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PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL

INSTITUTO DE BIOCIÊNCIAS
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FILOGENIA DE ELAENIINAE (AVES: PASSERIFORMES: TYRANNIDAE)

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PORTO ALEGRE
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Tese apresentada ao Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como requisito parcial à obtenção do título de Doutor em Biologia Animal.

Área de concentração: Biologia Comparada

Orientador: Prof. Dr. Márcio Borges Martins

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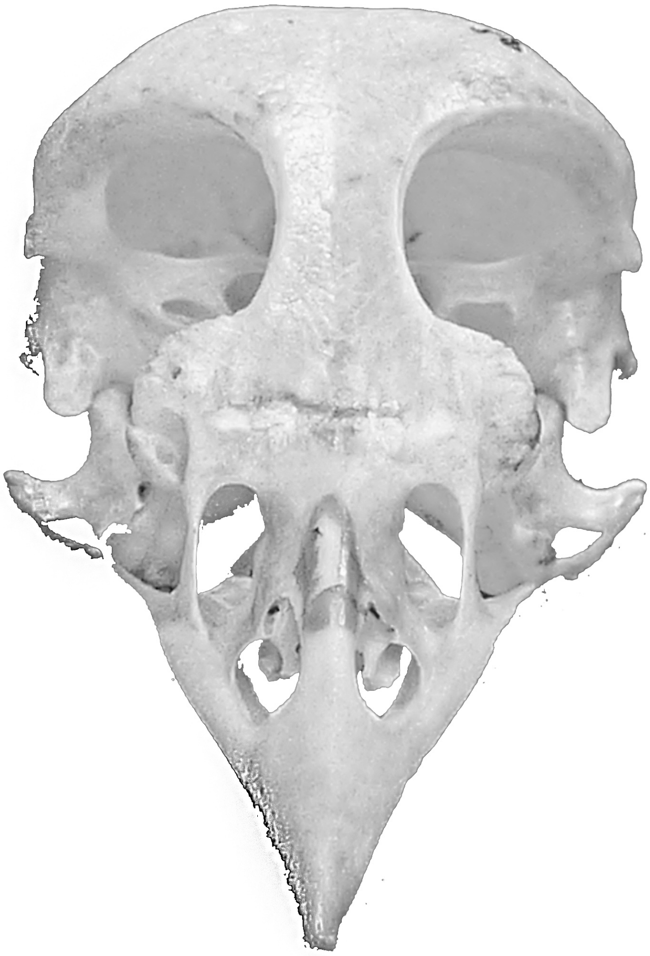

Elaenia dayi Chapman, 1929

guaracava-dos-tepuis

DEDICATÓRIA

Na última fase da minha formação que começou lá na infância e nunca deixou de ser estimulada, se é que isso tem um fim, não haveria como não dedicar esta tese, por completo, para Antonio e Ilani, meus pais e incentivadores.

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“Primero hay que saber sufrir,

Después amar, después partir

Y al fin andar sin pensamiento...”

(Virgilio Expósito)

SUMÁRIO

RESUMO

Comparada com outras notórias famílias de pássaros, Tyrannidae é menos conhecida em termos de relações internas, apesar de sua grande representatividade na avifauna americana (436 espécies). Elaeniinae compreende pequenos e inconspícuos pássaros que se alimentam de insetos em áreas abertas ou arbustivas, sendo uma das subfamílias mais diversas de aves (106 espécies). Membros do grupo estão entre as aves mais difíceis de se diferenciar morfologicamente. Neste estudo foi realizada uma análise filogenética, compreendendo 84 espécies no grupo interno e 28 no externo, a partir de uma nova matriz de caracteres osteológicos contendo 151 caracteres. Os poucos caracteres propostos na literatura foram discutidos e reavaliados. A árvore de consenso estrito, produzida por meio de "novas tecnologias" no software TNT, apresentou boa resolução. A subfamília foi recuperada como monofilética, diferente das suas duas tribos, não recuperadas. *Suiriri* foi identificado como táxon mais basal por compartilhar estados de caracteres com o grupo externo, que foi parcialmente resolvido. Todos os gêneros foram recuperados como monofiléticos, exceto: *Mecocerculus*, que apresenta ao menos dois grupos bem suportados, necessitando a descrição de um gênero novo; *Serpophaga* é polifilético, sendo necessária a ressurreição de *Ridgwayornis* para duas espécies (*R. nigricans* e *R. cinerea*); *Phyllomyias* é polifilético e pode apresentar diversos agrupamentos, necessitando mais terminais na análise. A topologia recuperada concorda em grande parte com as filogenias moleculares existentes, mas vai além e esclarece algumas relações até então desconhecidas. Essa similaridade entre as hipóteses é maior do que a do presente estudo com a pesquisa pioneira de Lanyon (1988), cujos problemas metodológicos são expostos. Este estudo demonstra inequivocamente a existência de sinal filogenético e utilidade das evidências fenotípicas nas reconstruções cladísticas.

ABSTRACT

Compared with other notorious passerine families, Tyrannidae is less known in terms of internal relationships, despite their remarkable representation in bird diversity across the Americas (436 species). Elaeniinae comprises small and inconspicuous passerines that feed on insects in open and woodland habitats, being one of the most speciose avian subfamilies (106 species). Members of the subfamily are among the world's most difficult bird species to distinguish morphologically. A phylogenetic analysis of the group was conducted, comprising 84 species in the ingroup and 28 in the outgroup, from a new matrix of osteological characters containing 151 characters. The few characters proposed in the literature were discussed and re-evaluated. The strict consensus tree, produced by means of "new technology search" in TNT software, exhibited good resolution. The subfamily was recovered as monophyletic, unlike its two unrecovered tribes. *Suiriri* was identified as the most basal taxon by sharing character states with the outgroup, which was partially resolved. All genera were recovered as monophyletic, except: *Mecocerculus*, which presents at least two well-supported groups, necessitating the description of a new genus; *Serpophaga* is polyphyletic, being necessary the resurrection of *Ridgwayornis* for two species (*R. nigricans* and *R. cinerea*); *Phyllomyias* is polyphyletic and may present several clusters, requiring more terminals in the analysis. The recovered topology greatly agrees with the existing molecular phylogenies, but goes beyond and clarifies some previously unknown relations. This similarity between the hypotheses is greater than the present one with the pioneering research of Lanyon (1988), whose methodological problems are exposed. This study unequivocally demonstrates the existence of the phylogenetic signal and the usefulness of the phenotypic evidences in cladistic reconstructions.

APRESENTAÇÃO

A presente tese de doutorado está estruturada na forma de um artigo científico, que foi idealizado e formatado visando à submissão para o periódico inglês *Zoological Journal of the Linnean Society*, que tem tradição em publicar estudos sobre anatomia comparada e sistemática filogenética, permitindo manuscritos extensos e que são de certo modo evitados em outros veículos de divulgação. As Normas aos Autores podem ser encontradas no Anexo 1. O artigo, que compõe o coração desta tese, está precedido de uma introdução geral, que não somente introduz a especificidade do tema explorado no artigo e do problema investigado, mas proporciona um breve panorama dos estudos de morfologia comparada em ornitologia, com ênfase nos Passeriformes. Algumas figuras e textos adicionais podem ter sido utilizados para ilustrar melhor a tese e não necessariamente comporão na íntegra o manuscrito à ser submetido. Por fim, uma seção de conclusões gerais sumariza os principais achados e exibe perspectivas. As referências a possíveis implicações taxonômicas advindas dos resultados diretos do estudo não têm, aqui, qualquer valor como ato nomenclatural.

INTRODUÇÃO GERAL

"Despite appearances, morphological characterization of birds for phylogenetic reconstruction still remains in its infancy."

(Livezey e Zusi 2006)

Do ponto de vista taxonômico (descobrimento, descrição e identificação de espécies), as aves são tidas como o grupo zoológico melhor conhecido (Gonzaga 2001). Em contraste, suas relações de parentesco internas, especialmente ao nível de família, subfamília e tribo, padecem de resoluções congruentes para grande parte dos grupos (Cracraft 1981). Nesse sentido, as décadas de 1990 e 2000 podem ser consideradas como um "divisor de águas", uma vez que um número expressivo de novas contribuições passaram a ser produzidas, especialmente por meio de filogenias moleculares (anteriormente, a sistemática de aves baseava-se em comparações fenéticas de elementos e sistemas anatômicos, geralmente entre poucos representantes dos grupos; Livezey e Zusi 2006). Esse cenário principiou com a clássica contribuição de Sibley e Ahlquist (1985) na forma de uma filogenia molecular da ordem Passeriformes (com ênfase nos "Suboscines do Novo Mundo"), surgindo como antítese para a classificação até então aceita de Wetmore (1960), essa praticamente inalterada desde Gadow (1893). À despeito de sua participação ínfima na classificação atual dos Passeriformes, é inegável que sua publicação (também Sibley *et al.* 1988, Sibley e Ahlquist 1990), juntamente com o advento de novas tecnologias para análises moleculares (*e.g.* PCR, década de 1980), alavancou sobremaneira essa nova fase da sistemática filogenética de aves (Ericson *et al.* 2003, Livezey e Zusi 2007, Vuilleumier 2003), ainda hoje em pleno desenvolvimento.

Tido como o grupo mais amplamente estudado e discutido em ornitologia e frequentemente utilizado como exemplo da evolução por seleção natural (Raikow 1977, Grant e Grant 1989), Passeriformes Linné, 1758 - os chamados pássaros - constitui a ordem mais rica entre as aves, compreendendo 6.456 espécies válidas (Gill e Donsker 2018), mais da metade de toda a diversidade global da classe. A causa de tamanho sucesso evolutivo foi alvo de calorosas discussões na década de 1980 (*e.g.* Raikow 1986, 1988, Fitzpatrick 1988, Kochmer e Wagner 1988, Vermeij 1988), tendo sido atribuída à capacidade do grupo em explorar de forma eficaz distintos nichos tróficos. Mas essa característica representa o efeito. A causa, na forma de novidades evolutivas responsáveis por proporcionar tal radiação adaptativa, os autores consideraram tão somente especulativa que tiveram de reconhecer as limitações de toda a explanação corrente. Para Raikow (1986), por exemplo, nenhuma das sinapomorfias dos Passeriformes possui significância histórica suficiente para ser considerada como novidade evolutiva, como a chave para sua elevada diversidade. Para Olson (2001), esse sucesso se deve não a adaptações morfológicas, mas sim comportamentais, relacionadas com sua habilidade de proteger ovos e filhotes. O monofiletismo dos Passeriformes é suportado por pelo menos seis caracteres fenotípicos, a saber: palato aegithognato (vômer largo e distalmente truncado, maxilopalatinos não se encontrando medialmente, mas encontrando a margem do basiesfenóide); músculo *tensor propatagialis brevis* ligado ao úmero; espermatozóide empacotado com cabeça enrolada e acrossoma grande; hálux aumentado; tendões plantares profundos do tipo VII; e divisão do músculo *pubo-ischio-femoralis* em superfícies caudal e cranial (Raikow 1982, 1986, Raikow e Bledsoe 2000). Passeriformes tem como grupo-irmão os Psittaciformes (Hackett *et al.* 2008, Suh *et al.* 2011, Wang *et al.* 2012; mas veja Pacheco *et al.* 2011). Posteriormente, a sua monofilia foi corroborada por meio de caracteres moleculares (*e.g.* Johansson *et al.* 2002). Igualmente importante tem sido a discussão, desde a década passada, sobre a sua origem biogeográfica, inicialmente defendida como sendo Gondwânica (Barker *et al.* 2002, Ericson *et al.* 2002; mas veja Edwards e Boles 2002) e posteriormente creditada à porção leste do hemisfério sul (Austrália/Nova Guiné, Nova Zelândia ou Antártica; Mayr 2013), tendo o grupo se originado antes do período Cretáceo-Terciário (Cracraft 2001, Ericson *et al.* 2002, Pacheco *et al.* 2011) e divergido aparentemente no Cenozóico (Brown e van Tuinen 2011, Mayr 2013).

