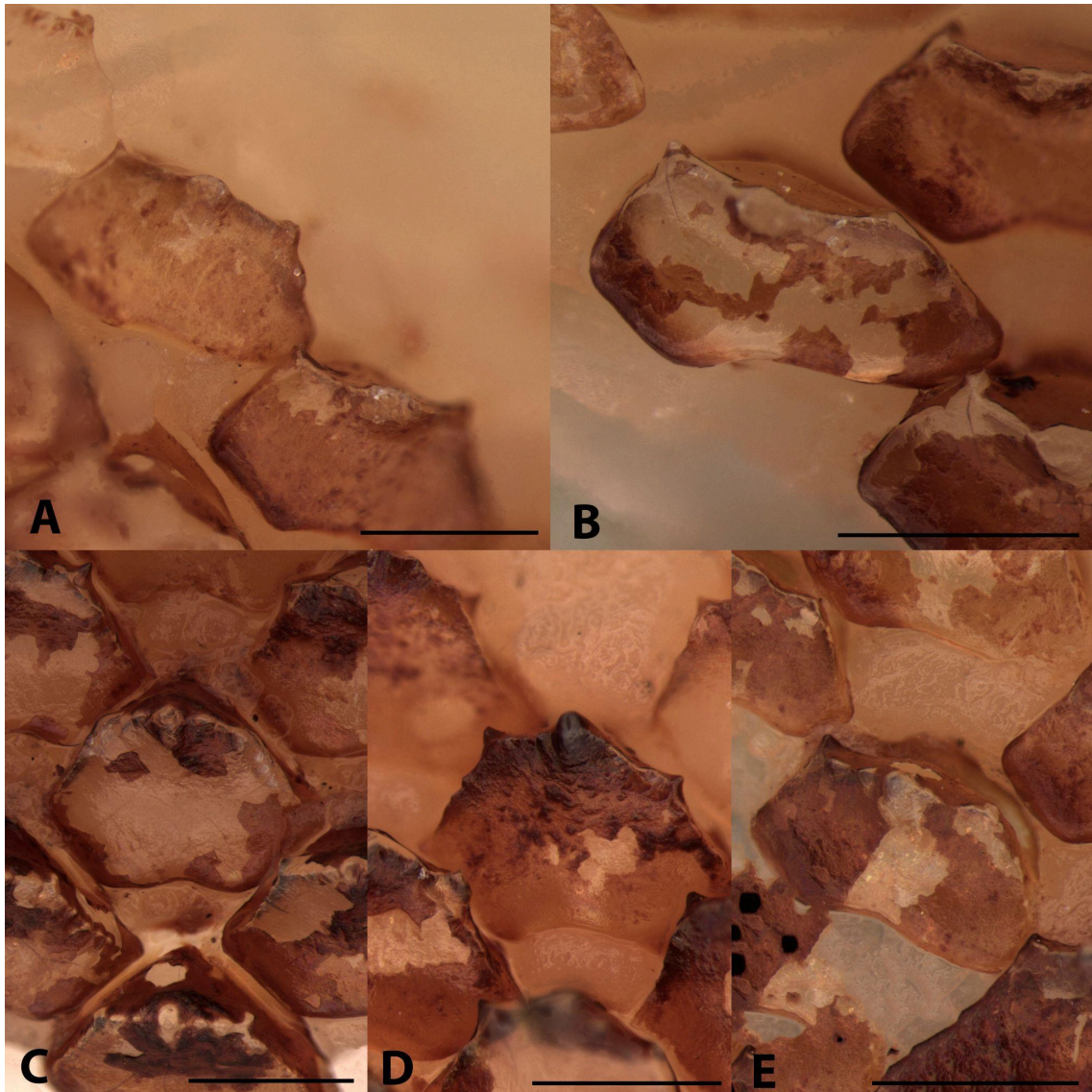


Figure 31. Occlusal view of teeth in a female of *Potamotrygon signata*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Lower teeth near symphysis (position 1). D - Lower intermediate teeth (position 2). E - Lower lateral teeth (position 3). In A-E labial to bottom. Scale bar = 0.5 mm.

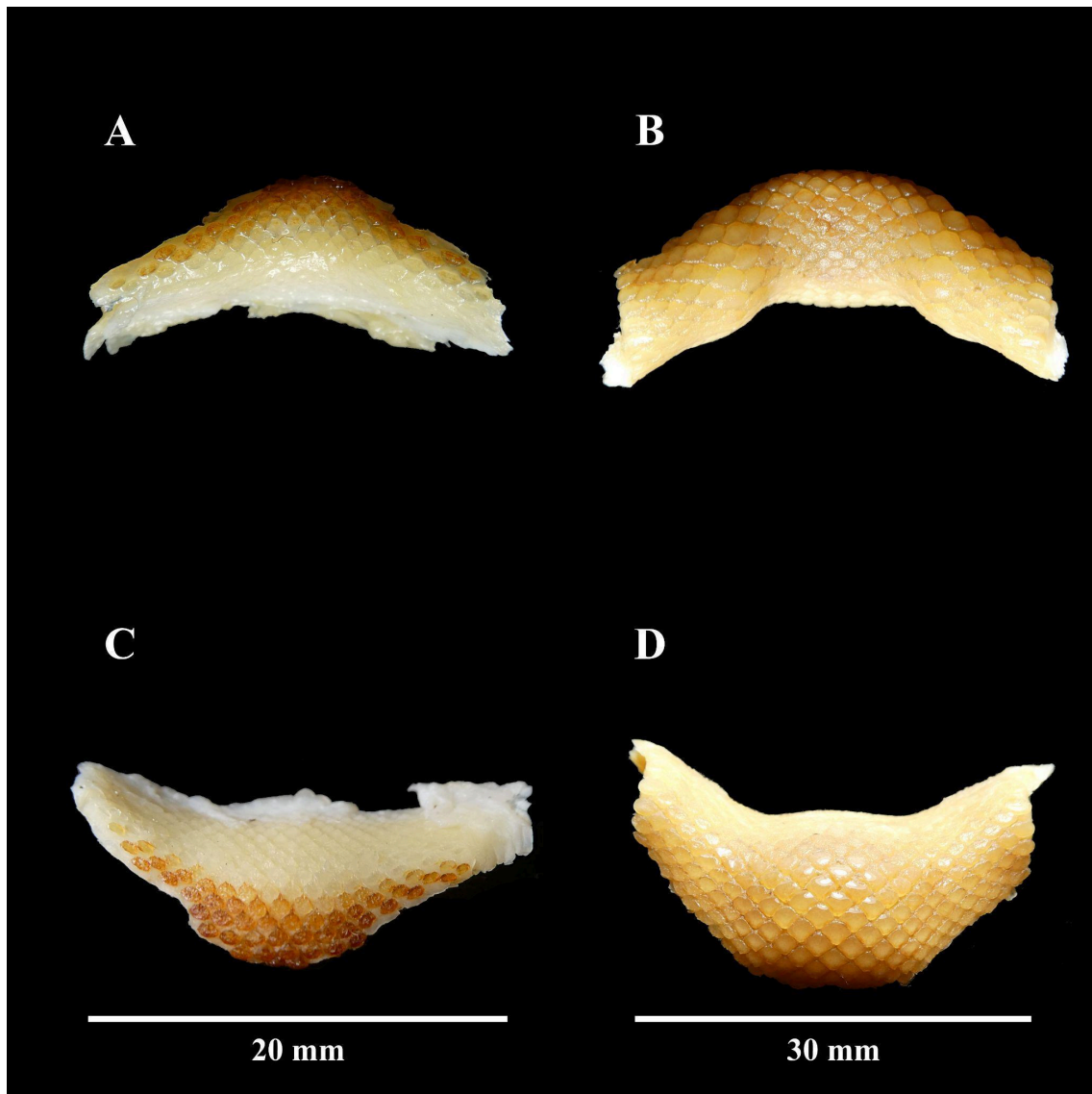


Figure 32. Occlusal view of the upper and lower plates of *Potamotrygon marquesi* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

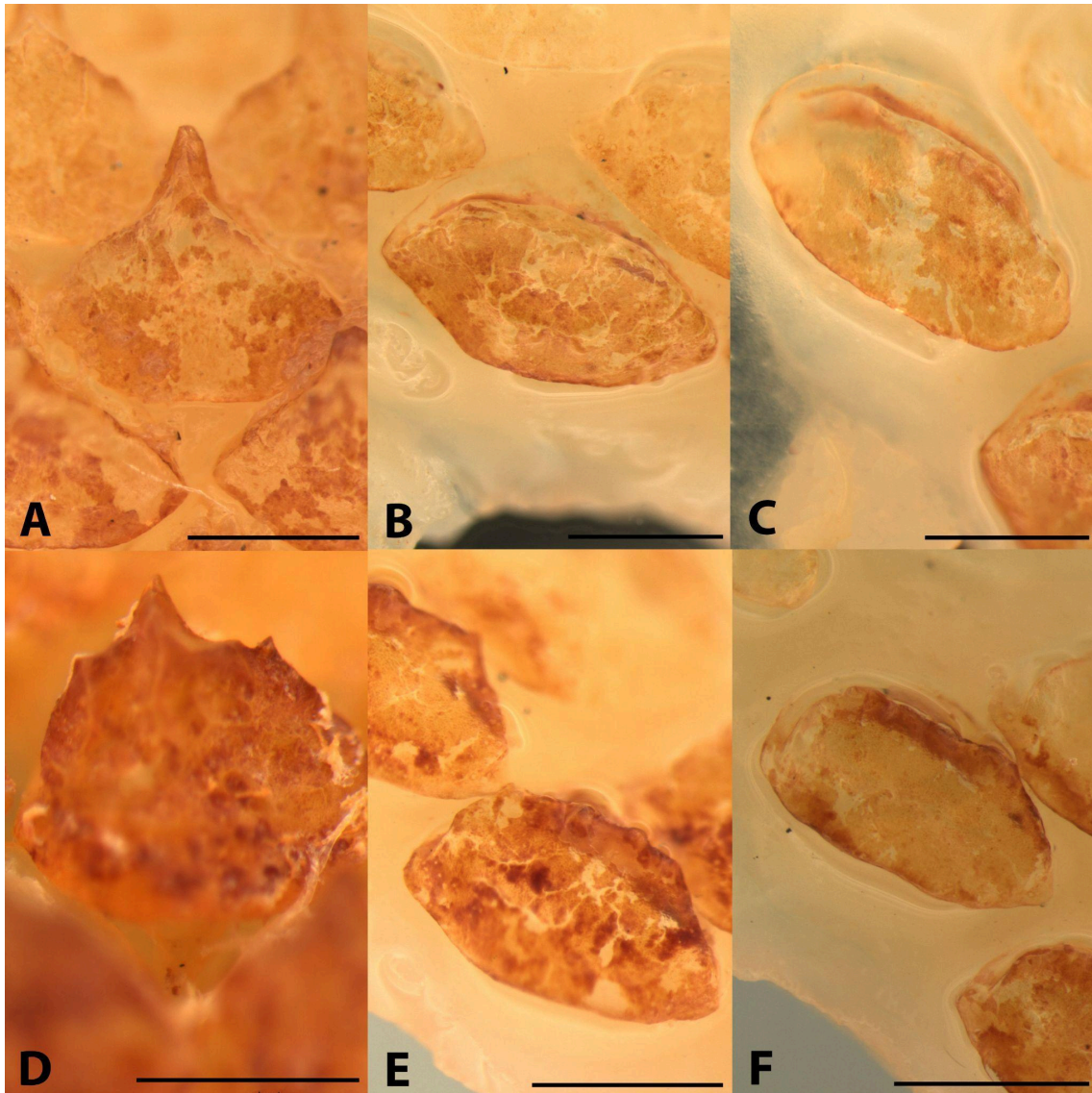


Figure 33. Occlusal view of teeth in a male of *Potamotrygon marquesi*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

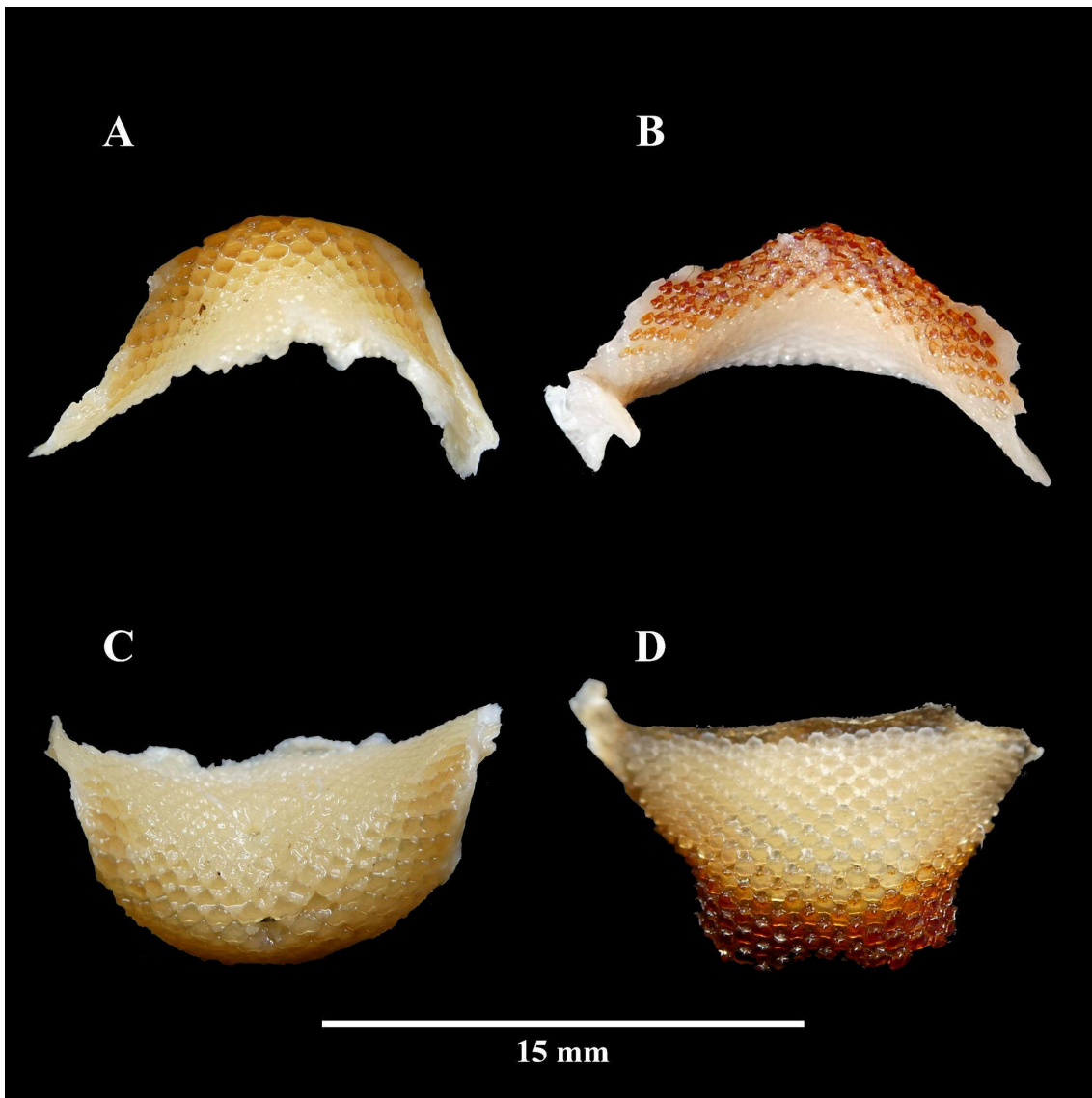


Figure 34. Occlusal view of the upper and lower plates of *Potamotrygon orbignyi* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