Três grandes divisões dos pássaros, categorizadas como subordens, são reconhecidas: os Acanthisitti Sundevall, 1872, grupo relictual endêmico da Nova Zelândia; os Passeri Linné, 1758, por muito tempo chamados de Oscines; e os Tyranni Wetmore e Miller, 1926, tradicionalmente denominados Suboscines (Sibley e Ahlquist 1990, Sick 1997, Tello *et al.* 2009); reconhecidas sobretudo pela estrutura da siringe (Ames 1971). Fenotipicamente, a monofilia dos Tyranni é suportada, entre outros, pela ocorrência de columela com uma base em forma de bulbo (Feduccia 1974, 1975). Já as relações internas de Tyranni têm sido assunto de importantes discussões em taxonomia (Cracraft 1981, Ericson *et al.* 2003). Sumariamente, com base na musculatura da siringe, pode-se dividí-los em dois grupos: os Tracheophonae (hoje, infraordem Furnariides; novo nome proposto por Moyle *et al.* [2009]), com um sistema muscular mais elaborado; e os Haplophonae (hoje, infraordem Tyrannides Wetmore e Miller, 1926, os “Suboscines do Novo Mundo”), de musculatura siringeal simples (Müller 1878, Tello *et al.* 2009). Os suboscines do Velho Mundo têm sido denominados Eurylaimides (Moyle *et al.* 2009, Tello *et al.* 2009). Níveis hierárquicos menos inclusivos dentro de Tyrannides apresentam grandes incongruências mesmo comparando-se as classificações resultantes apenas das filogenias moleculares (*e.g.*

Sibley e Ahlquist 1985, 1990, Ericson *et al.* 2003, Tello *et al.* 2009, Ohlson *et al.* 2013). Tais discordâncias revelam a necessidade de mais estudos de filogenia mesmo nas categorias mais inclusivas de Passeriformes.

Entre os Passeriformes Tyranni, a família Tyrannidae Vigors, 1825 destaca-se por sua elevada diversidade, congregando 436 espécies (Gill e Donsker 2018) de pássaros conhecidos como "tyrant-flycatchers", uma referência ao hábito de capturar insetos em voo (Fitzpatrick 1980, 1985). Anteriormente à Fitzpatrick *et al.* (2004), eram reconhecidas quatro subfamílias: Tyranninae, Tityrinae, Fluvicolinae e Elaeniinae. Com as filogenias moleculares subsequentes, os Tityrinae foram elevados ao nível de família e incorporados aos Cotingoidea (Tello *et al.* 2009). Ainda criou-se a família Onychorhynchidae (Tello *et al.* 2009) e também as subfamílias Hirundineinae (Ohlson *et al.* 2008, Tello *et al.* 2009) e Muscigrallinae (Ohlson *et al.* 2013). O agrupamento *Platyrinchus* + *Calyptura* + *Neopipo* anteriormente alocado em Tyrannidae foi incluído em Platyrinchidae (Ohlson *et al.* 2013), entre outras mudanças menos expressivas. Os gêneros *Piprites* (compreendendo duas espécies) e *Tachuris* (monotípico), mantidos como *incertae sedis* no início da década (CBRO 2011), foram incluídos em famílias próprias: Pipritidae e Tachurisidae (Ohlson *et al.* 2013, Franz 2015). Entretanto, a maior mudança na composição da família Tyrannidae se deu a partir da filogenia molecular de Tello *et al.* (2009), que ranquearam ao nível de família Rhynchocyclidae, a fim de incorporar os clados bem suportados de Pipromorphinae, Rhynchocyclinae, Todirostrinae e o grupo *Cnipodectes*. Uma vez que esse novo táxon inclui gêneros ricos em espécies (*e.g.* *Phylloscartes*, *Todirostrum*, *Hemitriccus*), Tyrannidae foi reduzida pela metade em número de espécies.

Conhecidos popularmente como piolhinhos, bico-chatos, guaracavas e afins, os Elaeniinae são caracterizados por pequenos pássaros geralmente esverdeados ou amarelados, com duas barras claras nas asas, bicos curtos (Figura 1) e reconhecidamente inconspícuos, de difícil determinação visual, como é o caso do rico e uniforme gênero *Elaenia* (Fitzpatrick *et al.* 2004, Straube 2013). A maior parte das espécies habita o sub-bosque e a parte baixa da vegetação em ambientes semi-florestais e florestais, onde forrageiam na folhagem densa a fim de capturar insetos ou coletar frutos, geralmente em voo, tática na qual são especialistas (Fitzpatrick 1980, 1985). Grupo exclusivamente Neotropical (salvo por *Camptostoma imberbe* que ocorre até o sul dos Estados Unidos), com formas exclusivamente andinas e de terras baixas, seus representantes distribuem-se até a Terra do Fogo, no extremo sul da América do Sul, com a maior diversidade nos trópicos. Duas espécies são endêmicas insulares: *Nesotriccus ridgwayi*, da ilha Cocos, 480 Km ao sul da Costa Rica, no Pacífico; e *Elaenia ridleyana*, uma das duas espécies de pássaros que colonizaram o arquipélago de Fernando de Noronha, no Atlântico (Ridgely e Tudor 1994, Sick 1997, Fitzpatrick *et al.* 2004). Cento e seis espécies são consideradas válidas conforme Gill e Donsker (2018), já incluindo os taxa recentemente descritos e desmembramentos em *Zimmerius* e *Elaenia*. Não obstante a subfamília Elaeniinae, objeto da presente tese, represente um dos clados de maior suporte e estabilidade taxonômica dentro de Tyrannidae, o histórico das suas relações filogenéticas internas demonstra incertezas e, sob alguns aspectos, é repleto de instabilidades. A explanação introdutória do artigo científico apresentado a seguir é uma tentativa de compilar de forma cronológica seus momentos mais importantes e apresentar o panorama geral de tal conhecimento, a classificação atual e os principais problemas.

Figura 1. Representantes da subfamília Elaeniinae. Da esquerda para a direita, de cima para baixo: *Elaenia cristata*, *Stigmatura napensis*, *Culicivora caudacuta*, *Pseudocolopteryx flaviventris*, *Serpophaga subcristata*, *Inezia caudata*, *Myiopagis gaimardii*, *Polystictus pectoralis*. Fotos: Ismael Franz.

A classificação de Elaeniinae adotada atualmente pelos comitês ornitológicos sul-americano (SACC 2018) e brasileiro (Piacentini *et al*. 2015) baseia-se nos resultados da filogenia molecular apresentada por Tello *et al*. (2009) e Ohlson *et al*. (2013), respectivamente. Nesta última (Figura 2), os autores reuniram os conjuntos de dados provenientes desse e de outros estudos moleculares (Ohlson *et al*. 2008, Irestedt *et al*. 2009) a fim de sintetizar os principais resultados em uma proposta de classificação para os grandes grupos de Passeriformes.

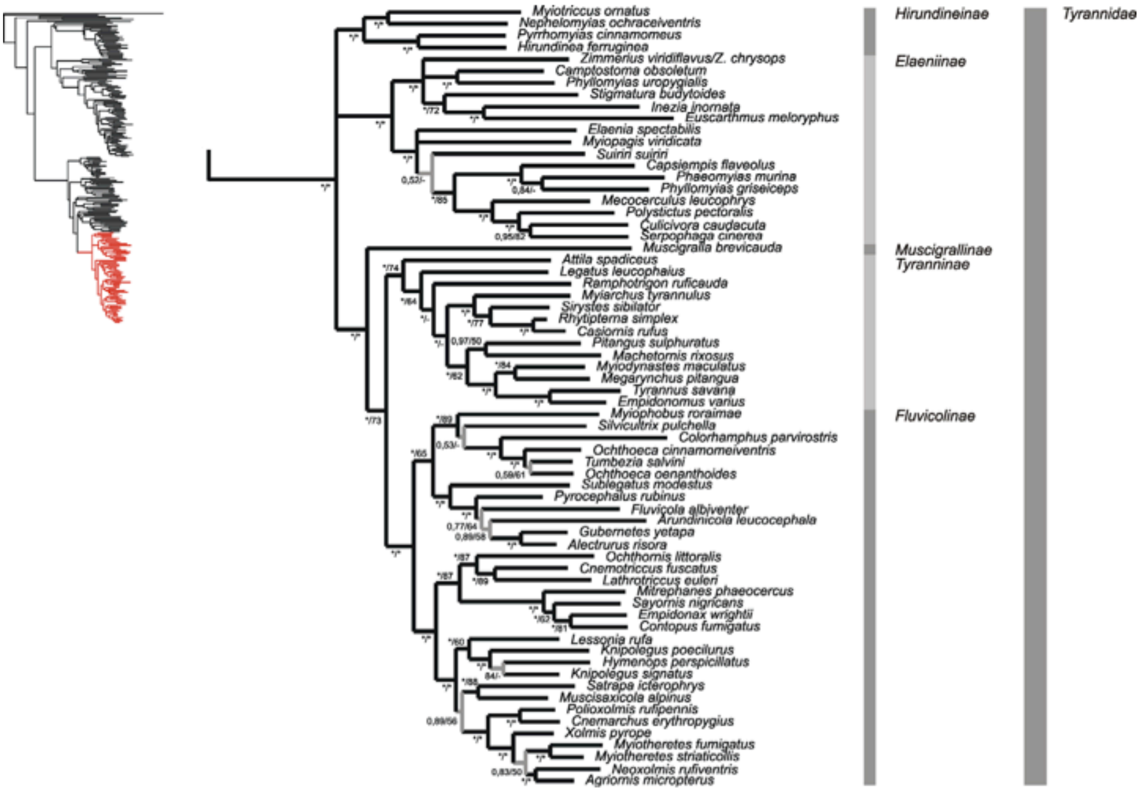

Figura 2. Posição filogenética de Tyrannidae entre os Passeriformes Tyranni (em vermelho, no detalhe) e relações internas da família, como aceito atualmente a partir das análises filogenéticas com base em caracteres moleculares de Ohlson *et al.* (2013).

A proposta de Ohlson *et al*. (2013) considera 25 gêneros ou agrupamentos genéricos ainda não nomeados na subfamília Elaeniinae, cuja riqueza seguindo a listagem de Gill e Donsker (2018) totalizaria 106 espécies (mas na referida filogenia foram incluídos somente 16 terminais pertencentes ao grupo), divididos em duas tribos, como segue:

Tribo Euscarthmini (von Ihering, 1904)

Zimmerius (11 espécies), *Stigmatura* (duas espécies), *Inezia* (quatro espécies), *Euscarthmus* (duas espécies), *Ornithion* (três espécies), *Camptostoma* (duas espécies), *Tyranniscus* (duas espécies), *Acrochordopus* (nove espécies), *Xanthomyias* (pelo menos três espécies) e grupo *Mecocerculus poecilocercus* (agrupamento genérico não nomeado, cinco espécies).

Tribo Elaeniini (Cabanis e Heine, 1860)

Elaenia (18 espécies), *Tyrannulus* (monotípico), *Myiopagis* (sete espécies), *Suiriri* (duas espécies), *Capsiempis* (monotípico), *Phyllomyias* (três espécies), *Phaeomyias* (duas espécies), *Nesotriccus* (provisório, monotípico), *Pseudelaenia* (monotípico), *Mecocerculus* (monotípico), *Anairetes* (oito espécies), *Polystictus* (duas espécies), *Culicivora* (monotípico), *Pseudocolopteryx* (cinco espécies) e *Serpophaga* (seis espécies).

Na literatura supracitada, o estudo pioneiro de Lanyon (1988) foi sempre mencionado como a referência única do conhecimento sobre a morfologia interna do grupo em questão e seu uso na inferência cladística. Aquele autor utilizou caracteres craniais, siringeais, alguns poucos reprodutivos e integumentários (n = 44 no total), codificados para representantes de todos os gêneros de Elaeniinae, à época. A subfamília foi diagnosticada com base unicamente na configuração do septo nasal, no qual está presente uma placa trabecular transversal que é ligeiramente elevada acima da margem ventral do septo, criando a aparência de uma crista sagital em vista ventral (Figura 3). O autor diagnosticou cinco grupos (que chamou "linhagens primárias"), a saber: grupo *Phylloscartes* (nove gêneros, 42 espécies), grupo *Stigmatura* (dois gêneros, sendo um descrito pelo autor [*Pseudelaenia*], três espécies), grupo *Euscarthmus*, grupo *Pseudotriccus* (dois gêneros, cinco espécies) e grupo *Elaenia* (18 gêneros, 65 espécies). Embora se reconheça o pioneirismo no que concerne o conhecimento gerado sobre a anatomia dos tiranídeos em uma série de trabalhos de Lanyon, os métodos analíticos adotados nos estudos devem ser observados quando se considera aquela uma verdadeira análise cladística a fim de se comparar com outros estudos filogenéticos. Lanyon (1988) analisou separadamente cada grupo e apresentou fenogramas individuais para estes “clados” recuperados, listando seus caracteres “sinapomórficos”. Se a matriz fosse analisada em conjunto ao invés de particionada em subconjuntos, os resultados seriam consideravelmente diferentes e o suporte diagnóstico dos agrupamentos seria modificado ou anulado, resultando em mais homoplasia. A árvore de consenso estrito apresentada por Birdsley (2002) utilizando uma matriz modificada de Lanyon (1988) é a prova disso (Figura 4). Portanto, não há uma hipótese final (com todos os terminais em uma matriz única) que possa ser considerada filogenética e apreciada como tal, dificultando a interpretação. Em se considerando o estudo de Lanyon (1988) tão somente uma descrição morfológica comparativa com implicações na classificação e diagnose ao invés de uma verdadeira análise de relacionamentos filogenéticos (*sensu* Hennig 1966), conclui-se que até então não existe um estudo da filogenia de Elaeniinae a partir de caracteres morfológicos. Ou, se a tentativa de Birdsley (2002) de reanalisar a matriz de Lanyon (1988) a partir dos preceitos da sistemática filogenética for considerada, ao menos fica claro que não existe uma matriz morfológica capaz de expressar as relações de parentesco no grupo (a baixa resolução pode ser verificada na Figura 4), ainda. Essas falhas têm sido inclusive utilizadas como amostra que corroboraria a tese sobre a "ineficácia deste tipo de evidência em sistemática de aves" ou do "alto grau de homoplasia" dos mesmos (Ohlson *et al*. 2008).

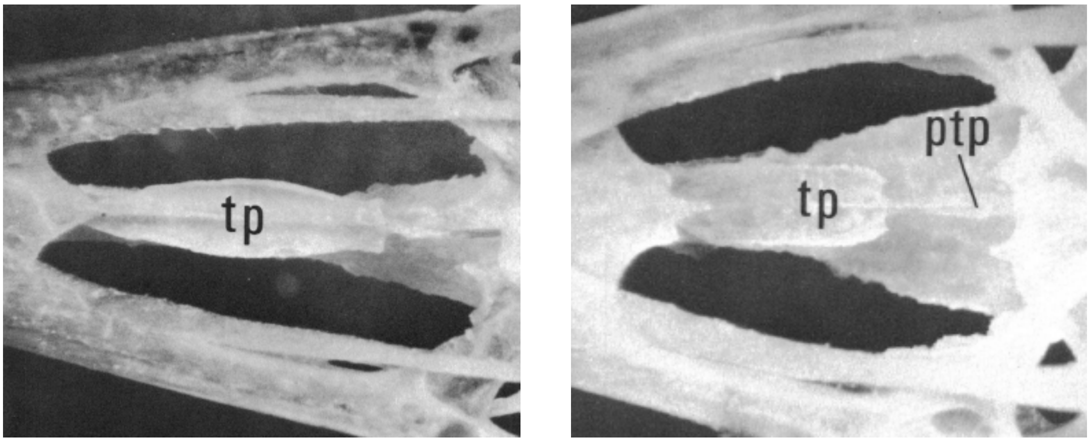

Figura 3. Caráter diagnóstico de Elaeniinae segundo Lanyon (1988): presença de placa trabecular transversal ("tp") na margem ventral do septo nasal, ilustrada em vista ventral dos crânios de *Euscarthmus meloryphus* (esquerda) e *Elaenia chiriquensis*. Modificado de Lanyon (1988). "ptp" = placa trabecular posterior.

Em geral, o presente projeto foi idealizado sob a luz da filosofia de Livezey e Zusi (2006). Esses autores, reconhecidos anatomistas, iniciaram em 1993 um expressivo projeto de análise filogenética com base em caracteres morfológicos (principalmente osteologia e miologia) de todos os grandes grupos de aves modernas (Neornithes), segundo eles, para "prover uma contraproposta morfológica empiricamente detalhada às reconstruções filogenéticas baseadas em evidências moleculares, pelo menos para proporcionar comparações das reconstruções moleculares com as classificações tradicionais das aves, essas últimas não qualificadas como hipóteses filogenéticas *per se*." Sua matriz, composta de incríveis 2.934 caracteres, comprova a possibilidade de se levantar quantidades suficientes de evidências fenotípicas, contrariando o pessimismo herdado desde Mayr (1976) com relação ao sinal filogenético presente na reduzida variação dos caracteres morfológicos das aves (Sibley e Ahlquist 1990), supostamente restringida pelas exigências do voo, principalmente nos Passeriformes (Colbert 1955, Romer 1968, Stahl 1974, Sick 1997). Contrariando essas opiniões historicamente bem arraigadas, Wyles *et al*. (1983) demonstraram quantitativamente que, comparadas aos demais grupos de vertebrados de mesma categoria taxonômica, as variações anatômicas das aves não são menores como se propusera.

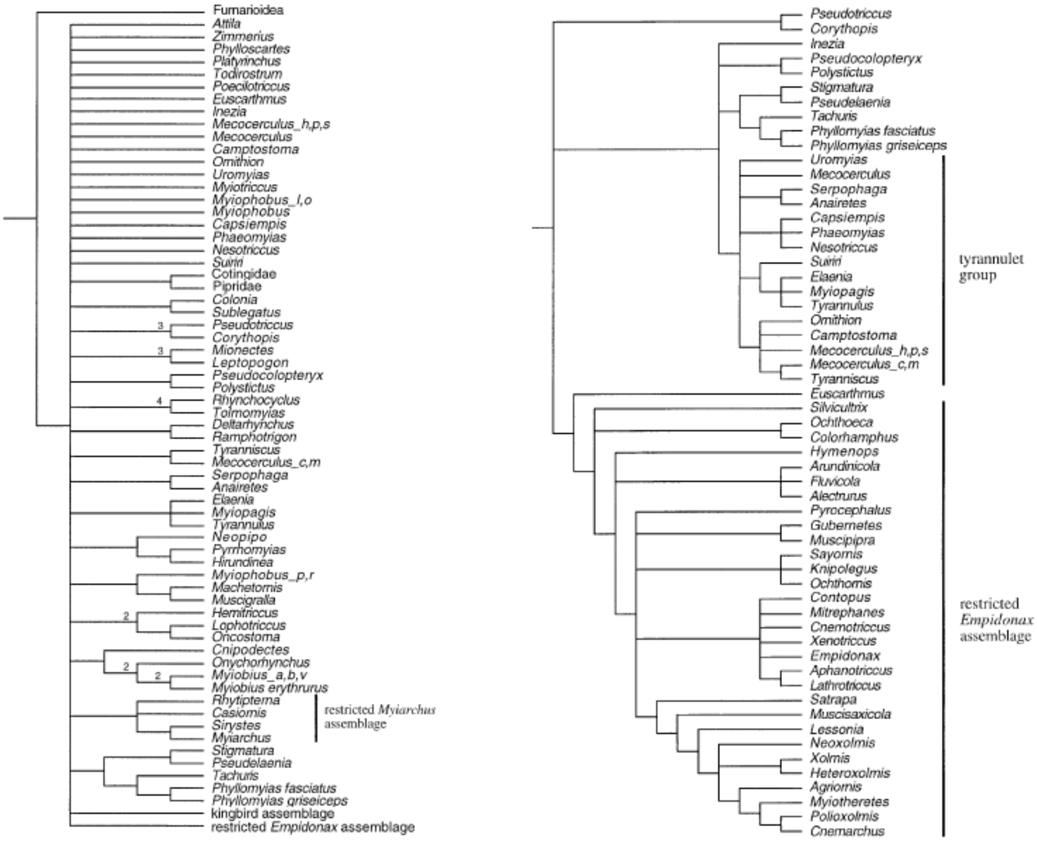

Figura 4. Árvores de consenso estrito (esquerda) e de consenso de Adams da análise filogenética com base em evidências fenotípicas de Birdsley (2002), majoritariamente baseada nos caracteres de Lanyon (1988).