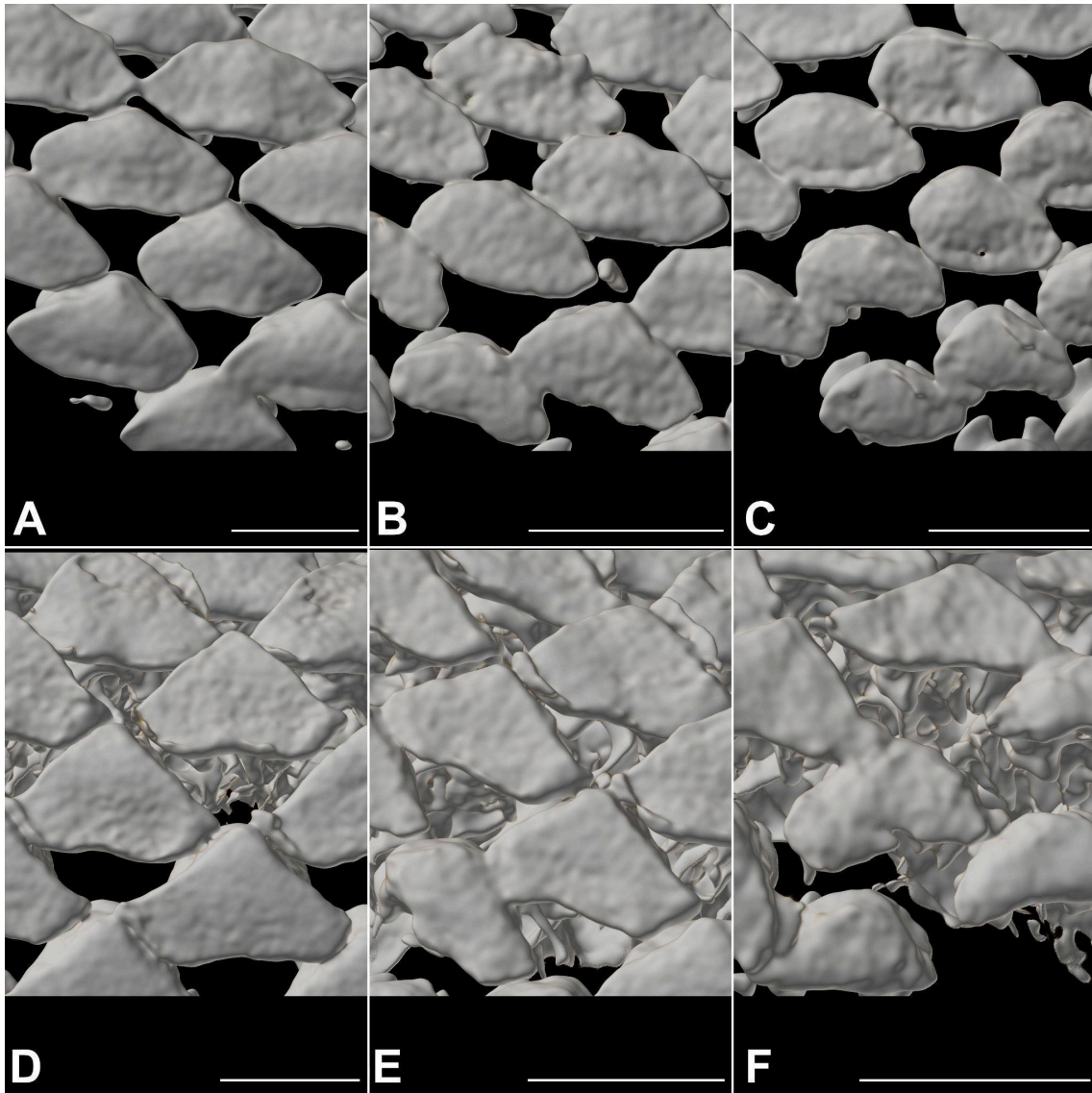


Figure 35. Occlusal view of teeth in a male of *Potamotrygon orbignyi*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

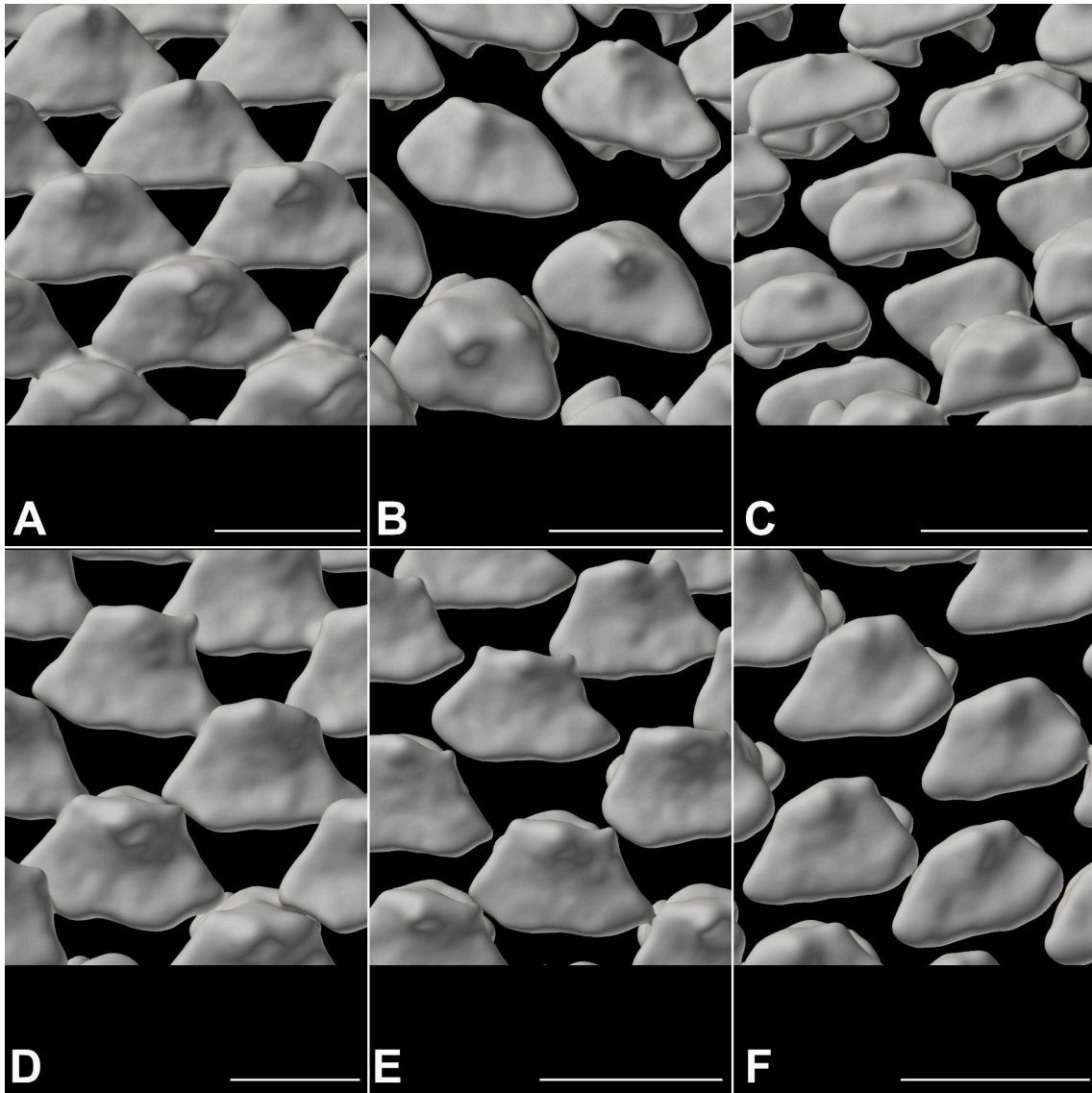


Figure 36. Occlusal view of teeth in a female of *Potamotrygon orbignyi*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

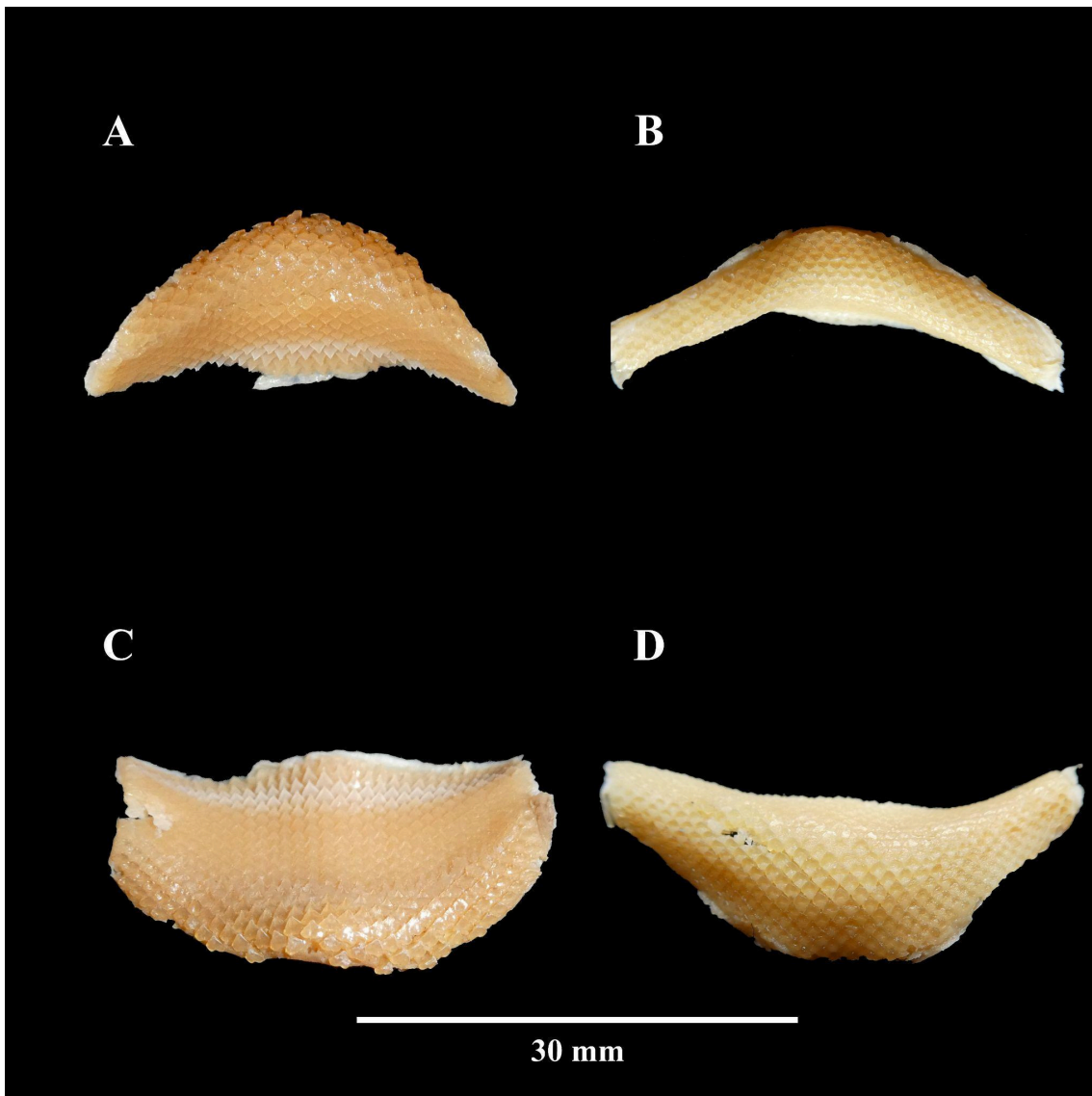


Figure 37. Occlusal view of the upper and lower plates of *Potamotrygon schroederi* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

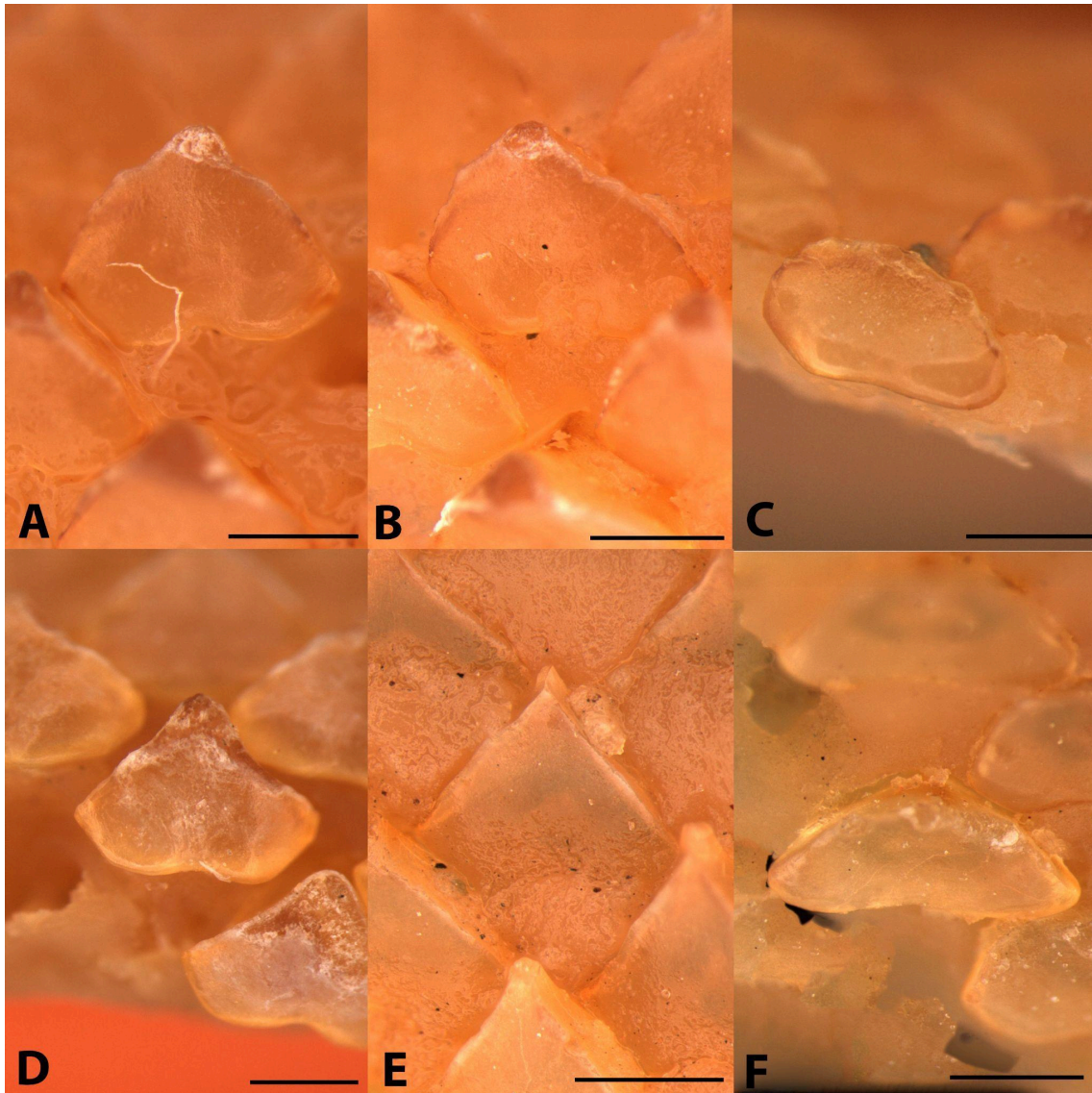


Figure 38. Occlusal view of teeth in a male of *Potamotrygon schroederi*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