Caracteres fenotípicos em inferência filogenética de aves: uma breve opinião

Desde as primeiras contribuições no século XVIII até final do século passado, a classificação das aves em todos os níveis baseava-se unicamente em densas análises de conjuntos de caracteres fenotípicos, notavelmente os osteológicos, siringeais e integumentários, conduzidas por renomados ornitólogos como Huxley, Müller, Ames, Wetmore, Lanyon, Bock, Zusi, Cracraft, Prum, entre outros. Essas trabalhosas análises permitiram que a maior parte dos agrupamentos nos níveis mais inclusivos se mantivesse incólume por um longo período de tempo, algumas persistindo até os dias de hoje, como as estáveis subordens Tyranni e Passeri, e diversas famílias.

Porém, com o advento de técnicas moleculares, a ciência da morfologia e anatomia entrou em uma etapa de gradual desuso, influenciada também pela hipótese antiga de retenção de caracteres anatômicos por pressão do voo (*e.g.* Mayr 1976; *contra* Wyles *et al.* 1983), hoje pouco aceita. Em comparação com o que aconteceu na ictiologia, herpetologia e mastozoologia, a ornitologia foi a área da zoologia em que essa mudança foi mais intensa. A dicotomia resultante dessa imersão repentina no campo da biologia molecular pode ser claramente identificada atualmente, em que a maior parte da classificação aceita é sustentada por filogenias unicamente moleculares, embora diversos métodos coalescentes, de Taxonomia Integrativa, Evidência Total e caracteres combinados estejam robustecendo as análises cladísticas e taxonômicas. Se Mooi e Gill (2010) causavam alvoroço na comunidade de ictiólogos ao provocar que "está na hora de mostrar algum caráter" e que "filogenias sem sinapomorfias" estavam sendo largamente produzidas, talvez fosse na ornitologia, em que se verifica a inexistência total de sinapomorfias ("não nucleotídicas" e, portanto, passíveis de avaliação prática) suportando mais de 90%

dos agrupamentos supraespecíficos atualmente aceitos (Franz e Borges-Martins *em prep*.), que tal insinuação coubesse de forma ainda mais plausível. Mesmo assim, à despeito do que acontecera com as demais ciências zoológicas, na ornitologia, o reconhecimento da importância dos estudos fenotípicos se deu apenas nos últimos anos, em que se julgou apropriado corroborar todo o conhecimento das relações de parentesco entre os grupos e dos padrões de diversificação dos organismos com o seu significado biológico e evolutivo, refletido na classificação.

Embora muito se pudesse explanar nesse sentido, é importante reconhecer que há um período de renascença das pesquisas anatômicas e morfológicas, não como uma contraproposta ao que se produziu até aqui, mas como uma forma de fortalecer ainda mais a compreensão dos padrões evolutivos das aves. No Brasil, em particular, identifica-se uma recente união de uma nova geração de anatomistas com pesquisadores brasileiros e estrangeiros reconhecidos mundialmente, preocupados em incorporar as novas tendências da sistemática filogenética, taxonomia, fisiologia, das análises morfofuncionais e da paleontologia e fazer uso de novas tecnologias e métodos analíticos, com vistas à unir as áreas de pesquisa em prol do conhecimento avançado em ornitologia.

As análises combinadas/de evidência total são raras no estudo das relações de parentesco entre as aves. Talvez o único grupo que se pudesse considerar assaz conhecido através desse tipo de método seja o dos tinamídeos, para o qual se dispõe de matrizes morfológicas e moleculares extensas para uma aferição próxima a desejada (veja Bertelli *et al.* 2014, Bertelli 2016). Quando as “filogenias sem sinapomorfias” são a regra, parece claro que a busca por caracteres diagnósticos práticos deveria ser prioridade e receber maior atenção. No caso dos Passeriformes, iniciativas globais de mapeamento genômico aproximam-se do momento de divulgar os primeiros resultados, em que todas as famílias, subfamílias, tribos e gêneros serão definidos e propostos com um nível de confiança nunca alcançado, mesmo considerando-se a zoologia geral. Mas esse novo e importante passo na ciência ornitológica está longe de representar o sepultamento da ciência da anatomia, por considerar-se que essa representará o futuro do descobrimento sobre os processos adaptativos e como a morfologia tem conduzido a evolução no tempo e espaço.

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Osteology-based phylogeny of the Elaeniinae tyrant-flycatchers (Aves: Passeriformes: Tyrannidae)

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The New World flycatchers (Tyrannidae) are poorly known in terms of phylogenetic relationships, despite their remarkable representation in bird diversity across the Americas (436 species). Elaeniinae comprises small and inconspicuous passerines that feed on insects in open and woodland habitats, being one of the most speciose avian subfamilies (106 species). Members of the subfamily are among the world's most difficult bird species to distinguish morphologically. A phylogenetic analysis of the group was conducted, comprising 84 species in the ingroup and 28 in outgroup, from a new matrix of osteological characters containing 151 characters. The few characters proposed in the literature were discussed and re-evaluated. The strict consensus tree, produced by means of "new technology search" in TNT software, exhibited good resolution. The subfamily was recovered as monophyletic, unlike its two unrecovered tribes. *Suiriri* was identified as the most basal taxon by sharing character states with the outgroup, which was partially resolved. All genera were recovered as monophyletic, except: *Mecocerculus*, which presents at least two well-supported groups, necessitating the description of a new genus; *Serpophaga* is polyphyletic, being necessary the resurrection of *Ridgwayornis* for two species (*R.*

nigricans and *R. cinerea*); *Phyllomyias* is polyphyletic and may present several clusters, requiring more terminals in the analysis. The recovered topology greatly agrees with the existing molecular phylogenies, but goes beyond and clarifies some previously unknown relations. This similarity between the hypotheses is greater than the present one with the pioneering research of Lanyon (1988), whose methodological problems are exposed. This study unequivocally demonstrates the existence of the phylogenetic signal and the usefulness of the phenotypic evidences in cladistic reconstructions.

ADDITIONAL KEYWORDS: birds, cladistics, comparative morphology, phylogenetic systematics, Tyranni.

Compared with tanagers (Thraupidae), cotingas (Cotingidae), manakins (Pipridae), antbirds (Thamnophilidae), ovenbirds (Furnariidae), tapaculos (Rhinocryptidae) and other notorious passerine families which have been studied in the last years (respectively, by Burns *et al.* 2014, Berv and Prum 2014, Ohlson *et al.* 2013, Bravo *et al.* 2014, Seeholzer *et al.* 2017, Maurício *et al.* 2012 and others), the New World flycatchers (Tyrannidae) are less known in terms of species boundaries and internal relationships (Fitzpatrick 2004), despite their remarkable representation in bird diversity across the Americas (436 species *sensu* Gill and Donsker 2018). One example of this scenario is the subfamily Elaeniinae, which comprises small and inconspicuous passerines that feed on insects mainly in open and woodland habitats in the Neotropical region, being one of the most speciose avian subfamilies, with 106 recognized species and close to 200 "subspecies". Members of Elaeniinae are among the world's most difficult bird species to distinguish morphologically. One example is the 21 species of *Elaenia* with generally greenish-gray plumage with yellowish wing bars (Rheindt *et al.* 2015), probably more challenging than the better-known *Empidonax* flycatchers.

Taxonomically, the subfamily includes numerous unresolved issues and cases that have not been investigated at all. More than the half of the tit-tyrants and tyrannulets have recognized subspecies and/or allopatric populations. And it is important to note that new taxa are still being discovered inside the group. This is the case, for example, of the recently described Chico's Tyrannulet *Zimmerius chicomendesi*, a member of the subfamily endemic to central Amazonian Brazil (Whitney *et al.* 2013), in addition to two new Andean subspecies, *Myiopagis olallai coopmansi* and *M. o. incognita* (Cuervo *et al.* 2014), and a non-described *Stigmatura* wagtail from the Orinoco delta in Venezuela. Few passerine subfamilies rival Elaeniinae in number of new forms discovered, proposed and pending taxonomic rearrangements over the last 20 years.

Phylogenetically, some puzzling problems are well known, including the apparent non-monophyly of some genera such as *Phyllomyias* and *Mecocerculus* (Lanyon 1988a, Rheindt *et al.* 2008, Tello *et al.* 2009), requiring extensive readjustments. The phylogenetic affinities of *Culicivora* (whose osteology has never been studied), *Euscarthmus* and other genera are unclear (Lanyon 1988a). *Tachuris* was excluded from Elaeniinae, with the description of Tachurisidae (Ohlson *et al.* 2013, Franz 2015). The Chapada Flycatcher, "*Suiriri*" *affinis* (formerly *S. islerorum*), was placed in a new genus, *Guyramemua*, and considered sister to *Sublegatus* within the subfamily Fluvicolinae, distant from Elaeniinae in the tyrant-flycatcher's tree (Lopes *et al.* 2017). Limits and composition of the two tribes - Elaeniini and Euscarthmini - need to be clarified with much more complete taxon sampling. Moreover, a small number of weak phenotypic diagnostic characters are acknowledged for the genera and tribes. Even the major “synapomorphy” of the entire subfamily - the presence of a transversal trabecular plate along the margin of the nasal septa (*sensu* Lanyon 1988a) - is questioned.

Additionally, many members of the subfamily are endangered, especially those restricted to certain South American open vegetation biomes, which have suffered extensive anthropogenic alteration in just the last few decades. Some examples are the Sharp-tailed Tyrant *Culicivora caudacuta* from the Cerrado, Chaco/Pantanal and south-temperate upland grasslands; the Chapada Flycatcher *Guyramemua affinis* from Cerrado; the Plain Tyrannulet *Inezia inornata* from Chaco woodlands; and the Gray-backed Tachuri *Polystictus superciliaris* from upland rocky grasslands. The taxon *Polystictus pectoralis bogotensis* has apparently been driven to extinction as a result of the rapid urbanization throughout its entire range, the Savannas of Bogotá, Colombia.

Thus, it is clear that the Elaeniinae subfamily needs to be better studied to resolve pending taxonomic and phylogenetic issues and characterize yet-unknown cryptic taxa. For this, it is considered fundamental to initially circumscribe the inter- and intra-subfamilial phylogenetic relationships and produce a new matrix of phenotypic characters in order to evaluate the monophyly, boundaries and real synapomorphies of the named taxa. Here we present a phylogenetic hypothesis based on a new matrix of osteological characters involving representatives of all genera and discuss the consequences for classification.