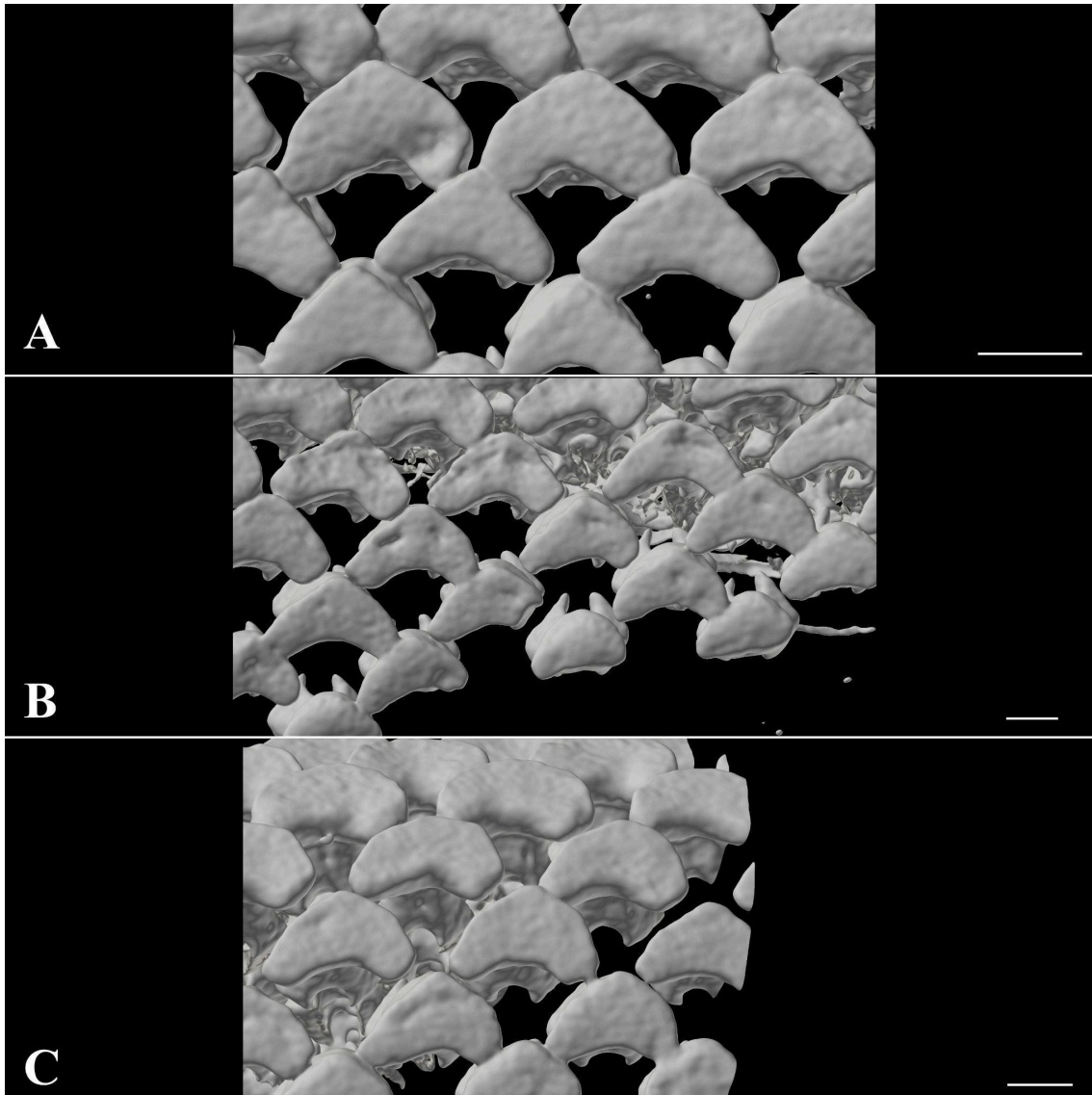


Figure 39. Occlusal view of teeth in a female of *Potamotrygon schroederi*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3).

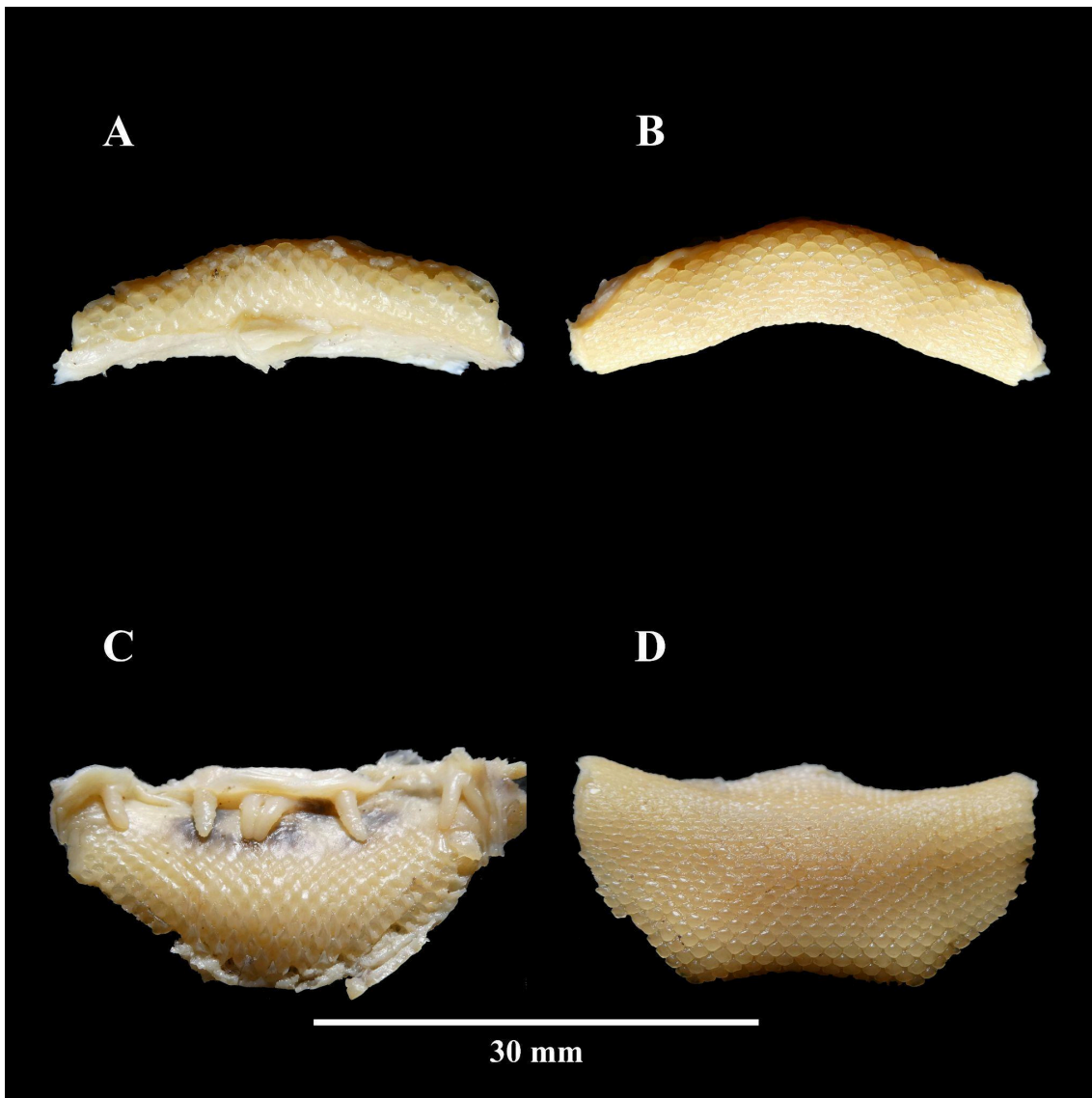


Figure 40. Occlusal view of the upper and lower plates of *Potamotrygon albimaculata* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

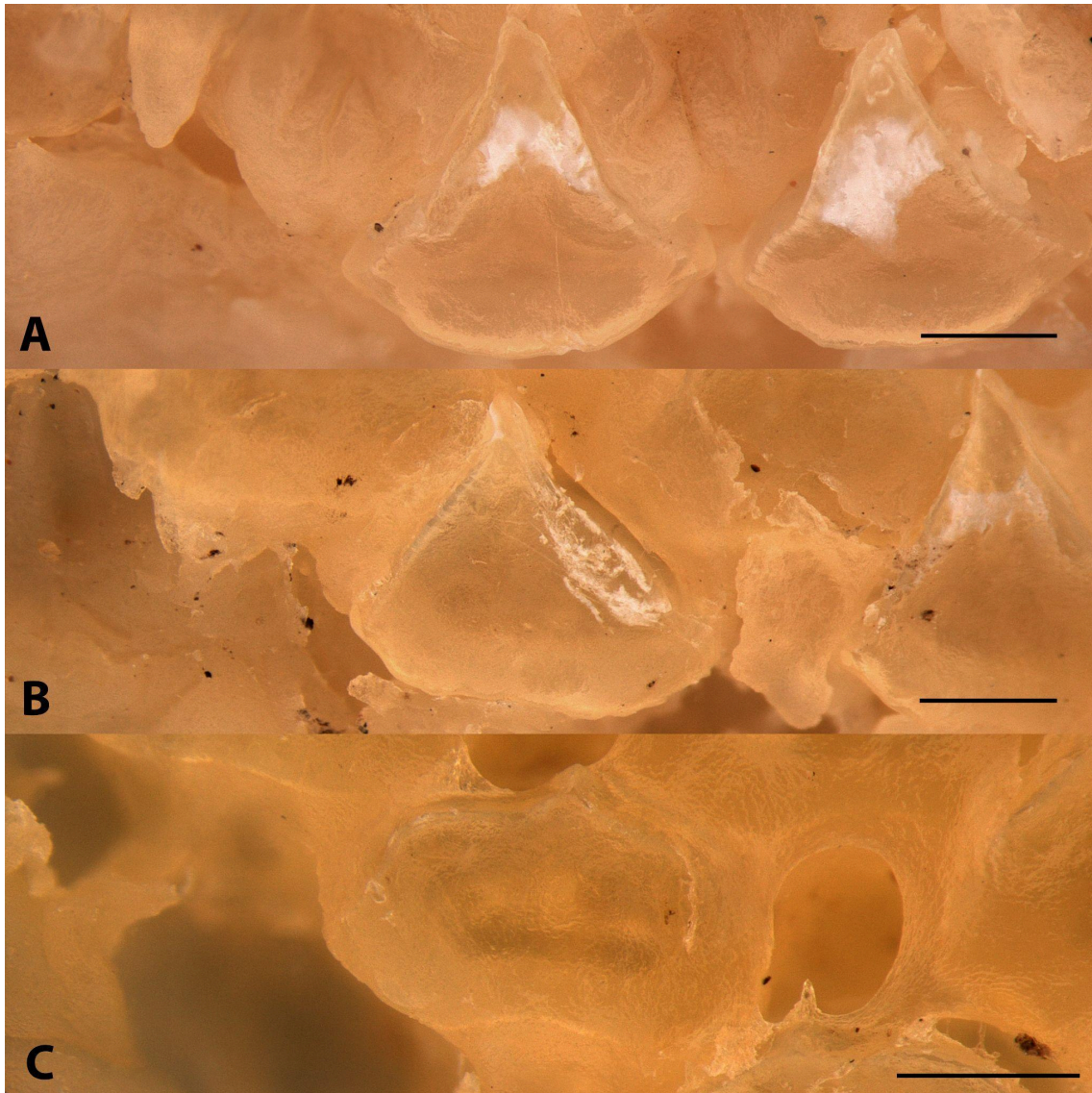


Figure 41. Occlusal view of teeth in a male of *Potamotrygon albimaculata*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). In A-C labial to bottom. Scale bar = 0.5 mm.

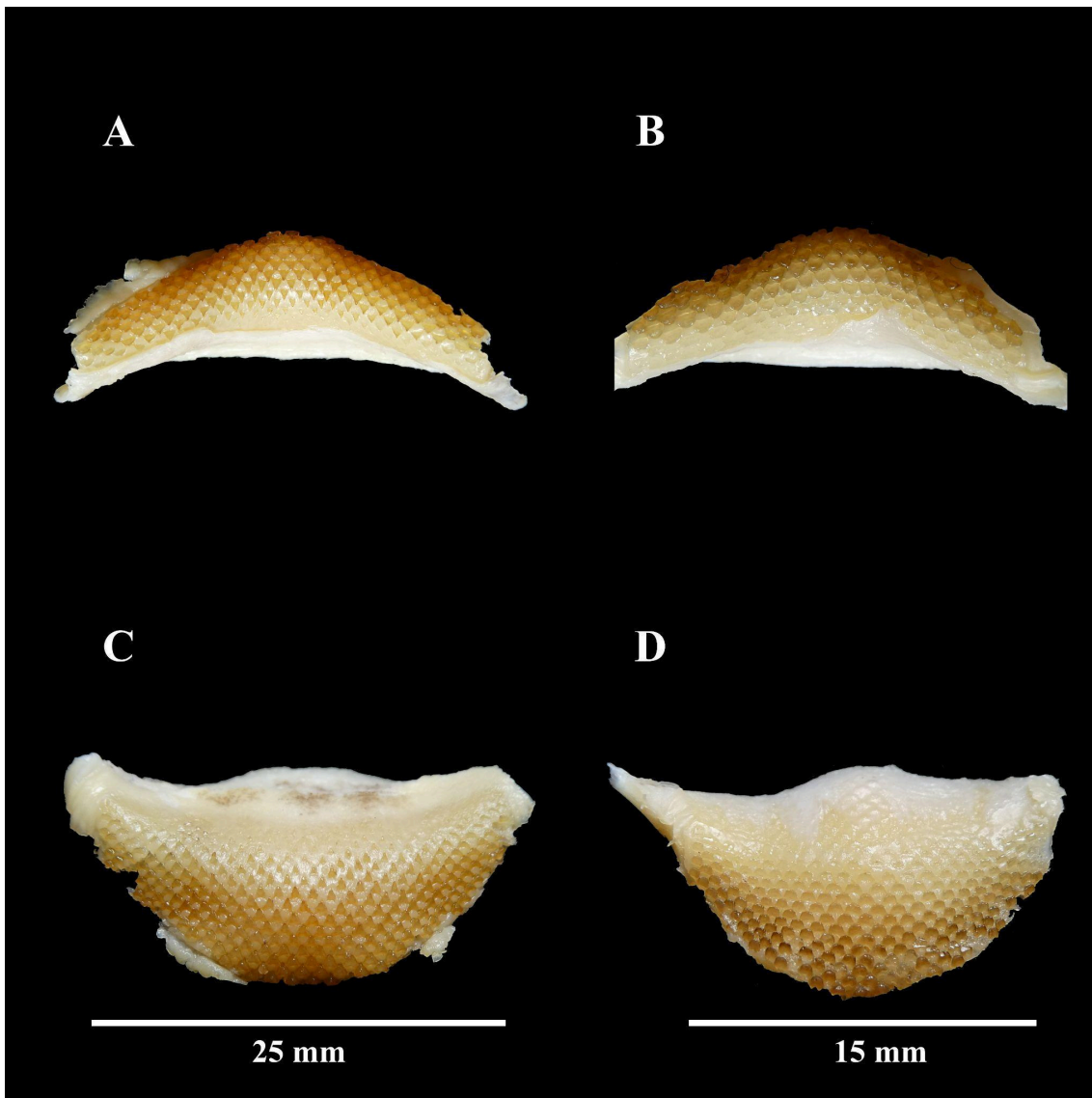


Figure 42. Occlusal view of the upper and lower plates of *Potamotrygon humerosa* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

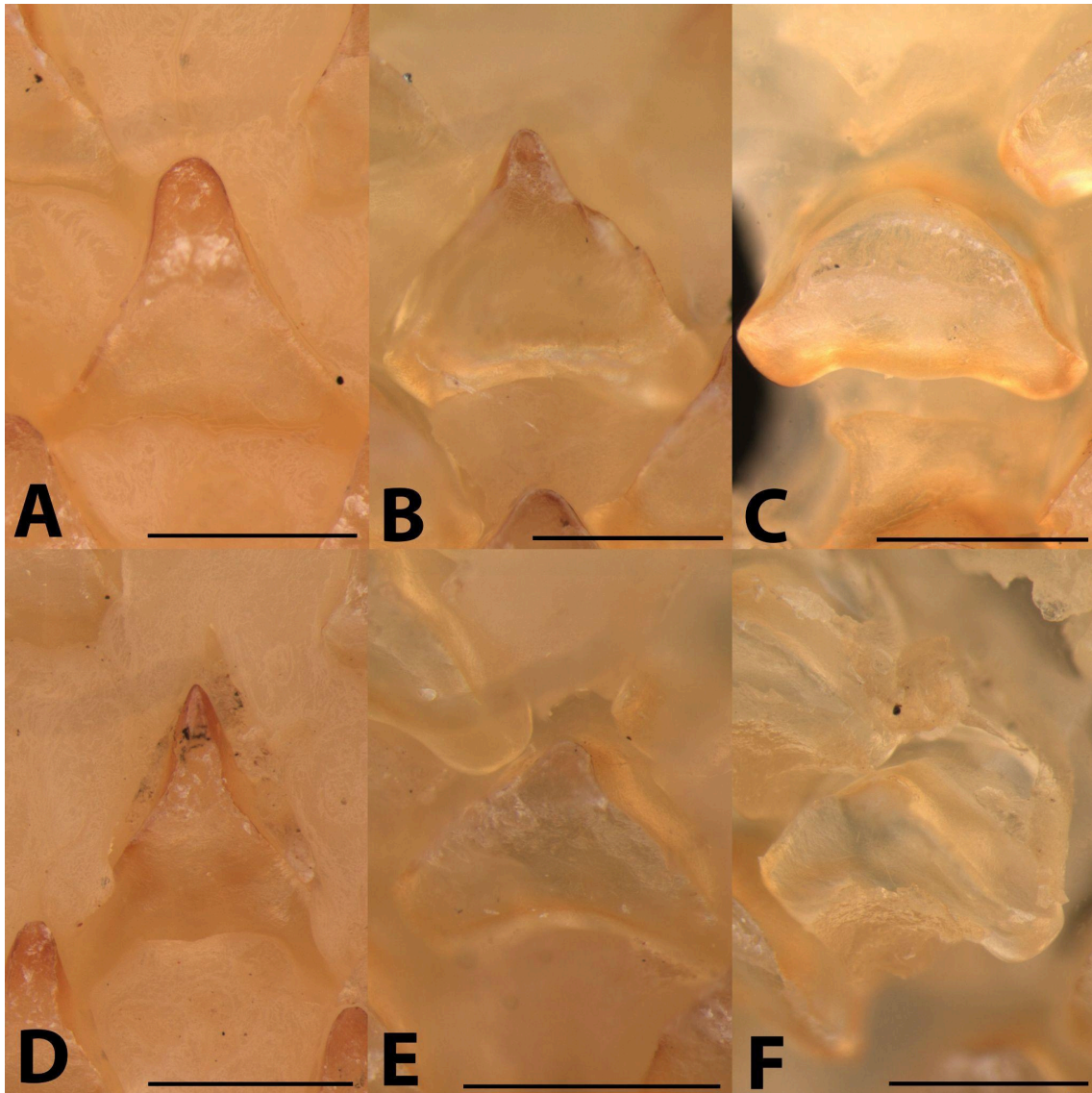


Figure 43. Occlusal view of teeth in a male of *Potamotrygon humerosa*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

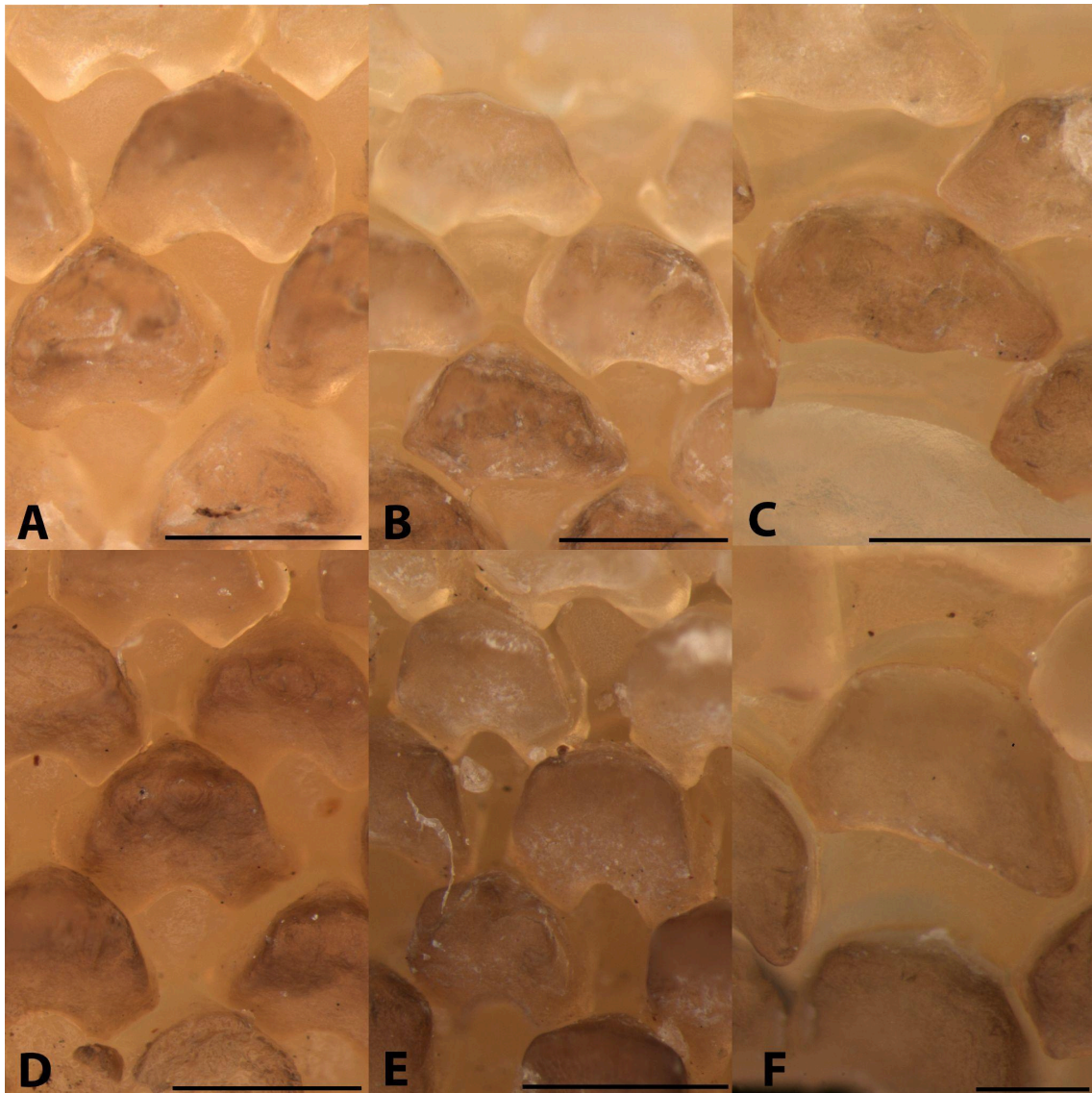


Figure 44. Occlusal view of teeth in a female of *Potamotrygon humerosa*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

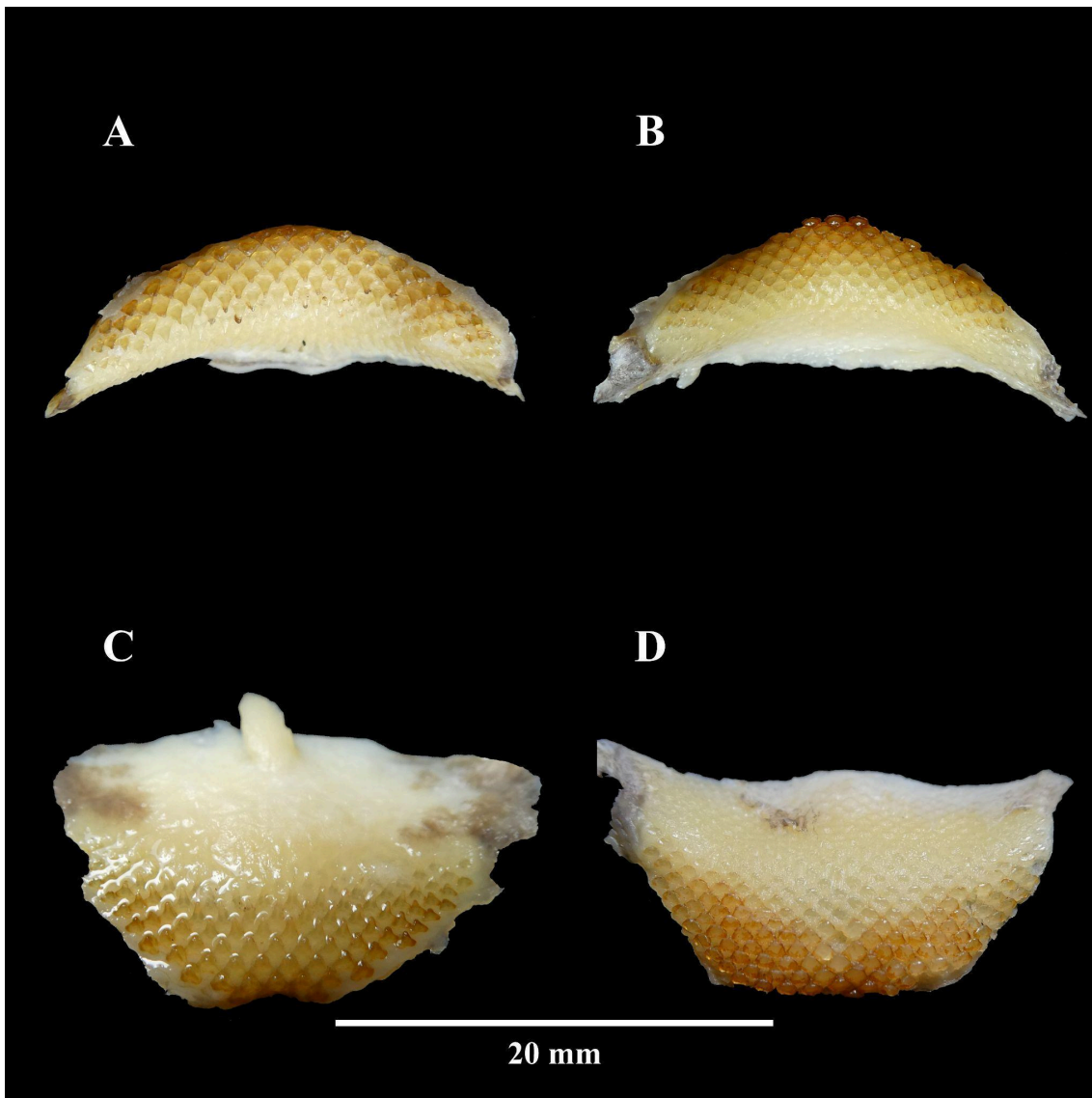


Figure 45. Occlusal view of the upper and lower plates of *Potamotrygon amandae* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

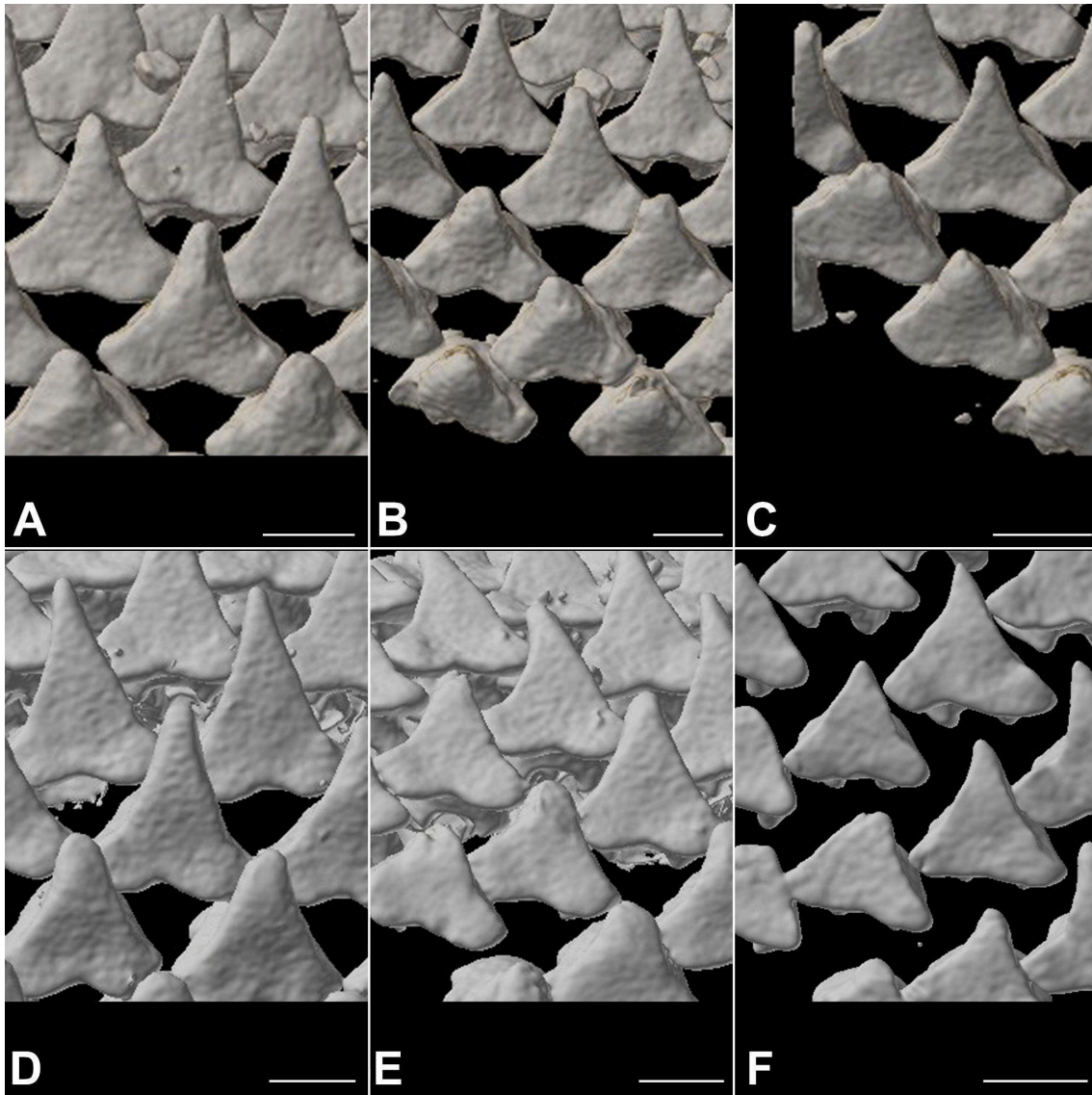


Figure 46. Occlusal view of teeth in a male of *Potamotrygon amandae*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