Chronology of Elaeniinae systematics

The subfamily "Elaininae" (type: *Elaenia* Sundevall, 1836) was described in 1860 by Jean L. Cabanis and Ferdinand Heine, congregating representatives of the genera *Leptopogon*, *Pipromorpha* (= *Mionectes*), *Capsiempis*, *Rhynchocyclus* (= *Tolmomyias*), *Phyllomyias*, *Tyranniscus*, *Tyrannulus*, *Myiopatis* (= *Phaeomyias*), *Elainea* (= *Elaenia*), *Legatus*, *Myiozetetes*, *Saurophagus* (= *Philohydor* + *Pitangus*) and *Megarrynchus* (= *Megarynchus*) (Cabanis and Heine 1860). The authors did not present a formal description or a diagnosis for the group. Sclater (1888, p.109), in volume XIV of the British Museum's bird catalogue, uses the Elaineinae spelling, and gives a brief description of the group, especially diagnosing it from Platyrhynchinae Bonaparte (1854) (and not Sclater, 1862 according to Tello *et al.* [2009]) for having, among other characteristics, the compressed and smooth bill (*vs*. depressed and bristled). It also mentions the primarily Neotropical distribution of the subfamily, except for *Ornithion imberbe* (= *Camptostoma imberbe*) with occurrence in the Neartic region. Ihering (1904) proposes a rearrangement of the four subfamilies accepted by Sclater (1888; Taeniopterinae, Platyrhynchinae, Elaineinae and Tyranninae), dividing the Platyrhynchinae into two groups, which he calls Euscarthminae and Serpophaginae; excluding from Elaeniinae the Pitanginae (*Pitangus*, *Myiodynastes*, *Legatus*, *Myiozetetes* among others) and grouping them with Tyranninae, the "true flycatchers"; and relocating *Rhynchocyclus* from Elaeniinae to Euscarthminae. Ridgway (1906) considers the arrangements of Sclater (1888) “merely provisory” and "obviously erroneous" his allocations of those genera in the subfamilies, agreeing with the rearrangements proposed by Ihering (1904). The author also suggests, based on the type of tarsal scutellation, the withdrawal of several genera of the family Tyrannidae, among them *Stigmatura*, *Hapalocercus* (= *Pseudocolopteryx*), *Habrura* (= *Polystictus*), *Myiopagis*, *Tyrannulus*, *Ornithion* and *Culicivora*, all included currently in Elaeniinae. Cory and Hellmayr (1927) endorse these subfamilies (except for still maintaining Platyrinchinae including the genera *Platyrinchus*, *Cnipodectes*, *Tolmomyias*, *Rhynchocyclus* and *Ramphotrigon*) and, finally, correct the spelling for Elaeniinae based on the correct spelling of *Elaenia* (previously, "Elaenea", "Elainia", "Elainea" and "Elania"), listing 16 genera for the subfamily, plus 25 genera on Euscarthminae and nine genera on Serpophaginae.

Müller (1878), in a pioneering study, compared the support elements and musculature of the syrinx among representatives of Passeriformes, including *Elaenia pagana* (= *Elaenia flavogaster*), other tyrannids such as *Elaenia brevirostris* (= *Sublegatus modestus*, Fluvicolinae) and *Tyrannus crudelis* (= *Tyrannus melancholicus*, Tyranninae), some "Todinae" (partial junction of Rhynchocyclidae and Elaeniinae) and Platyrhynchidae, among others. Müller (1878) identified some differences in the number of bronchial rings and in the presence of muscles between the main groups in Picarii (= "Suboscines"), advocating the division of the Tyrannidae into Tyranninae, Fluvicolinae and "Todinae". More important than the classification itself was its demonstration of the potential use of syrinx structures as taxonomic characters, serving as a reference for subsequent studies (Ames 1971).

Although not supported by the phylogenetic framework, the contributions of John T. Zimmer between the 1930’s and 1950’s through the extensive series Studies of Peruvian Birds, notably the numbers XXXV (Zimmer 1940) and XXXVI (Zimmer 1941), which presents, respectively, taxonomic revisions of representatives of several genera of Elaeniinae, such as *Euscarthmus*, *Pseudocolopteryx*, *Uromyias*/*Anairetes*, *Stigmatura*, *Serpophaga* and *Mecocerculus*; and several taxa in *Elaenia* and

Myiopagis, both contributing with the description of new subspecies (*e.g. Serpophaga hypoleuca venezuelana* and *Elaenia obscura sordida*) and proposition of splits and lumps. Recently, *E. o. sordida* described by Zimmer has been tentatively treated as a full species (del Hoyo *et al*. 2018) based on genetic studies (Rheindt *et al*. 2008) and on vocal differentiation (Minns 2017).

Warter (1965), analyzing cranial osteology characters, recognizes the difficulty in establishing the boundaries between the subfamilies of "little tyrannids". In conclusion, the author suggests the hierarchical lowering of the subfamilies in tribes, Elaeniini and Serpophagini.

Ames (1971) produced an important study on the morphology of the syrinx in order to establish the intergeneric relations and among the main groups of Passeriformes, including 19 species of Euscarthminae (the genera *Euscarthmus*, *Capsiempis*, *Habrura* [= *Polystictus*] and *Pseudocolopteryx*), seven Serpophaginae species (including the genera *Serpophaga*, *Stigmatura*, *Inezia* and *Mecocerculus*) and 23 "true" Elaeniinae species, totalling 33 species of “Elaeniinae *lato sensu*”. According to the author, the genera *Elaenia*, *Suiriri*, *Phaeomyias*, *Camptostoma* and *Microtriccus* (= *Ornithion*) share several characters, such as three or more A elements fused to the drum, directly inserted *sternotrachiales* muscles, two pairs of intrinsic muscles, among others. More importantly, Ames (1971) found two synapomorphies for Elaeniinae: presence of fully fused tympanum and presence of the *obliquus lateralis* muscle. In addition, most of the species had a well-developed *obliquus ventralis* muscle, originating in a raphe connected to the tympanum; and the internal cartilage as narrow, curved bars, usually with narrow ventral extensions. Finally, the author contested some taxonomic decisions of his predecessors, suggesting alterations in the composition of Elaeniinae, for example, with the relocation of the genera

Pseudocolopteryx, *Stigmatura* and *Polystictus* and the withdrawal of *Mionectes*, classifications accepted until now (*sensu* Tello *et al*. 2009 and others).

Traylor (1977) has architected his new classification of Tyrannidae mainly by integrating the anatomical evidence of Warter (1965; cranial characters) and Ames (1971; syringeal characters) along with additional reproductive and plumage characters (Fitzpatrick 1985). Of the seven subfamilies of Cory and Hellmayr (1927), four of them were unified into one, which was given the oldest name, Elaeniinae. Thus, Elaeniinae incorporated the Platyrinchinae, Euscarthminae and Serpophaginae. Many of the genera of Cory and Hellmayr (1927) were synonimized (*e.g.* *Xanthomyias*, *Oreotriccus*, *Acrochordopus* and some *Tyranniscus* in *Phyllomyias*) and a new genus was described, *Zimmerius*, composed of five species.

Sibley and Ahlquist (1985), from their pioneering molecular analysis, designated the Mionectidae family, including taxa formerly belonging to Elaeniinae (Traylor 1977), such as *Mionectes*, *Leptopogon*, *Pseudotriccus*, *Corythopis*, *Hemitriccus* and *Todirostrum*. The other Elaeniinae that were part of the analysis (*Camptostoma*, *Phaeomyias*, *Suiriri*, *Tyrannulus*, *Myiopagis*, *Mecocerculus*, *Anairetes* and *Euscarthmus*) formed a monophyletic group, agreeing with the classifications based entirely on morphological characters proposed until then.

Expressly influenced by the studies of Warter (1965) and Ames (1971), Lanyon (1988a) justified his analysis by stating that the two authors working independently with their distinct sets of characters would not accumulate enough information to adequately establish the phylogenetic relationships of the groups. In this way, he combined cranial and syringeal characters with a few reproductive and plumage ones (n = 44 characters in total), coded for 117 species representing all 32 genera of Elaeniinae. The monophyly of the subfamily (his "Elaenia assemblage") was established based solely on the nasal septum configuration, in which a transverse trabecular plate is present and slightly elevated above the ventral margin of the septum, creating the appearance of a sagittal crest in ventral view. Some representatives of *Phyllomyias*, *Tachuris* and *Culicivora*, for not sharing such a character, were removed from the subfamily. Intergeneric relations were largely supported by the syringeal characters, followed by cranial characters. The author recognized five groups, which defined as "primary lineages", namely: *Phylloscartes* group (nine genera, 42 species), *Stigmatura* group (two genera, one being described by the author [*Pseudelaenia*], three species), *Euscarthmus* group, *Pseudotriccus* group (two genera, five species) and *Elaenia* group (18 genera, 65 species), recovered on the basis of one or two "synapomorphies". Strangely, Lanyon (1988a) performed analyzes separately for each group, and consequently presented individual trees for these recovered “clades”, listing the "synapomorphic" characters for each of these groups. With this, there is no final hypothesis (with all terminals and character sets) that can be appreciated, making interpretation difficult. Certainly, these characters pointed out by the author as synapomorphic, if analyzed together, could show a different evolutionary history, some ceasing to be synapomorphic. Therefore, the data were not adequately analyzed, so the author did not seek the best explanatory power in a phylogenetic context (Franz *in prep*., Ohlson *et al*. 2008).

Fitzpatrick *et al*. (2004) warned for the existence of conflicts, hitherto lacking in reasonable resolutions, involving serious inconsistencies in the morphological and behavioural characters widely considered diagnostic of subunits recognized in the Tyrannidae family, such as Elaeniinae. They emphasized, among the attempts to integrate such characters in a modern phylogenetic context, the Birdsley (2002) study. Summarily, this author collected the sets of characters that Lanyon (1984, 1985, 1986, 1988a, b, c) used to define each of his five "assemblies" together with new characters (ecological, behavioural and plumage) in a single matrix and performed a real phylogenetic analysis. The strict consensus tree presented minimal resolution, apparently as a consequence of the reduced number of characters in relation to the number of terminals and the high degree of homoplasy contained especially among its new plumage characters. Such failure led Fitzpatrick *et al.* (2004) to recommend "detailed molecular analyses in order to resolve the phylogenetic relationships between Tyrannidae at the subfamily and tribe levels". Fitzpatrick's call came into effect, as will be seen below.

The phylogenetic analysis of Birdsley (2002) was carried out from 68 characters to 106 species, being 10 cranial, 33 syringeal, 13 integumentary (plumage) and 7 behavioural/ecological (as seen, it is the basis of Lanyon's [1984, 1985, 1986, 1988a, b, c] morphological matrix). Unlike Lanyon, the author included the Furnarioidea as an additional outgroup and assigned equal weights to the characters. Interestingly, in the analysis, the author did not find support for Lanyon's "*Elaenia* assemblage" (1988a), nor for the other groups, which led him to abandon his strict consensus and analyses trees from the Adams consensus (Adams 1972). In this analysis, Elaeniinae was partially recovered, being polyphyletic (for example, *Euscarthmus* joined the "*Empidonax* assemblage" - today, Fluvicolinae with modifications [Ohlson *et al.* 2013]) -, presenting high support for this branch (Birdsley 2002). A "tyrannulet group" (Lanyon [1988a], now the modified Elaeniini tribe) was supported on all the optimal trees by the fusion of the A elements of the trachea into a tympanum (the Ames 1971 drum). But the study by Birdsley (2002) was not well accepted by the community, being rarely cited and considered, although Lanyon's (1988a; the same matrix analysed in a "sectioned" way, as seen), along with his studies of the other related groups (aforementioned) for many years supported the accepted classification of Tyrannidae and to date is taken as a reference in family morphological characters (clades are compared, for example, with the most recent classification of Ohlson *et al.* 2013), despite of the alert by Fitzpatrick *et al.* (2004). Birdsley (2002), finally, emphasizes the need for more data in the search to solve the phylogenetic relationships of Tyrannidae.

The publication of the volume of the Handbook of the Birds of the World (HBW) which included the Tyrannidae (Volume 9, Fitzpatrick *et al.* 2004) represents the most comprehensive review of the state of the art of group knowledge at the time, and greatly influenced the classifications adopted. The subfamily had 203 species, which represents almost double the number of species included today (*sensu* Gill and Donsker 2018). This disparity is due to the fact that Fitzpatrick *et al.* (2004) kept all the early "Platyrinchinae" within Elaeniinae, contrary to much of the authors of the last decades. According to the authors, the subfamily was divided into two tribes in order to represent the distinct groups: Elaeniini (133 species, Lanyon's "*Elaenia* assemblage" [1988a] with modifications, or the "true Elaeniinae") and Platyrinchini (70 species).

From the mid-2000's, the first molecular phylogenies including more representatives of tyrant-flycatchers were produced. Ericson *et al.* (2006) conducted a phylogenetic analysis based on two genes (4,283 bp) for 26 species of the internal group and found three monophyletic groups in Tyrannidae (Tyranninae, Fluvicolinae and Elaeniinae), agreeing to the division into subfamilies of Traylor (1977). Only five species of Elaeniinae were sequenced (*Myiopagis viridicata*, *Elaenia flavogaster*, *Serpophaga subcristata* [later identified as a female of *Myiopagis caniceps*, Ohlson *et al.* 2008], *Inezia inornata* and *Stigmatura budytoides*), according to the authors themselves a modest taxonomic coverage, not showing changes in known relationships.

Ohlson *et al*. (2008) for the first time sought to infer the relationships of Tyrannidae at the generic level based on molecular data with a broader taxonomic coverage. They sampled 103 species, being 25 of Elaeniinae, by means of three nuclear introns (702 bp in total). The authors recovered the clade corresponding to the subfamily Elaeniinae composed essentially of the "*Elaenia* group" of Lanyon (1988a), with the inclusion of *Zimmerius*, *Stigmatura*, *Euscarthmus* and *Inezia*. It also included *Culicivora* (not analyzed by Lanyon [1988a]) and two species of *Phyllomyias* (*P. fasciatus* and *P. griseiceps*), which the latter author considered *incertae sedis* based on the "aberrant morphology of the syrinx". *Mecocerculus* and *Phyllomyias* were polyphyletic, as already pointed out by Lanyon (1988a). Three subclades in Elaeniinae were well supported by the Bayesian inference analysis, but their internal relationships could not be resolved. Finally, the authors conclude that the syringeal characters of Lanyon (1988a) are “extremely homoplastic" and suggest a greater sampling of taxa and more molecular markers in order to clarify the evolutionary history and the intergeneric boundaries of Elaeniinae.

Rheindt *et al*. (2008), in a similar proposal, sequenced 1,715 bp (Fib5 and ND2 genes) of representatives of 48 genera of Tyrannidae, this time prioritizing the species of the Elaeniini tribe, in what represented up to that time the greater coverage of Elaeniinae representatives in molecular phylogenies. As in Ohlson *et al*. (2008), Elaeniinae was recovered with composition identical to the "*Elaenia* group" of Lanyon (1988a). *Phyllomyias* showed to be polyphyletic, grouping the "true members" (*P. griseiceps* and *P. fasciatus*) distant of *P. uropygialis* and *P. plumbeiceps*. A close affinity was revealed between *Phaeomyias* and *Capsiempis*, agreeing with Lanyon (1988a), as well as between *Camptostoma* + *Ornithion* + *Tyranniscus* and *Tyrannulus* + *Myiopagis*.

Tello *et al*. (2009) presented a robust phylogenetic analysis of Tyrannides from 4,024 bp (RAG-1 and RAG-2 genes) of representatives of 141 genera. Using both sequencing and subordination criteria, the authors proposed an equally robust phylogenetic classification. Of more significant implications is the elevation of Rhynchocyclinae to the family level (Rhynchocyclidae), a strongly supported clade that now includes the tody-tyrants (Todirostrinae) and flatbills (Rhynchocyclinae) of Lanyon (1988a), all Platyrinchinae and some Elaeniini from Fitzpatrick *et al*. (2004), and the Mionectidae/Pipromorphinae of Sibley and Ahlquist (1985, 1990). In this way, Elaeniinae begins to congregate the Elaeniini of Fitzpatrick *et al*. (2004), without *Myiotriccus*, *Pseudotriccus*, *Corythopis*, *Phylloscartes*, *Pogonotriccus*, *Leptopogon*, *Mionectes* and *Tachuris*. Internally, the subfamily is divided into Euscarthmini tribe (a new rank that includes *Tyranniscus burmeisteri*, *Euscarthmus rufomarginatus*, *Stigmatura budytoides* and *Zimmerius viridiflavus*, without any known morphological diagnosis) and Elaeniini tribe, comprising the rest of the analyzed species. The polyphyly of *Phyllomyias* is again corroborated. In order to allocate two species (*P. uropygialis* and *P. burmeisteri*), the authors resurrected the genus *Tyranniscus* Cabanis and Heine (1859-60), which have priority in relation to *Acrocordopus* Berlepsch and Hellmayr, 1905. A group consisting of *Serpophaga*, *Pseudocolopteryx*, *Polystictus*, *Culicivora* and *Anairetes* + *Uromyias* is defined ("*Culicivora* group"), partially supported by phenotypic evidence (Traylor 1977, Lanyon 1988a).

Chebez and Agnolin (2012) outlined an analysis of the phylogenetic relationships of "Serpophagini" from 20 characters of plumage and behaviour for 32 species. The "new combination" Serpophagini was proposed based on the "*Culicivora* group" of Tello *et al*. (2009), supported by the authors and diagnosed by means of external morphology and reproductive characters. Strangely, within Serpophagini, the grouping "Culicivorina", without category, is proposed to group *Culicivora*, *Polystictus* and "*Holmbergphaga*", a supposed new genus that would include *Serpophaga nigricans*, *S. hypoleuca* and *S. cinerea*. It is well known that the characters used in this study have limited phylogenetic value.

At the same time, studies looked for particular taxonomic (based on morphology and voice) or phylogenetic (mostly DNA-based) resolutions in Elaeniinae. For example, Zimmer and Whittaker (2000) analysed the boundaries between the four valid subspecies of *Inezia subflava* and, based on vocalizations, plumage, behaviour, biometry and iris coloration, proposed the separation of two full species. Roy *et al*. (1999) performed a phylogenetic analysis using molecular characters of *Anairetes* (six species) + *Uromyias agilis* (rooted in *Stigmatura*), identifying *Uromyias* among the *Anairetes*. The phylogeny of the clade was later reviewed by Dubay *et al*. (2012) based on more characters (6,407 bp), who found both genera as monophyletic sister clades, supporting the separation. Another genus intensively studied through DNA and external morphology was *Zimmerius*, initially finding polyphyly at the subspecific level for *Z. chrysops* (a split and a not described taxon) and *Z. gracilipes* (two splits, Rheindt *et al*. 2008) and identifying vocal characters as more effective tools than plumage patterns to seek boundaries between entities. After, Rheindt *et al*. (2013) increased the number of terminals, comprising all nine species of *Zimmerius* and identifying again new cryptic taxa. In this genus, a new species (*Z. chicomendesi*) was described from populations of the upper Madeira-Tapajós interfluve in the Brazilian central Amazon (Whitney *et al*. 2013).

Nowadays, the knowledge of the phylogenetic relationships of Elaeniinae is entirely based on the molecular phylogenies presented. As seen, some studies have been debating their relationships in this and the past decade, culminating with the classification proposition of Ohlson *et al*. (2013), although extensive coverage of taxa has not always been employed (studies have prioritized the relationships between more inclusive groups such as Passeriformes and Tyrannides). The classification most widely adopted today is based on the results of the molecular phylogenies presented by Tello *et al*. (2009) and Ohlson *et al*. (2013). In the latter, the authors used new data sets enhanced with other published molecular studies (Ohlson *et al*. 2008, Irestedt *et al*. 2009) in order to synthesize the main results in a classification proposal for large groups of Passeriformes. It considers 25 genera or not yet named generic groups in the subfamily Elaeniinae (although they have sequenced only 16 species), totalling 106 species (*sensu* Gill and Donsker 2018), divided into two tribes.

In contrast, it is clear the tortuous path that was followed in terms of the knowledge of the morphology and anatomy of the group and the importance of these character sets for the reconstruction of parental relationships within Tyrannidae: Elaeniinae. From Lanyon (1988a), it can be affirmed that no contribution has brought novelties with respect to the morphological characters with phylogenetic value. As regards osteology, the most significant set of morphological characters in phylogenetic systematics of birds, that study presented only 10 characters, all of the skull (nasal and interorbital septa). Thus, it is considered that the production of an osteological matrix is an open field and, therefore, represents the main objective of the present study. With a new matrix, we aimed to perform a cladistic analysis in order to discuss the relationships recovered and the phylogenetic signal of the characters identified and their diagnostic power. More specifically, we aimed to (1) compile from the literature and reanalyse the existing osteological character sets for the subfamily, notably those of Lanyon (1988a), (2) propose new characters based on comparative osteology analyses, (3) test the monophyletic hypotheses of the Euscarthmini and Elaeniini tribes, (4) evaluate the monophyly of Elaeniinae genera, especially of the taxonomically controversial units, (5) compare the phylogenetic hypothesis found with the pre-existing ones, analysing possible differences in the topologies between morphological and molecular phylogenies and their implications for group classification, and (6) serve as a morphological basis for future combined analyses.

METHODS

Osteology was chosen as the source of the characters because of its potential to find a satisfactory amount of information (at least between 100 and 200 characters, depending on the group), of the recognized phylogenetic signal, and the availability of material that, although not ideal and presenting several practical gaps, is more reasonable than the situation of material suitable for myology or in the form of syrinx, for passerines (Franz and Borges-Martins *in prep*). For this, the primary source of terminology was the traditional *Nomina Anatomica Avium* (Baumel and Witmer 1993), with the inclusion when necessary of the nomenclatural refinement and new terms proposed by Livezey and Zusi (2006) and Zusi and Livezey (2006), and consultation of osteological matrices of passerines (*e.g.* James 2004, Maurício *et al.* 2012). Whenever possible, bone elements were referred to in English, especially those already mentioned in the literature in this language (*e.g.* Proctor and Lynch 1993), maintaining Latin for more exclusive and difficult to translate elements, in this case in italic for differentiation.