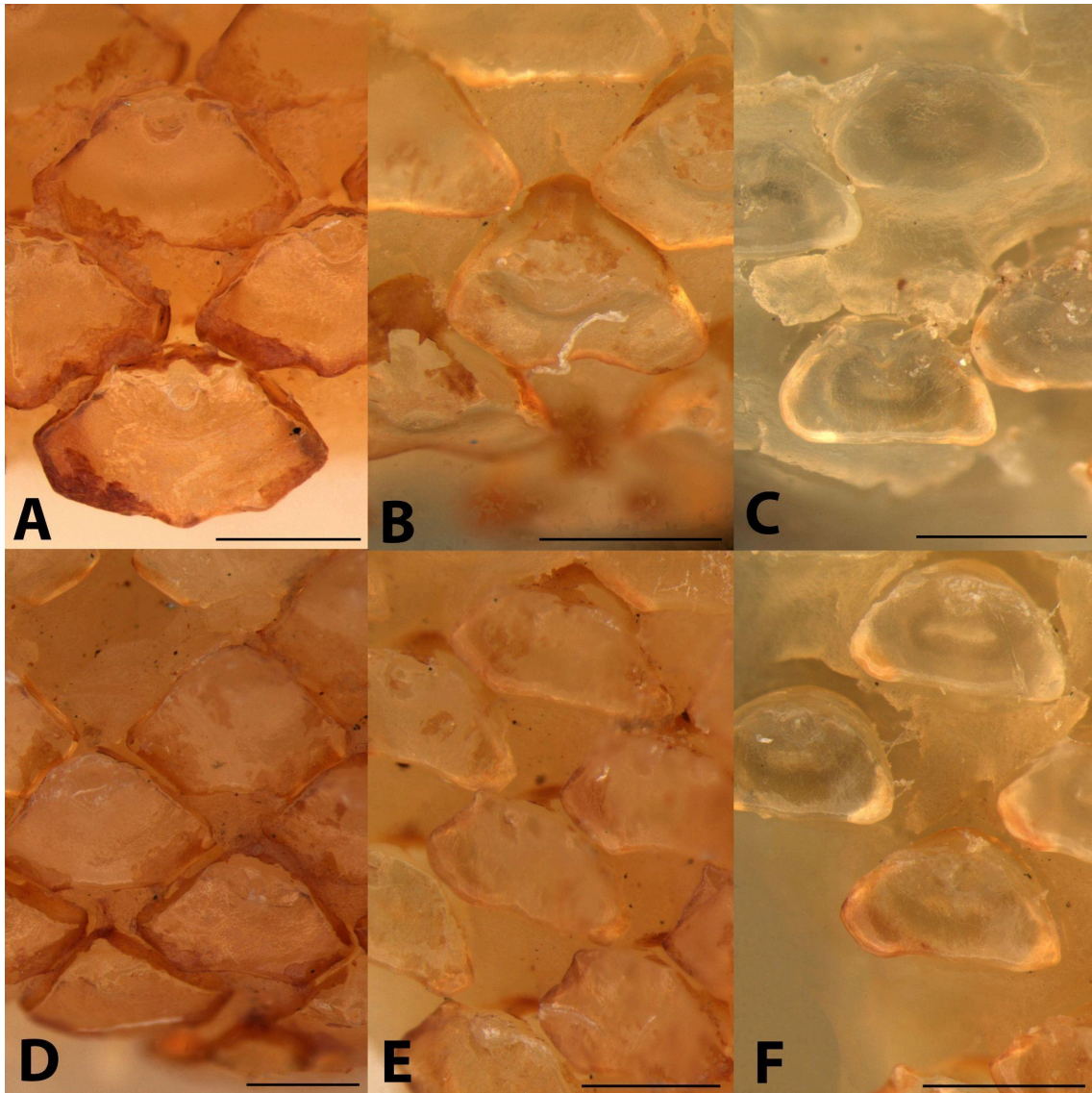


Figure 47. Occlusal view of teeth in a female of *Potamotrygon amandae*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

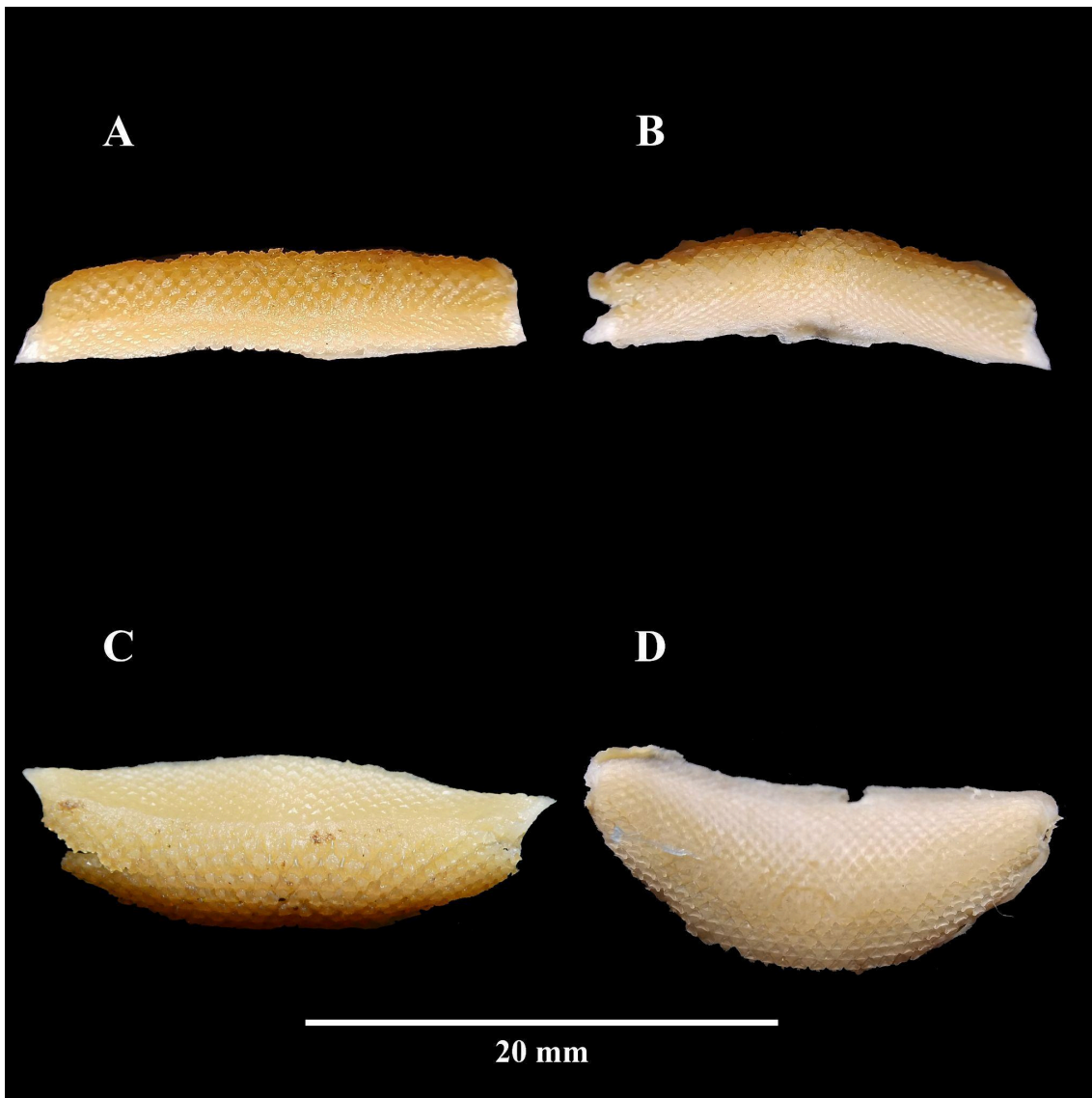


Figure 48. Occlusal view of the upper and lower plates of *Potamotrygon wallacei* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

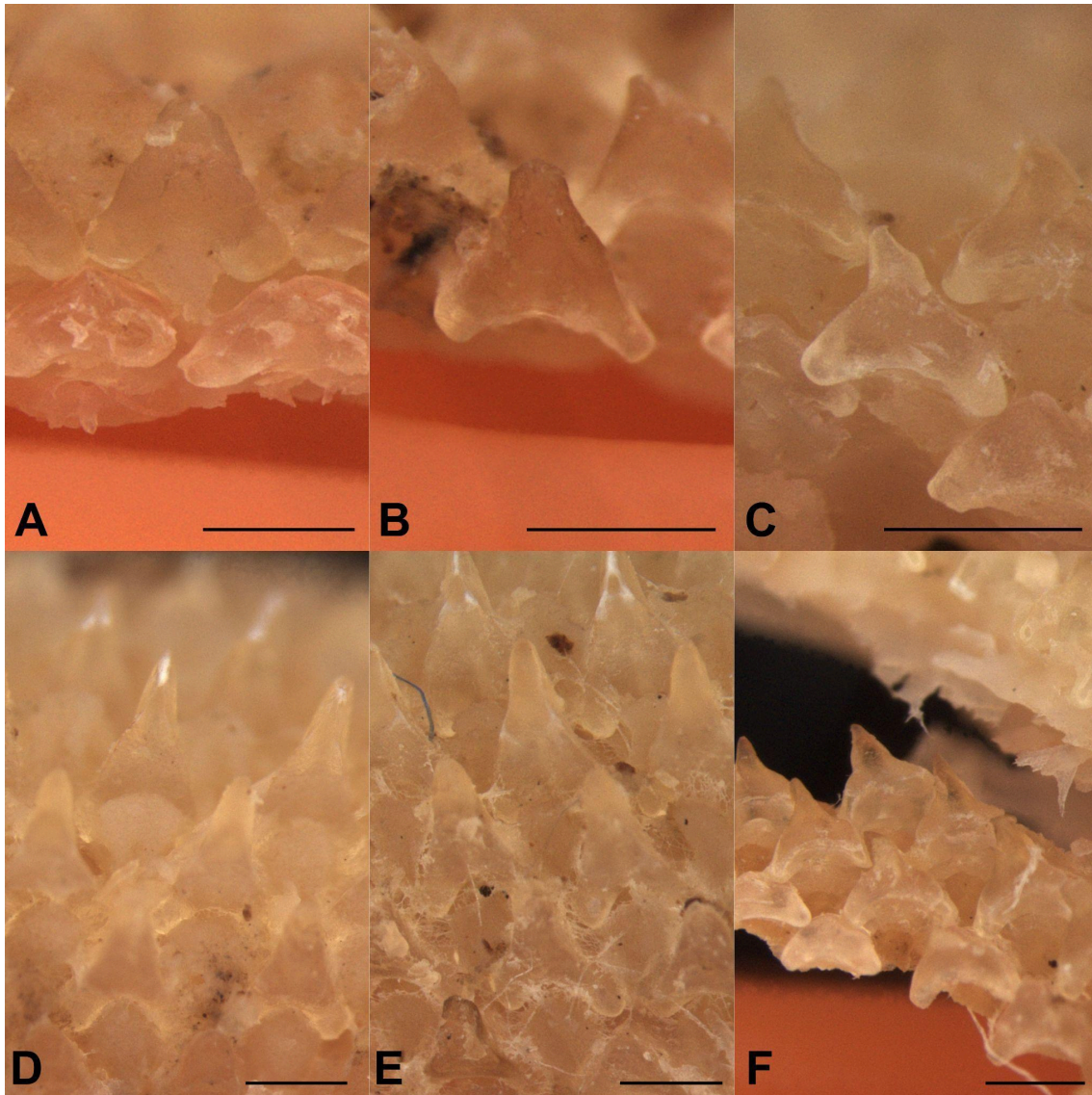


Figure 49. Occlusal view of teeth in a male of *Potamotrygon wallacei*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

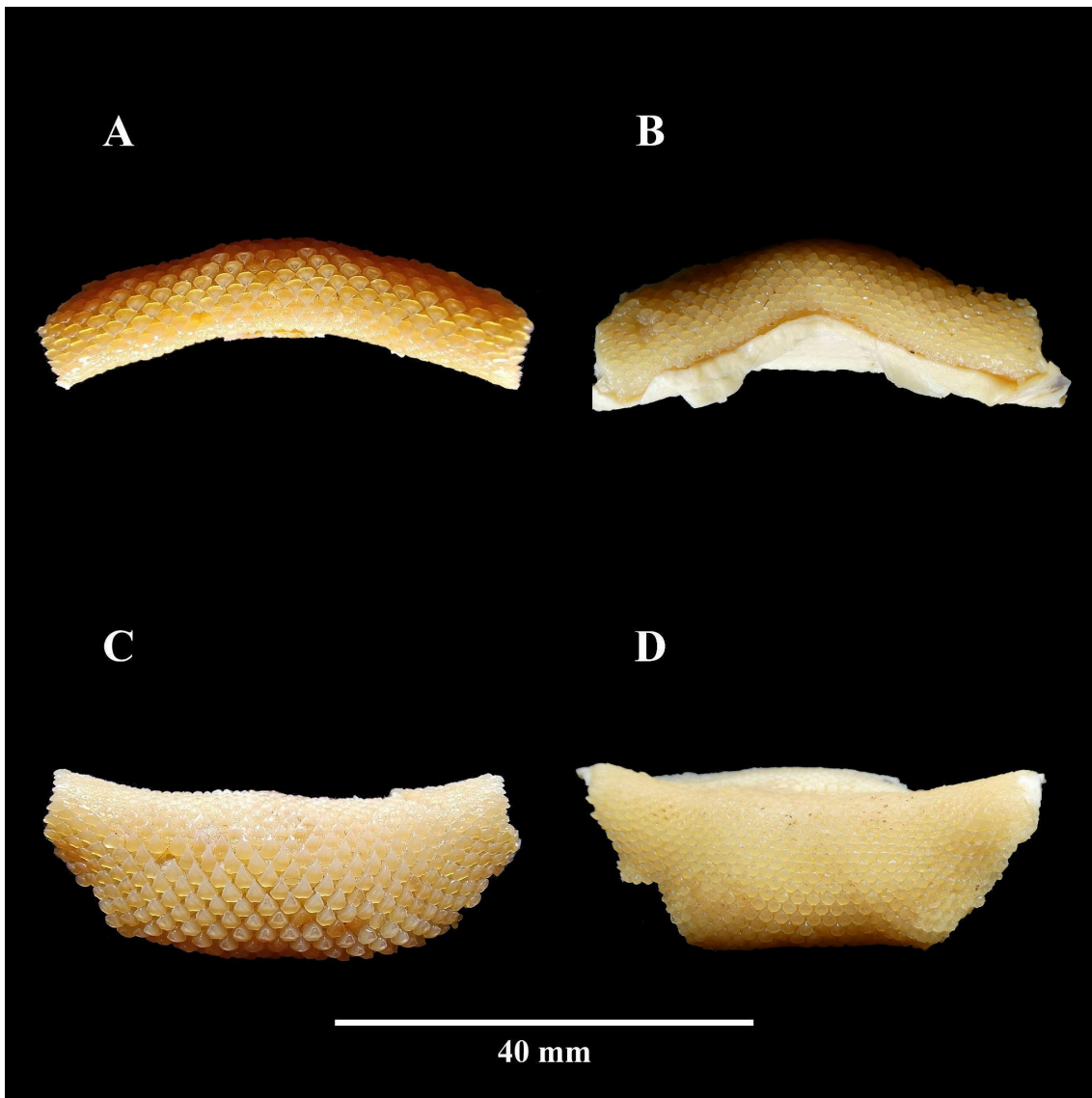


Figure 50. Occlusal view of the upper and lower plates of *Potamotrygon limai* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

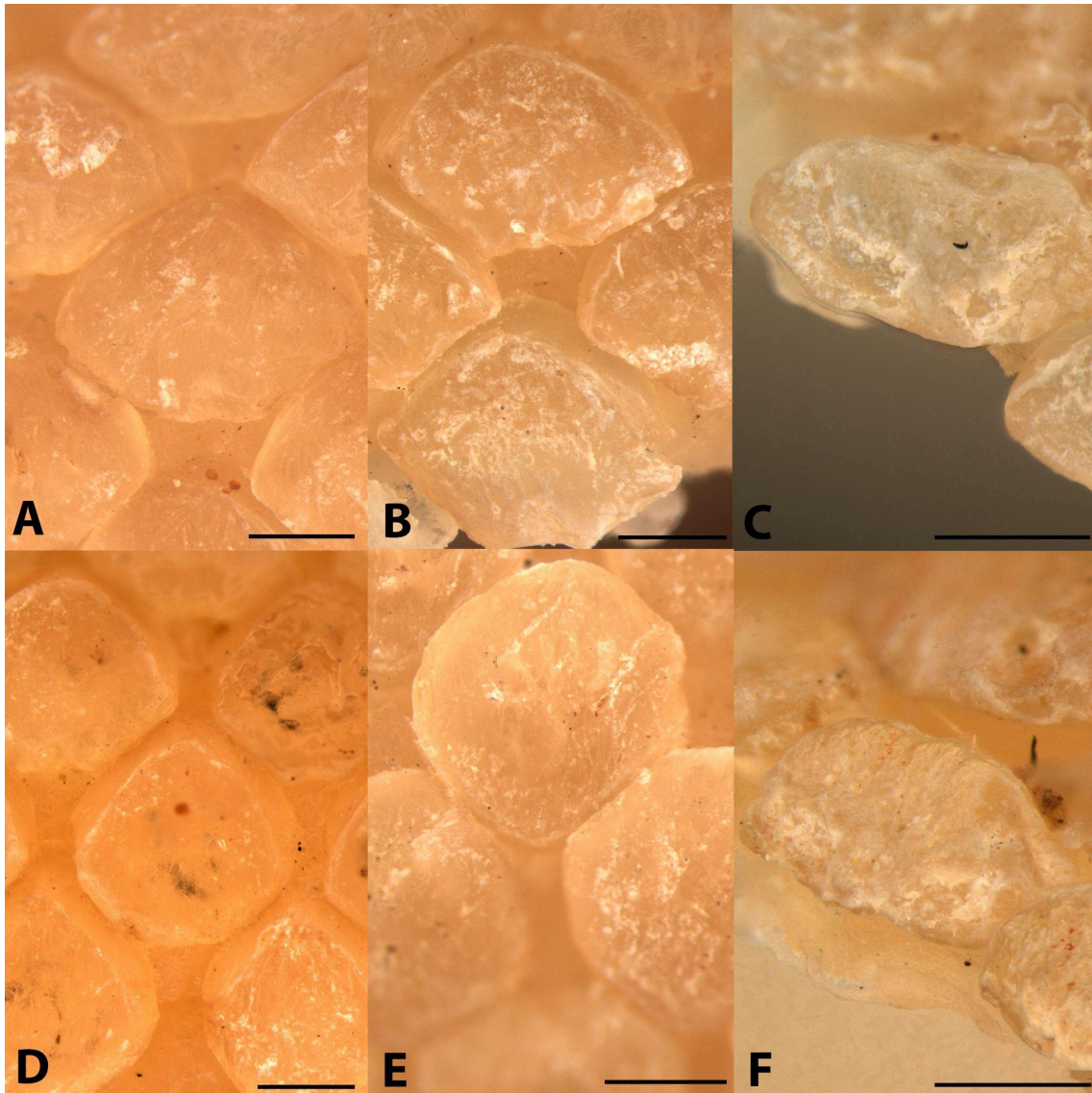


Figure 51. Occlusal view of teeth in a female of *Potamotrygon limai*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

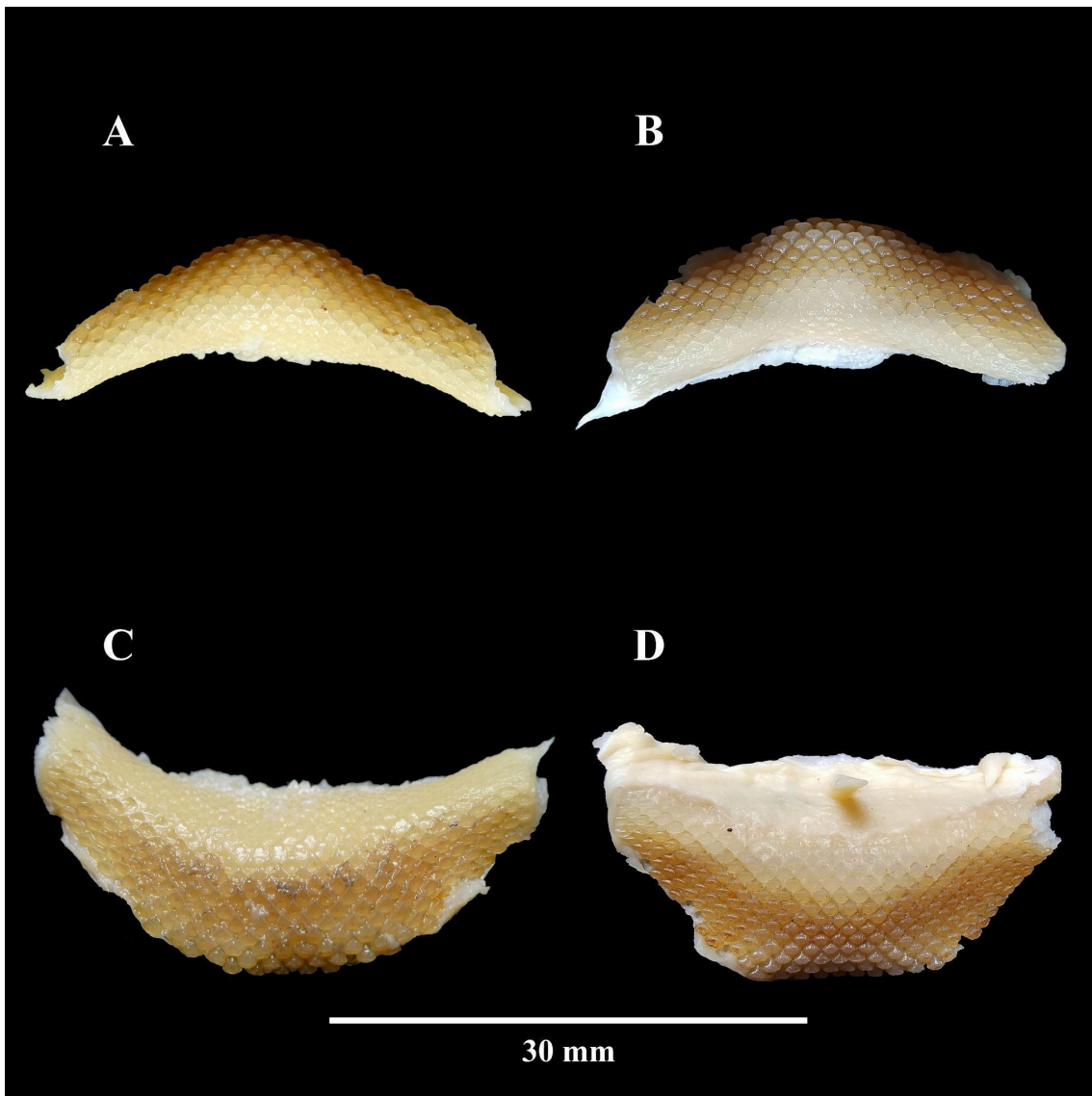


Figure 52. Occlusal view of the upper and lower plates of *Potamotrygon scobina* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

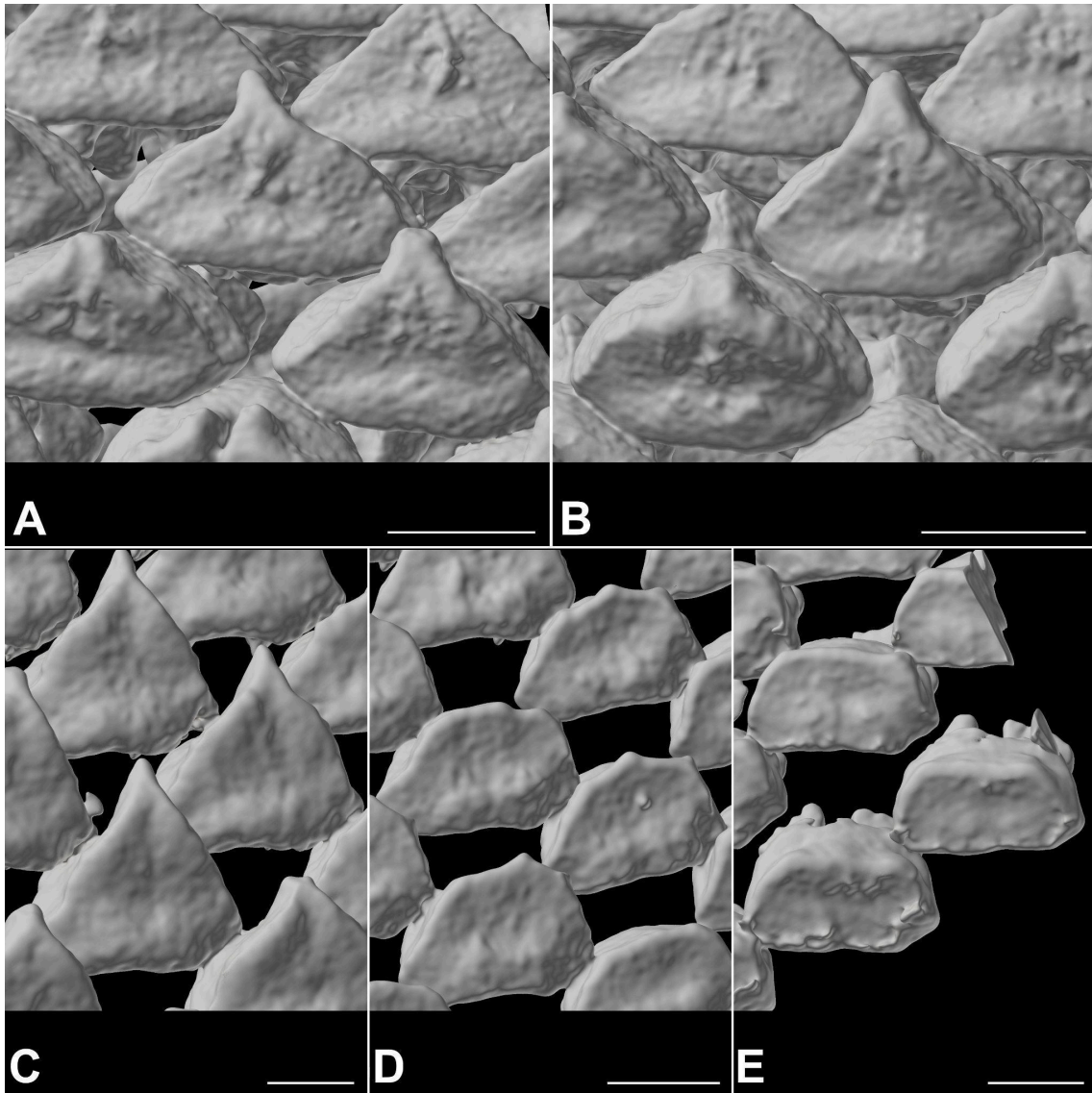


Figure 53. Occlusal view of teeth in a male of *Potamotrygon scobina*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Lower teeth near symphysis (position 1). D - Lower intermediate teeth (position 2). E - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

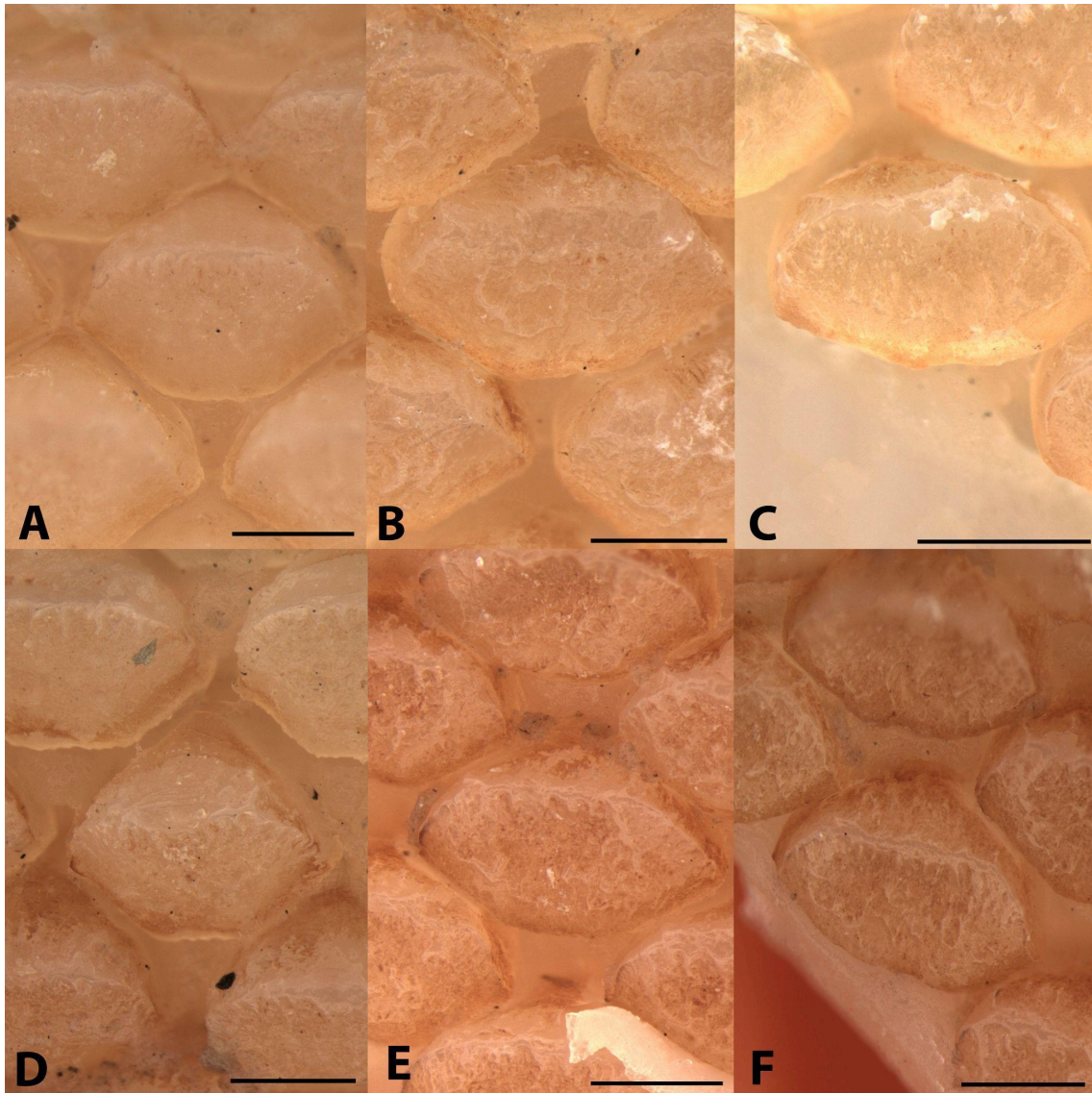


Figure 54. Occlusal view of teeth in a female of *Potamotrygon scobina*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