Material access and preparation

Material from the following institutions was accessed: Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (MCP); Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (MCN); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP); Museu Paraense Emílio Goeldi, Belém (MPEG); Museu Nacional do Rio de Janeiro, Rio de Janeiro (MNRJ); American Museum of Natural History, New York (AMNH); Cornell University Museum of Vertebrates, Ithaca (CUMV); Louisiana Museum of Natural History, Baton Rouge (LSUMZ); U.S. National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM); Field Museum of Natural History, Chicago (FMNH); Yale Peabody Museum of Natural History, New Haven (YPM); Academy of Natural Sciences of Drexel University, Philadelphia (ANSP); Natural History Museum, Tring (NHM, formerly BMNH); and Muséum National d'Histoire Naturelle, Paris (MNHN). The complete list of material examined can be consulted in the Appendix 1. The richest osteological collection (USNM) served as the basis for the concentration of most of the material and comparative studies. Selected specimens used in the study of Lanyon (1988a) were re-examined.

In addition, field expeditions were carried out aiming at the direct collect of sparsely represented species in collections, especially those that needed preparation of complete and/or better quality osteological material. The expeditions focused on the open and forest areas of the Amazon and Atlantic Rainforests, the "dry diagonal" areas (Cerrado, Caatinga and Chaco regions) and the Pampa, covering all Brazilian biomes. The specimens were collected by means of Ecotone 16 mm mist nets installed in understory and canopy and attraction through playback, as well as the use of compressed air .177-caliber carbine (Amaral *et al.* 2012) and 6 mm airsoft gun (Franz *in prep.*). The referred capture and collect license was issued by the Brazilian government via Sisbio/ICMBio (license number 41384-4) for the execution period of the collection phase.

Collected birds were taxidermized according to the standard procedures in ornithology (Piacentini *et al.* 2010, Winker 2000), prioritizing the preparation in the form of shmoo (skin without skeleton), and deposited in Brazilian collections. Both the collected material and the complete carcases or specimens in alcohol deposited in collections ("spirit"/fluid specimens) were prepared for osteological analysis in two ways according to the size of the birds. Larger skeletons (> 13-15g) were prepared with use of dermestid beetles and subsequent cleaning or by manual discarding and maceration in water; kept, therefore, in dry collections. Smaller skeletons (< 12g) were cleared and stained (c&s) for bone according to the protocol of Taylor and Van Dyke (1985) with modifications (Franz and Zusi *in prep.*). Unlike other groups (*e.g.* fishes and amphibians), diaphanization is not a commonly used procedure in anatomical studies of birds, and is applied primarily to nestlings or to parts such as syrinx. In recent years, the author has tested the technique on small size adult birds, obtaining satisfactory results in comparison to the dry preparation of small species (Franz and Zusi *in prep.*). As pointed out by Lanyon (1988a), just a little remains of some parts in skeletons of dry collections, such as the important nasal septum, character that diagnoses Elaeniinae and other flycatcher subfamilies. According to Zusi (2013), cleared and stained specimens are “especially useful for (1) determining the nature of cartilaginous structures in the nasal region and patterns of ossification, (2) verifying delicate ossifications in the prepalatal upper jaw, (3) verifying presence of bones often lost in skeleton preparation (*e.g.* sesamoids of the tail, free ribs, phalanges), and (4) clarifying syringeal structure."

Specimen identification

To ensure the correct determination of the osteological specimens, we adopted some procedures when selecting the material for examination: we prioritize skeletons (1) associated with specimens in the form of dry skin and/or that had their vocalization recorded and deposited in a sound collection, although this last case is rare; we verified if (2) the bird prepared as skeleton was collected on the same day or on the same expedition as specimens in the form of skin correctly identified by the collectors (some collectors "separate" specimens to skeleton or fluid after a minimum acceptable amount of skins already reached in the expedition); we evaluate the (3) distribution, considering as less susceptible of error when in the locality of collection there is no record of another morphologically similar taxon that could be confused; we evaluated subjectively whether (4) the collector had previous knowledge with the species, for example, when he has already collected specimens of the species before, prepared them in the form of skin and these skins were correctly identified after our examination; we compared (5) the osteological specimens with other skeletons in which we could confirm the correct identification (such as those collected by ourselves or those that passed criterion 1). With this care, we certify that only skeletons whose determination has been filtered are part of the material examined. To select fluid specimens (carcasses or whole specimens) for skeletal preparation, priority was given to those that could be safely identified by plumage characteristics (whole specimens in alcohol) and/or that were associated with the respective vouchers in the form of shmoo skins and any proof of identity (*e.g.* vocalization recordings).

Material examination

The specimen examination was performed under a Zeiss Stemi 1000 binocular dissecting microscope with an external light source. Osteological characters were investigated in at least two or more individuals from each terminal taxon in order to identify possible intraspecific variations (polymorphisms), except in cases where only one specimen was found in all collections (*e.g. Oxyruncus cristatus*). Documentation of character states was obtained from stacking photos (a composition from 10-15 images in different depths) with an Olympus DSX-100 opto-digital microscope at the Imaging Lab of the Smithsonian Institution's National Museum of Natural History, and with a Nikon Z100 digital stereomicroscope at the Zoology Department of the Federal University of Rio Grande do Sul.

Taxon sampling

Species-level taxa were considered the terminals. The supra-specific classification was adopted according to Ohlson *et al.* (2013) and the species composition following Gill and Donsker (2018), both for the Elaeniinae and the other Tyrannides. The latter already considers the recent and complex splits in *Zimmerius* (Rheindt *et al.* 2013) and *Elaenia* (Rheindt *et al.* 2015). In addition, we adopted the splits of *Euscarthmus fulviceps*, *Polystictus brevipennis*, and *Suiriri burmeisteri* (Franz *et al. in prep*.).

Ingroup. Representatives of all genera of Elaeniinae, belonging to 84 species, were analysed. In the case of rich genera in which it was not possible to examine all species, species that represented the gradients of variation were prioritized, a decision that was applied using the criteria of Maurício *et al.* (2012), namely: (1) to analyse the species-type of the genus, (2) to analyse species with a wide geographic coverage, representative of the distribution of the genus (for example, the northern, central and middle portions of the Andes and Southeast Brazil), (3) to analyse species with different vocal patterns in the genus, (4) to analyse species with distinct patterns of plumage in the genus, (5) to analyse extremes of variation in body size of the genus (smaller and larger species), and (6) to analyse controversial taxa with potential for taxonomic rearrangements. These criteria were applied, for example, to the most problematic genus in terms of available material in the world's largest collections, which is *Phyllomyias lato sensu*, in which 50% of the species were accessed (seven out of 14). The sample belonged to the genus included the most distinct representatives among them, including those previously allocated in the questioned genera *Tyranniscus*/*Acrochordopus* and *Xanthomyias*.

Outgroup. As the external group, we selected at least two representatives (when not monotypic) of each family of the superfamily Tyrannoidea (Oxyruncidae, Onychorhynchidae, Tityridae, Pipritidae, Platyrinchidae, Tachurisidae, Rhynchocyclidae), of all subfamilies of Tyrannidae (Hirundineinae, Muscigrallinae, Tyranninae, Fluvicolinae) and of the families Cotingidae and Pipridae. Thus, all major groups within the parvorder Tyrannida (Tyrannoidea + Cotingidae + Pipridae) were sampled, with a full sampling within Tyrannidae (all subfamilies included). The only case in which it was not possible to include two species was in the family Pipritidae, composed of two species and whose material of the species *Piprites pileata* was not found in the accessed collections. The monotypic groups were Oxyruncidae (*Oxyruncus cristatus*), Tachurisidae (*Tachuris rubrigastra*) and Muscigrallinae (*Muscigralla brevicauda*). In this way, it was possible to test the monophyly of Elaeniinae. In addition to the present classification, taxa that previously composed the Elaeniinae subfamily and were subsequently relocated (Traylor 1977, Lanyon 1988a, Fitzpatrick et al., 2004, Ohlson et al., 2013) were also incorporated. This is the case, for example, of some Rhynchocyclidae (*e.g. Phylloscartes*, *Corythopis*), Fluvicolinae (*e.g. Sublegatus*), *Tachuris* and *Platyrinchus*. This criterion of inclusion in the Outgroup made it possible to evaluate the support of such relocations in a morphological context. Applying our selection criteria based on previous knowledge of phylogenetic relationships, the number of terminal taxa in outgroup was 28 species, including the root species. In each suprageneric taxon (family and subfamily), the choice of the two or more representatives was according to the extremes of variation (see Ingroup criteria) and classification. The rooting of the analysis was made in a taxon external to the Tyrannida parvorder, belonging to the superfamily Furnarioidea: *Furnarius rufus*. The total number of terminals (ingroup + outgroup) in the analysis was 116 species.

Character presentation and phylogenetic analyses

Characters were presented according to the logical structure recommended by Sereno (2007): in the initial statement (*i.e.* the "title" of the character), the first words correspond to the locator terms, that is, the name or set of names of structures that allow to locate the character unambiguously, while the last terms correspond to the variable, that is, the aspect that varies (*e.g.* length, shape, insertion). The states of the character are then described, and comments on its use by other authors and variation in the group studied can be written.

In order to reconstruct the phylogenetic relationships of Elaeniinae representatives, the cladistic method, based on character analysis, was employed (Hennig 1966, Wiley 1981). In this method, the establishment of monophyletic groups in the construction of phylogenetic relationship hypotheses is based exclusively on the sharing of derived characters (synapomorphies) by the members of each hierarchical group. The choice of characters was based on the presence of variation of the osteological characteristics, as seen. Parsimony seeks to find the simplest tree for the explanation of the observed variation of a given phenomenon based on the least number of transformations (*i.e.* steps). The multi-state characters were previously treated as unordered, so as to avoid subjectivity in relation to their transition.

Characters and their observed states and coding for each species made up the binary matrix of characters, which was made and organized in the Mesquite software (Maddison and Maddison 2011). The parsimony analysis method was implemented in TNT v. 3.5 (Goloboff 1999). For this analysis we used the heuristic search method through the Ratchet algorithm, which consists of randomly adding taxa in the RAS (Random Addition Sequence), in which tree branching reconnections (TBR) are applied to get one or two trees to start. On these trees are made new rearrangements of branches with a given percentage of the characters with disturbed weights (duplicated or zeroed), finding new optimal trees. Finally, the matrix is returned to the original weights and a new rearrangement is applied, and so on until the stability of optimal trees is reached in the search. The main advantage of employing Ratchet's method is the possibility of escaping more easily from the tree islands, and thus inspecting a much larger portion of the universe of possible relationship hypotheses.

From the optimal trees obtained in the analyses, a strict consensus tree (Sokal and Rohlf 1981) was elaborated for the final hypothesis. The support measure was calculated using the Goodman-Bremer or Bremer index (Bremer 1988), which considers the number of extra steps needed to collapse a branch node.

RESULTS

Description of characters

We described 151 characters of the osteology, 144 of the cranium and seven additional of the postcranium, which were coded for 112 terminal taxa, 84 ingroup and 28 outgroup species. Of this total, 144 characters are new in Tyrannidae, that is, they were delineated from the comparative analysis of all available material and the variation found, whose homology was tested *a posteriori*. Polymorphic characters were strictly avoided, except when they could be coded consistently. And seven were modified from characters or morphological features already suggested, notably those of Lanyon (1988 and others). These characters are described below, indicating the coding between the terminals and, where necessary, accompanied by a graphic representation. Multistate characters were treated as unordered, and the resulting matrix used in the cladistic analyzes can be found in Appendix 2.