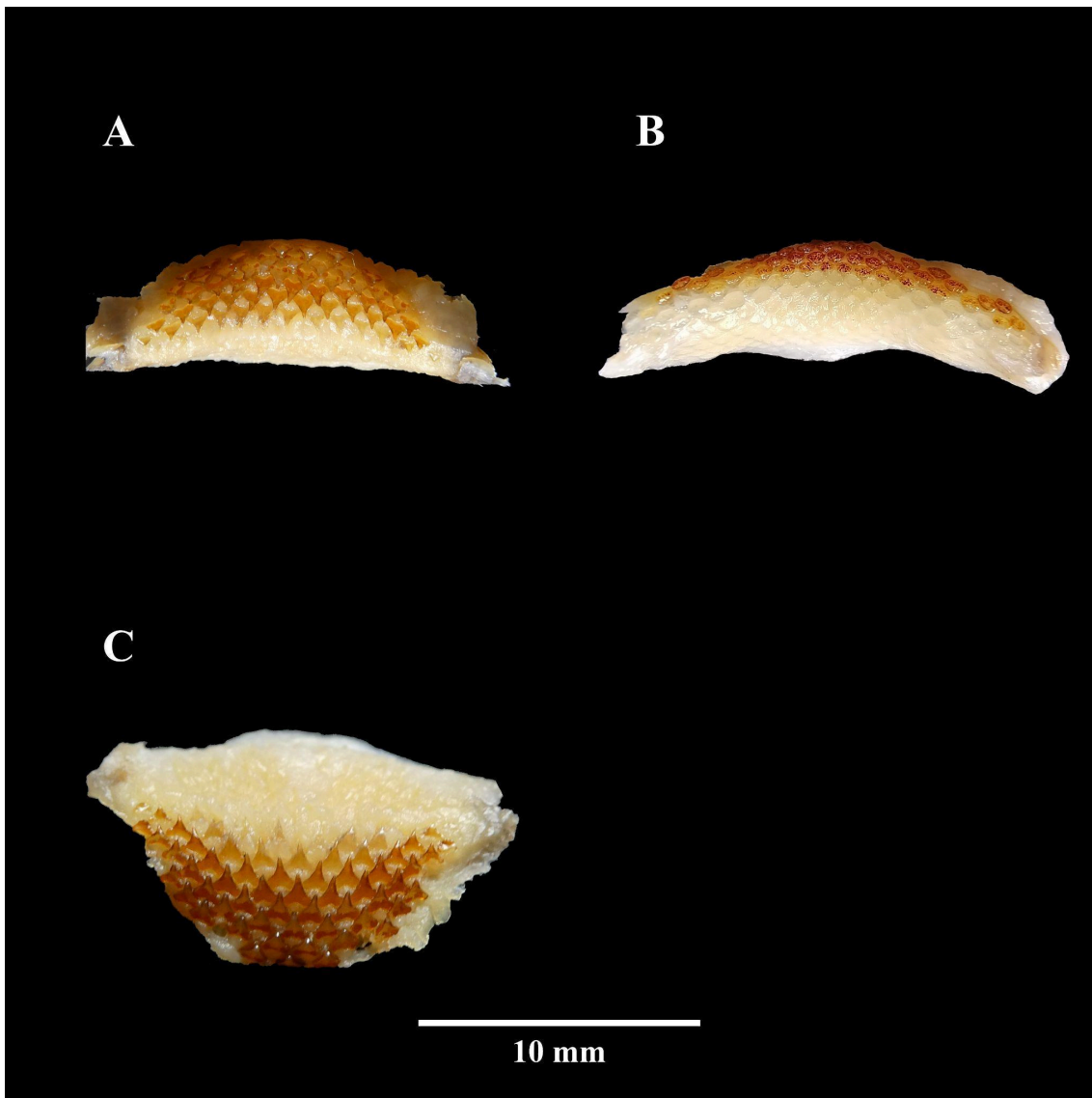


Figure 55. Occlusal view of the upper and lower plates of *Potamotrygon hystrix* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. In A and B labial to top; In C labial to bottom.

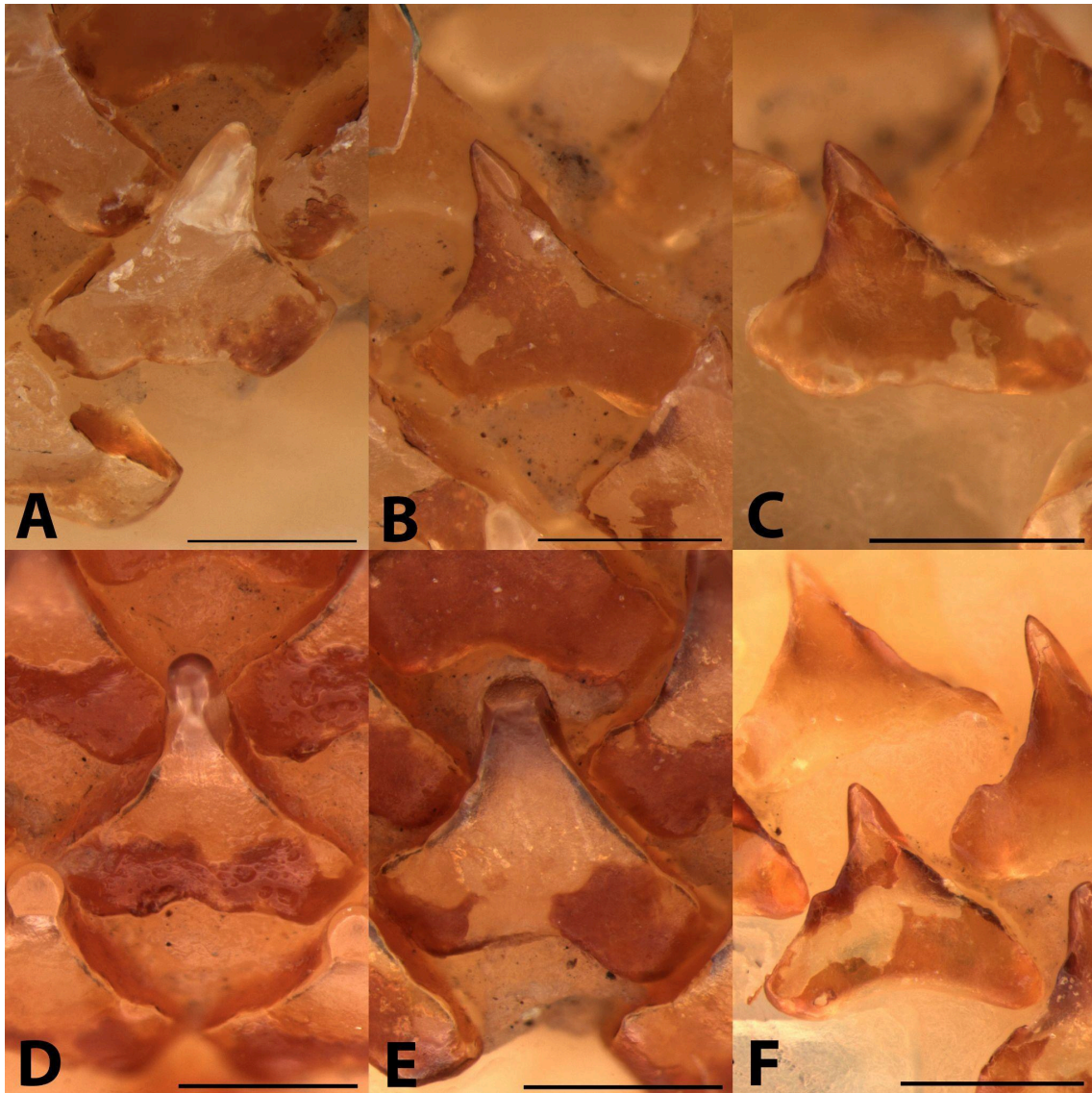


Figure 56. Occlusal view of teeth in a male of *Potamotrygon hystrix*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

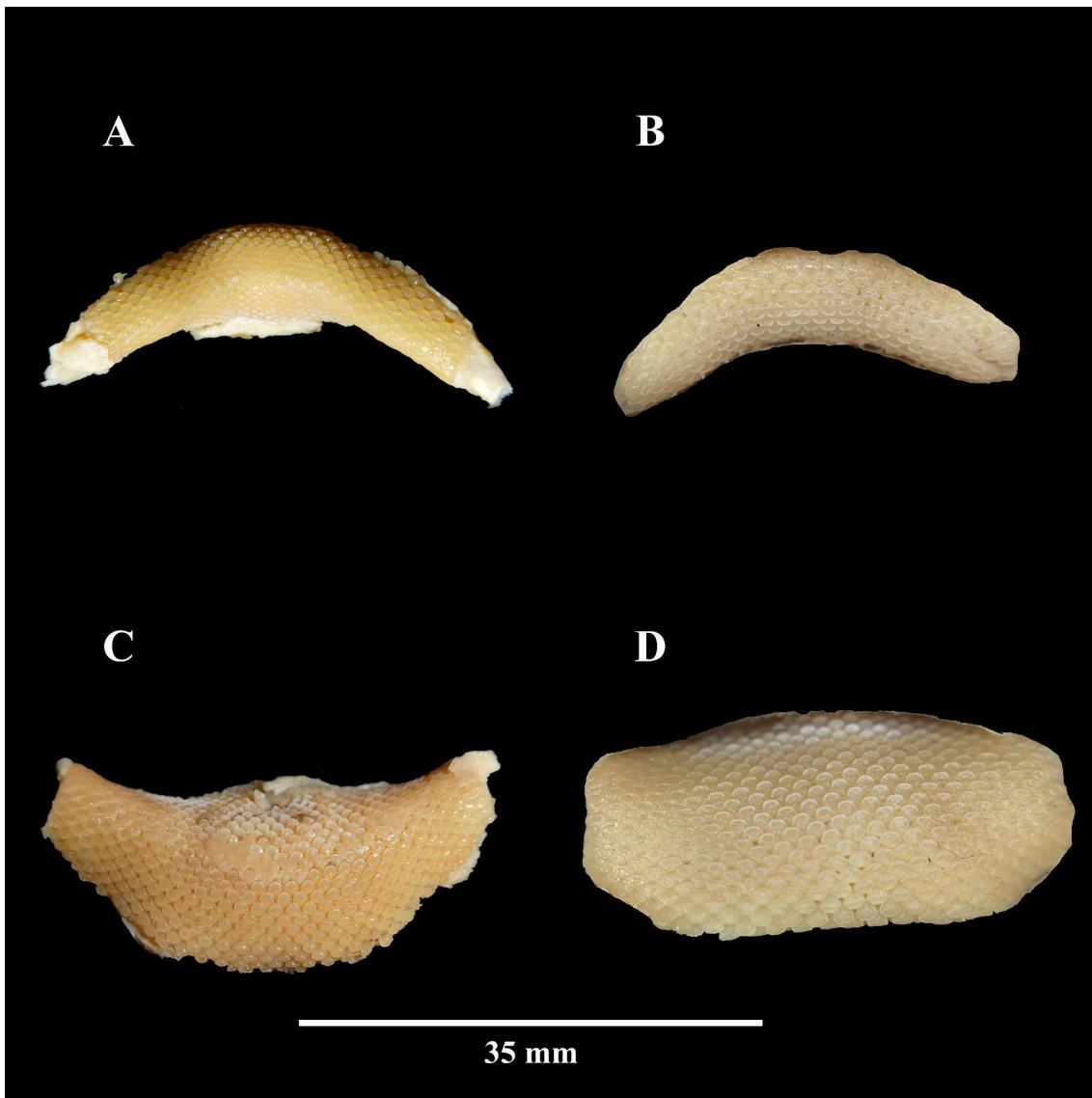


Figure 57. Occlusal view of the upper and lower plates of *Potamotrygon falkneri* plates. A – Upper male plate. B – Lower male plate. C – Upper female plate. D – Lower female plate. In A and B labial to top; In C and D labial to bottom.

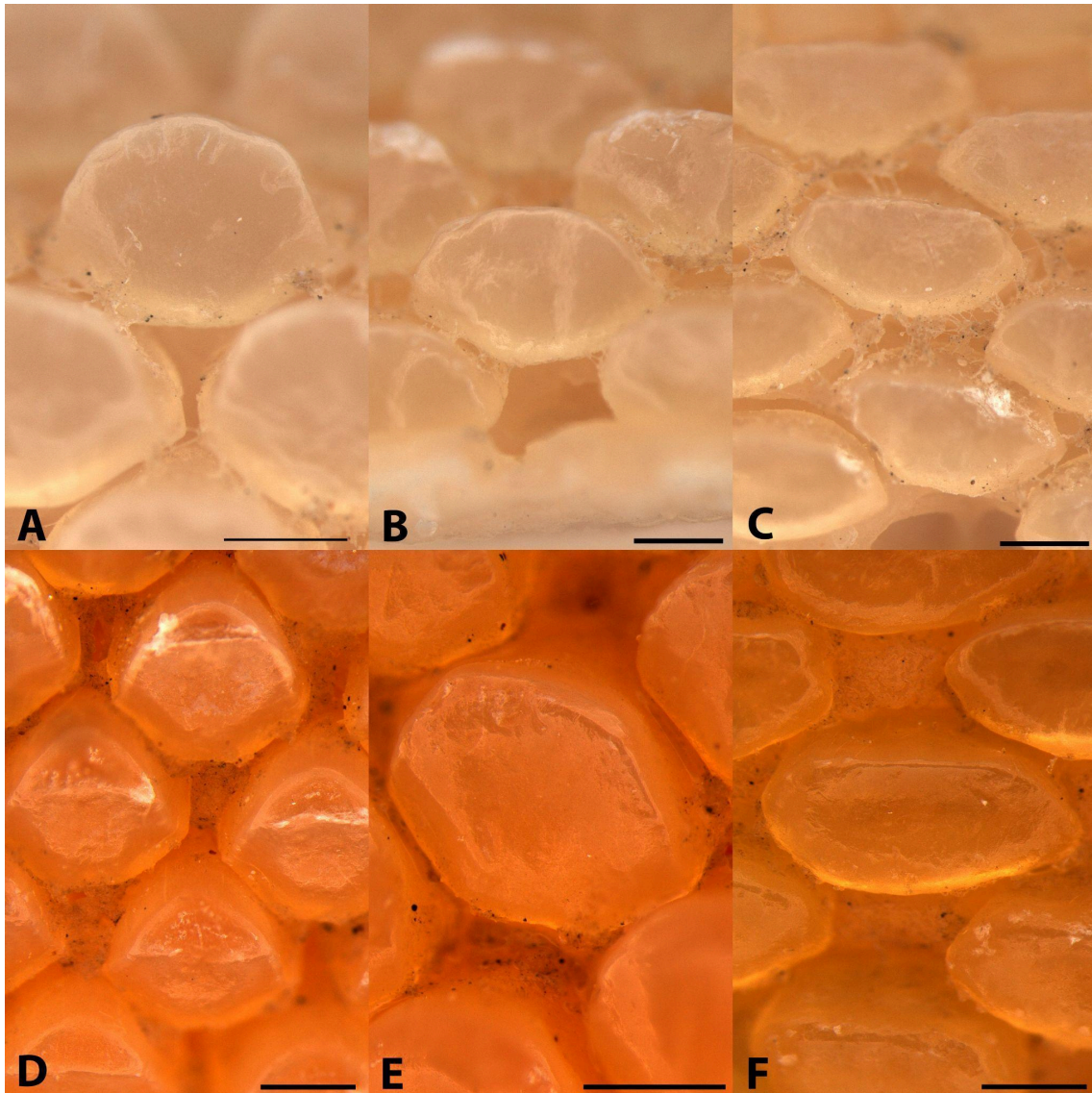


Figure 58. Occlusal view of teeth in a male of *Potamotrygon falkneri*. A - Upper teeth near symphysis (position 1). B - Upper intermediate teeth (position 2). C - Upper lateral teeth (position 3). D - Lower teeth near symphysis (position 1). E - Lower intermediate teeth (position 2). F - Lower lateral teeth (position 3). In A-F labial to bottom. Scale bar = 0.5 mm.

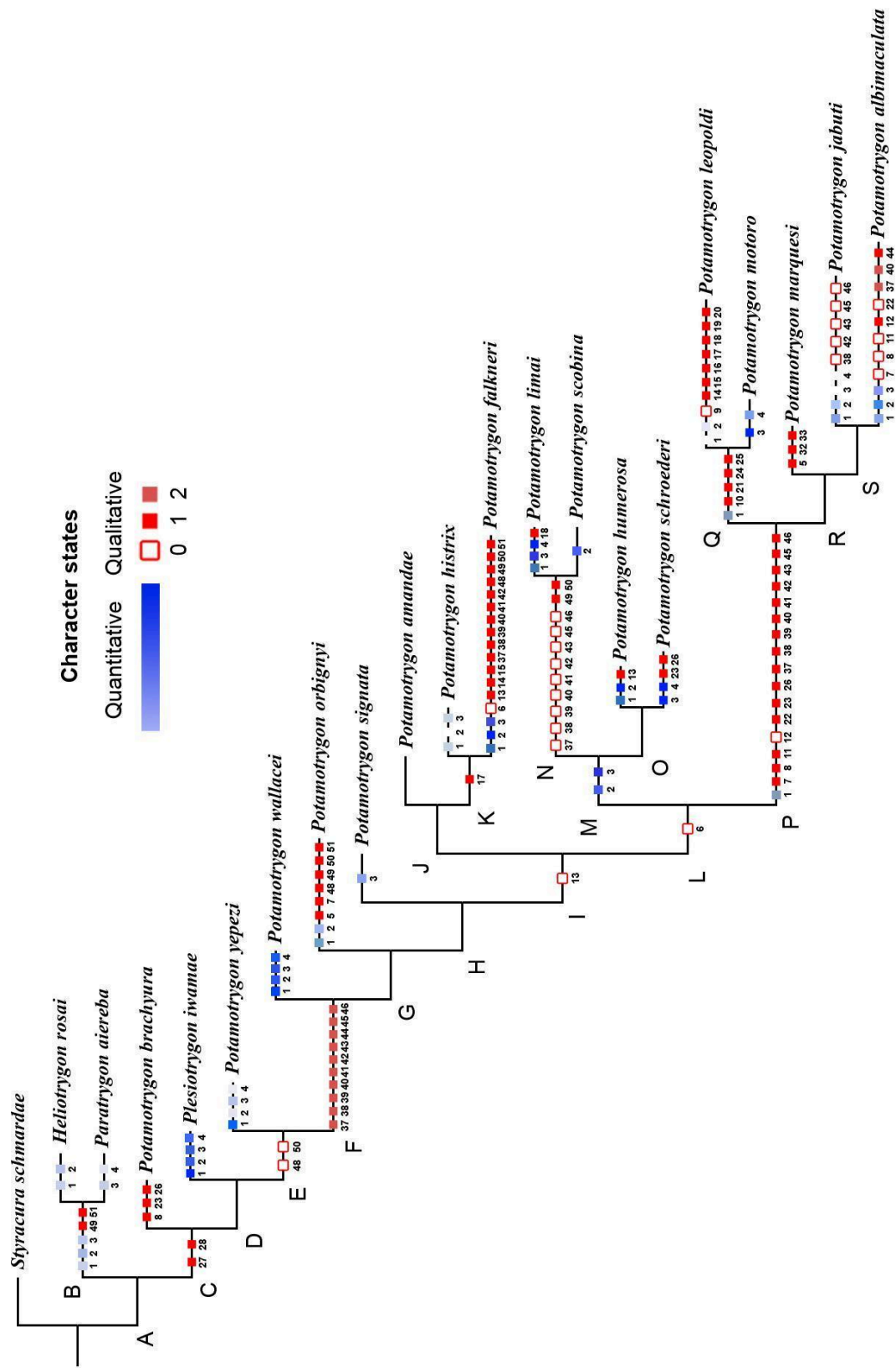


Figure 59. Most parsimonious cladogram of relationships of potamotrygonids based on the combined data set analyzed under POS and $k = 4.61909$ ($L = 1799,862$; $Fit = 157,82434$).

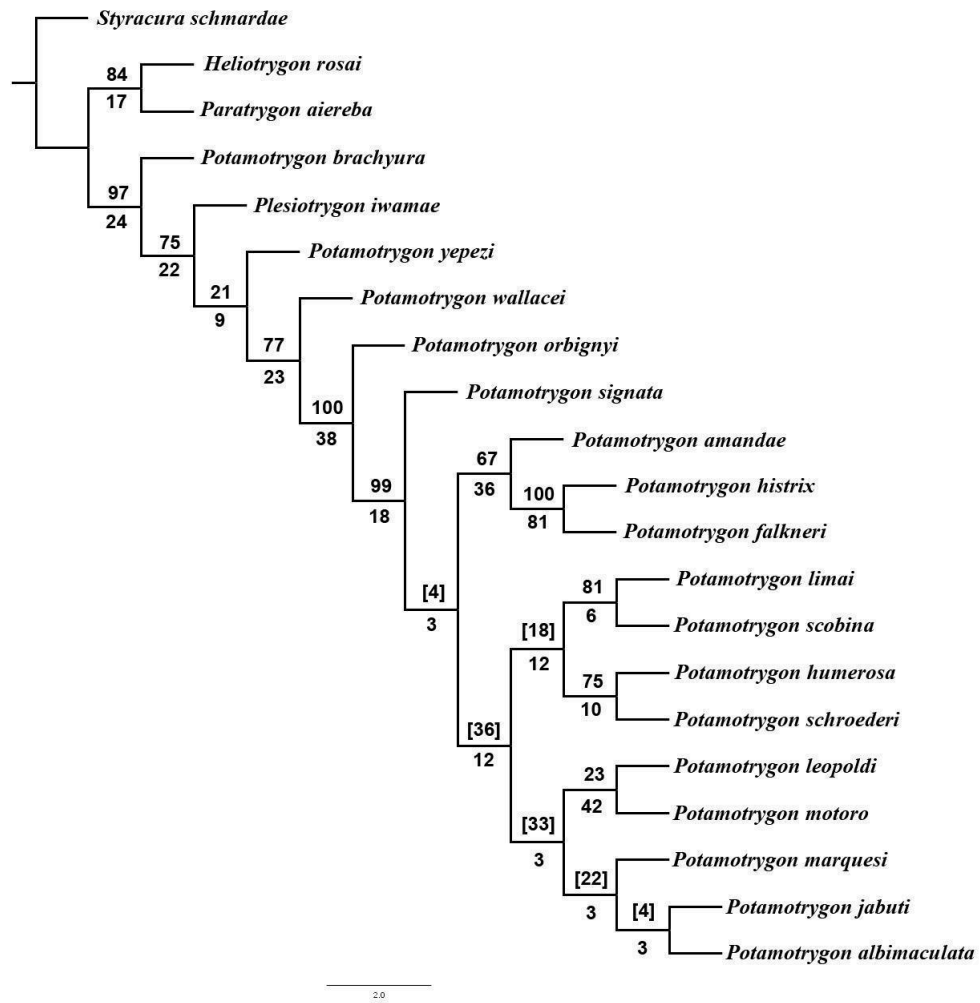


Figure 60. GC and relative bremer support (RBS) of each clade. Values over each branch correspond to GC support. Values under each branch correspond to Relative Bremer supports.

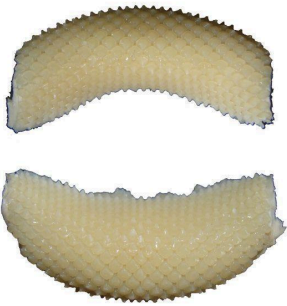
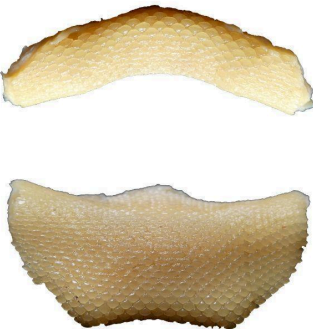
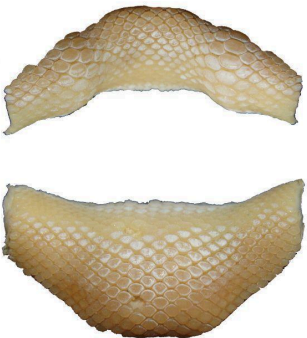
Clutching type	<i>Heliotrygon rosai</i> <i>Paratrygon aiereba</i>	
Crushing type	<i>Styracura schmardae</i> , <i>Plesiotrygon iwamae</i> , <i>Potamotrygon hystrix</i> , <i>P. brachyura</i> , <i>P. humerosa</i> , <i>P. albimaculata</i> , <i>P. amandae</i> , <i>P. limai</i> , <i>P. falkneri</i> , <i>P. scobina</i> , <i>P. orbignyi</i> , <i>P. wallacei</i> , <i>P. yepezi</i> , <i>P. schroederi</i> , <i>P. signata</i>	
Crushing-grinding type	<i>Potamotrygon jabuti</i> <i>P. motoro</i> <i>P. leopoldi</i> <i>P. marquesi</i>	

Figure 61. Adaptive dental types (Cappetta, 2012) and corresponding species of potamotrygonides.

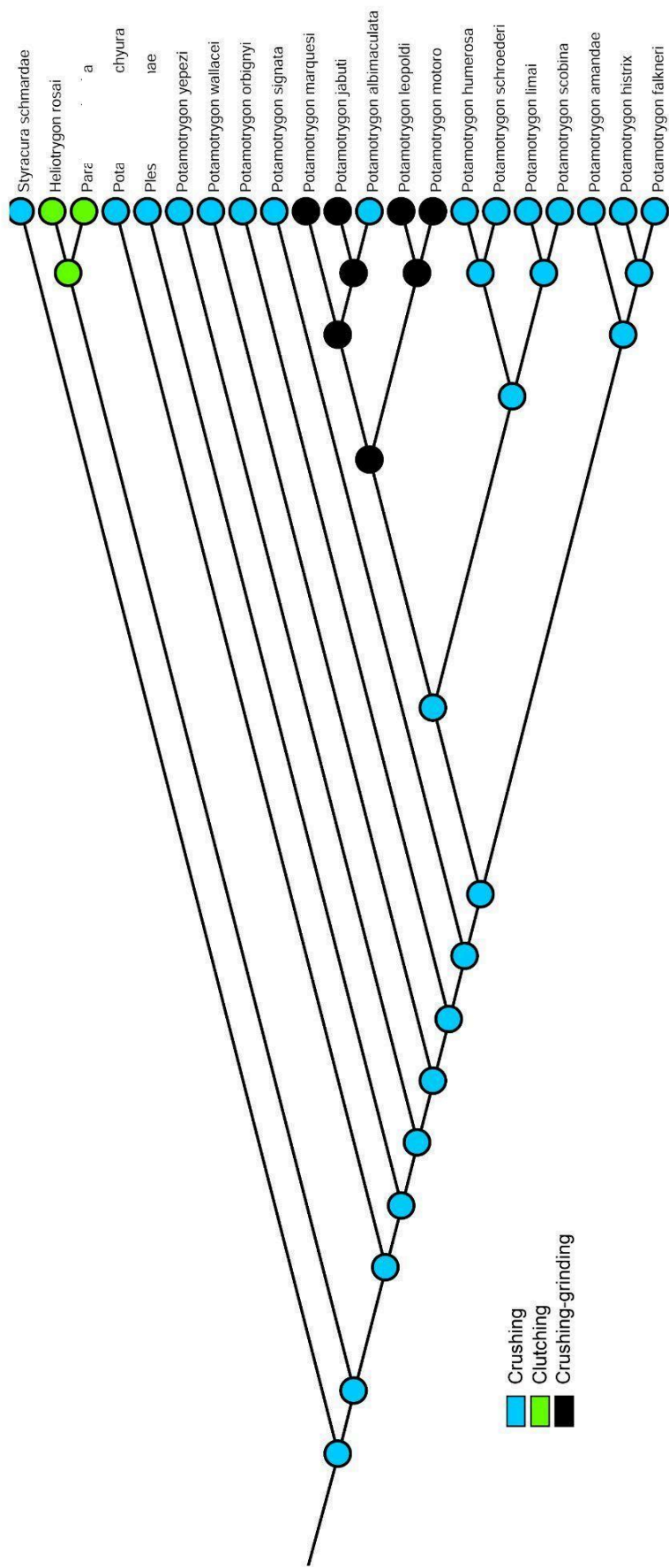


Figure 62. Evolution of adaptive dental types in Potamotrygonidae using maximum parsimony reconstruction and the unordered characters option in Mesquite

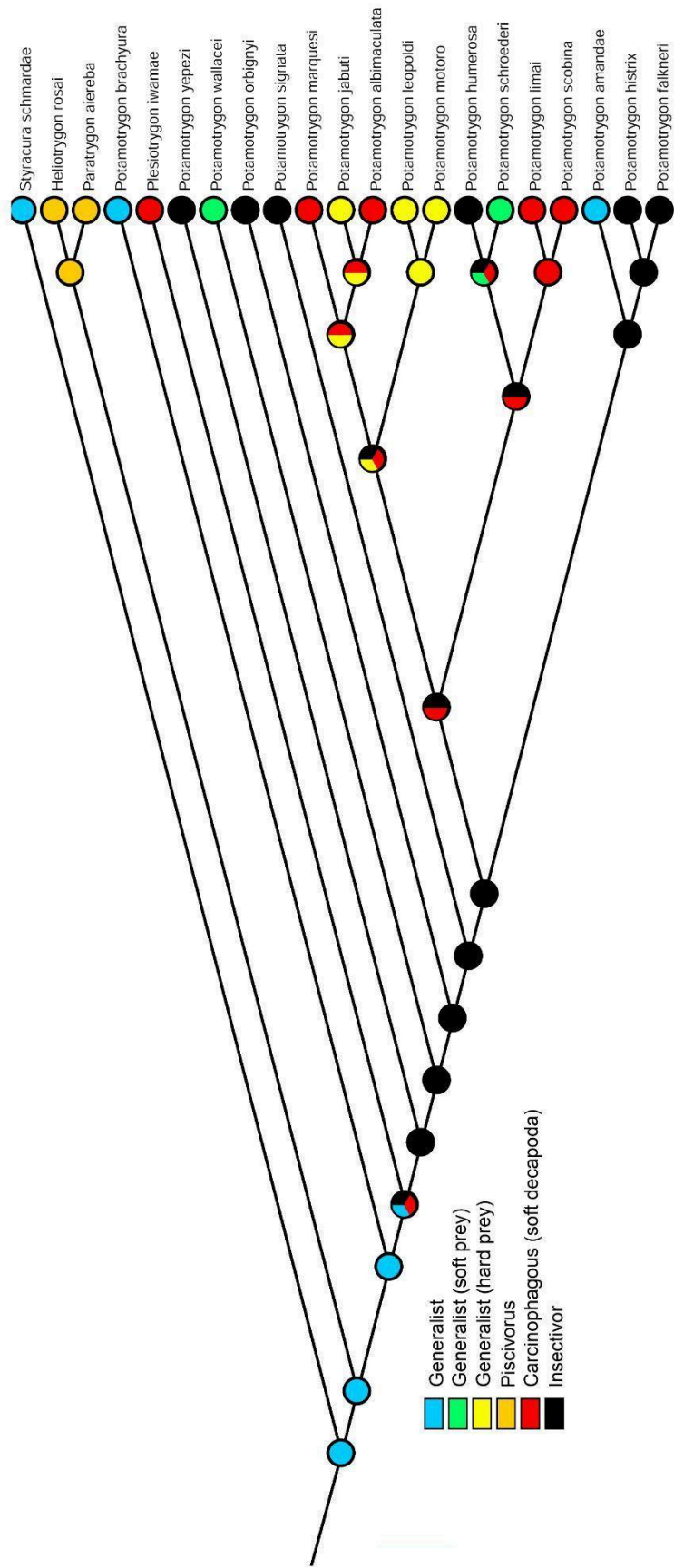


Figure 63. Evolution of feeding habits in Potamotrygonidae using maximum parsimony reconstruction and the unordered characters option in Mesquite.

ATTACHMENT

[File S1](#). TNT matrix with morphological and molecular characters used for phylogenetic tree construction (Figures 66 and 67);

[File S2](#). Distortion coefficient (DC);

[File S3](#). Subtree pruning and regrafting (SPR);

[File S4](#). Wincladtree of the resulting phylogenetic tree.