Mandible (1-43)

Character 01. Mandible, *pars caudalis*, posterior coronoid process, position: rostral, more distant in relation to the retroarticular process than the lateral-medial processes distance, or with equivalent distance (0); caudal, less distant in relation to the retroarticular process than the lateral-medial processes distance (1).

In the species that presents the apomorphic state (part of the outgroup representing Pipritidae, Tityridae and Pipridae on the matrix: *Piprites chloris*, *Tityra cayana*, *Pachyramphus polychopterus*, *Xenopipo atronitens* and *Chiroxiphia caudata*), the posterior coronoid process is positioned more caudally, what can be verified comparing the distance between it and the retroarticular process/caudal margin of the lateral cotyla with the lateral-medial processes distance (Figure 1B). Additionally, on those taxa the posterior coronoid process reaches the pseudotemporal tubercle. In the other species (rest of the outgroup including the root species - *Furnarius rufus* - and the ingroup), the posterior coronoid process is rostrally positioned in the mandibular rami, so the distance used for comparison is greater or similar, and the process never reaches the pseudotemporal tubercle (Figure 1A). In the species that lacks the structure, the character was coded as inapplicable (see character 03).

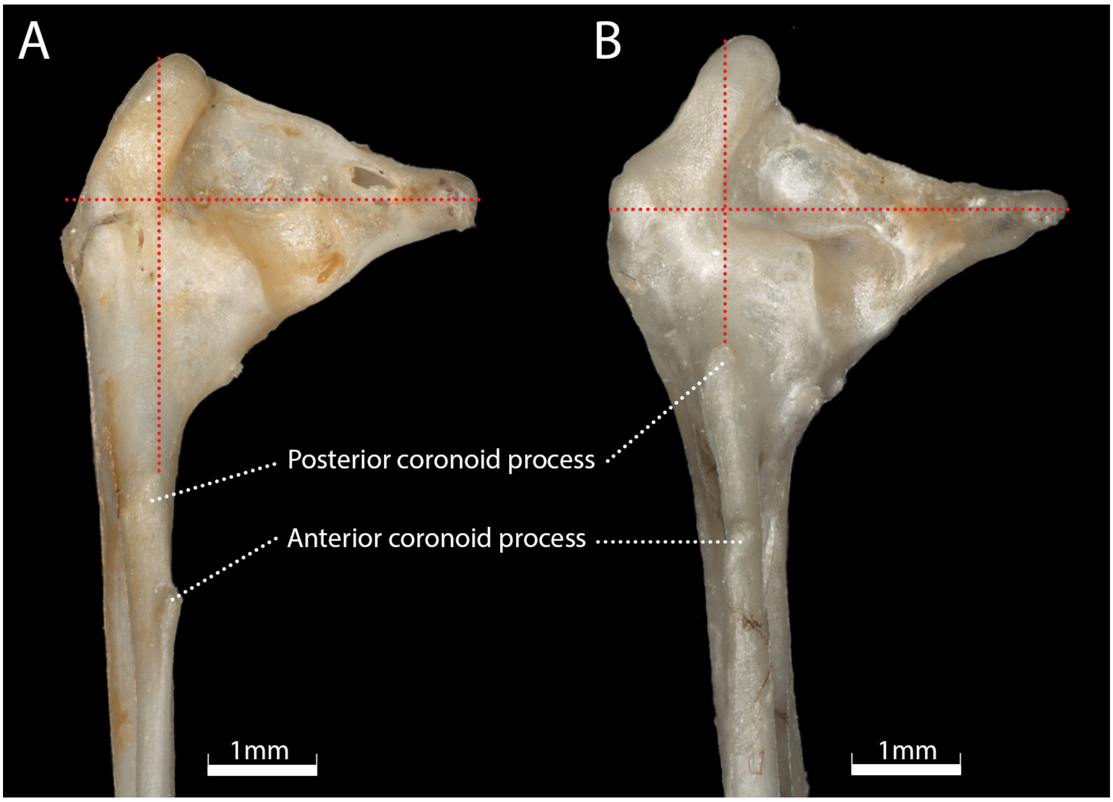

Figure 1. Dorsal view of the caudal part of the right mandibular ramus of *Elaenia flavogaster* (A; USNM 492275) and *Piprites chloris* (B; USNM 622076) illustrating character 01 and its postulated states, respectively: rostral position of the posterior coronoid process (state 0) *vs*. caudal position of the posterior coronoid process (state 1). Red dotted lines indicates the distances used to discretize the character (see notation).

Character 02. Mandible, *pars caudalis*, posterior coronoid process, shape: dome shaped (0); fold shaped (1).

Dome shaped posterior coronoid process (Figure 2A) is present in part of the ingroup including *Anairetes*, *Uromyias*, *Polystictus*, part of *Serpophaga* (*S. subcristata*, *S. munda* and *S. hypoleuca*), part of *Zimmerus* (*Z. minimus* and *Z. parvus*), *Suiriri suiriri* and outgroup represented by the root species *Furnarius rufus*, Tyrannidae:

Fluvicolinae (*Myiophobus fasciatus*, *Sublegatus modestus*, *Pyrocephalus rubinus*, *Knipolegus cyanirostris*) and the analyzed species representing Rhynchocyclidae (*Pseudotriccus pelzelni*, *Phylloscartes ventralis*, *Corythopis torquatus*). Fold shaped posterior coronoid process Figure 2B) was observed in most of the species, with some degree of variation, particularly regarding the orientation, being perpendicular, transversal or oblique in the ramus. Inapplicable for species that lacks the posterior coronoid process (*Myiotriccus*, *Hirundinea*, *Todirostrum*, *Platyrinchus*, *Neopipo*).

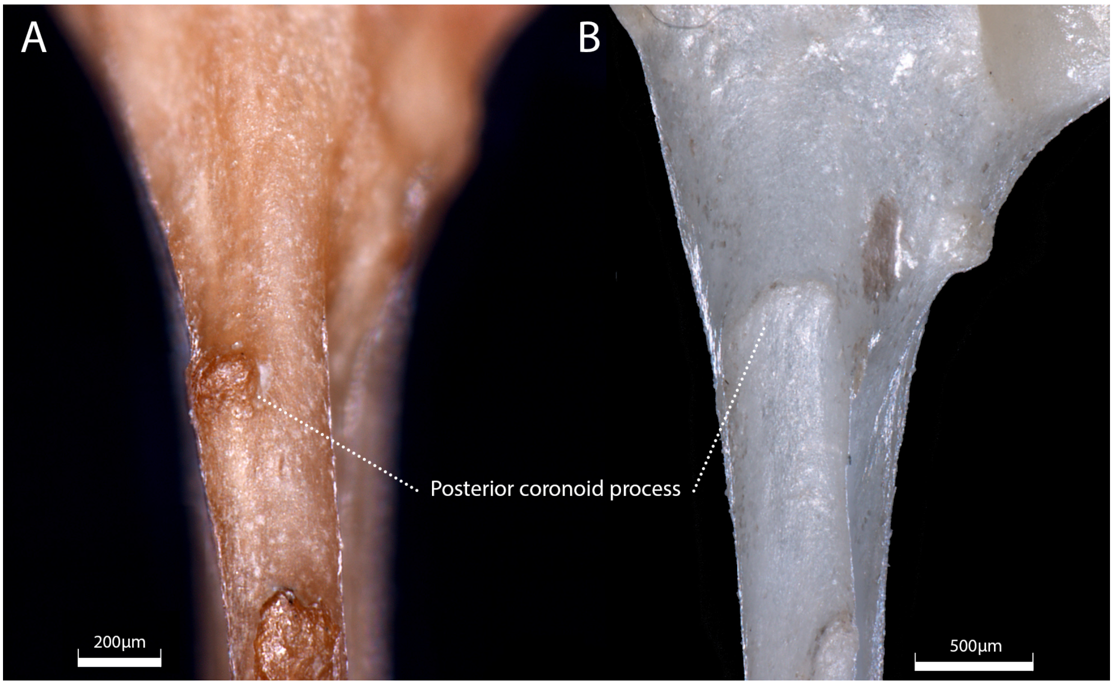

Figure 2. Dorsal partial view of the caudal part of the right mandibular ramus of *Zimmerius parvus* (A; USNM 343855) and *Elaenia ruficeps* (B; USNM 621782) illustrating character 02 and its postulated states, respectively: dome shaped posterior coronoid process (state 0) *vs*. fold shaped posterior coronoid process (state 1).

Character 03. Mandible, *pars caudalis*, posterior coronoid process, degree of development: well developed, comparable in size or larger than the anterior

coronoid process or occupying half or more than half of the ramus width (0); poorly developed, smaller than the anterior coronoid process and occupying less than half of the ramus width (1); vestigial or absent (2).

In the root species and most of the ingroup and outgroup taxa the posterior coronoid process is prominent, occupying at least half of the ramus width. The extreme of variation (a protuberant posterior coronoid process) was observed in the root species, *Furnarius rufus*. The state 1 was observed in part of *Serpophaga* (*S. cinerea* and *S. nigricans*) and *Pseudocolopteryx*. The state 2 is present in part of the outgroup representing Platyrinchidae (*Platyrinchus mystaceus* and *Neopipo cinnamomea*) and Tyrannidae: Hirundineinae (*Hirundinea ferruginea* and *Myiotriccus ornatus*). In the analyzed specimens of these species, the structure appears only like a vestigial mark or is absent.

Character 04. Mandible, *pars caudalis*, anterior coronoid process: present (0); absent (1).

The anterior coronoid process is absent in Onychorhynchidae (*Onychorhynchus coronatus* and *Myiobius barbatus*) and Platyrinchidae (*Platyrinchus mystaceus* and *Neopipo cinnamomea*). The apomorphic state was also observed in species of these two families not included in the matrix (*Onychorhynchus mexicanus*, *Myiobius atricaudus*, *Terenotriccus erythrurus* and *Platyrinchus saturatus*, pers. obs.). The single coronoid process present in *O. coronatus* and *M. barbatus* was identified as the anterior coronoid process based on shape and particularly in its position in the mandibular ramus. *P. mystaceus* was the only species with none coronoid process (characters 03 and 04).

Character 05. Mandible, *pars caudalis*, anterior coronoid process, position: rostral, not reaching the posterior coronoid process (0); caudal, reaching the posterior coronoid process (1).

In the species that present the apomorphic state, the anterior coronoid process is situated so caudally that reaches the posterior coronoid process (Figure 3B), at least in its base. This state was observed in part of *Serpophaga* (*S. cinerea* and *S. nigricans*) and in *Pseudocolopteryx*. In the remaining species, the anterior coronoid process is clearly distant from the posterior coronoid process (Figures 1A-B, 2A-B, 3A). The character was coded as inapplicable in the species that lacks the structure (see character 04).

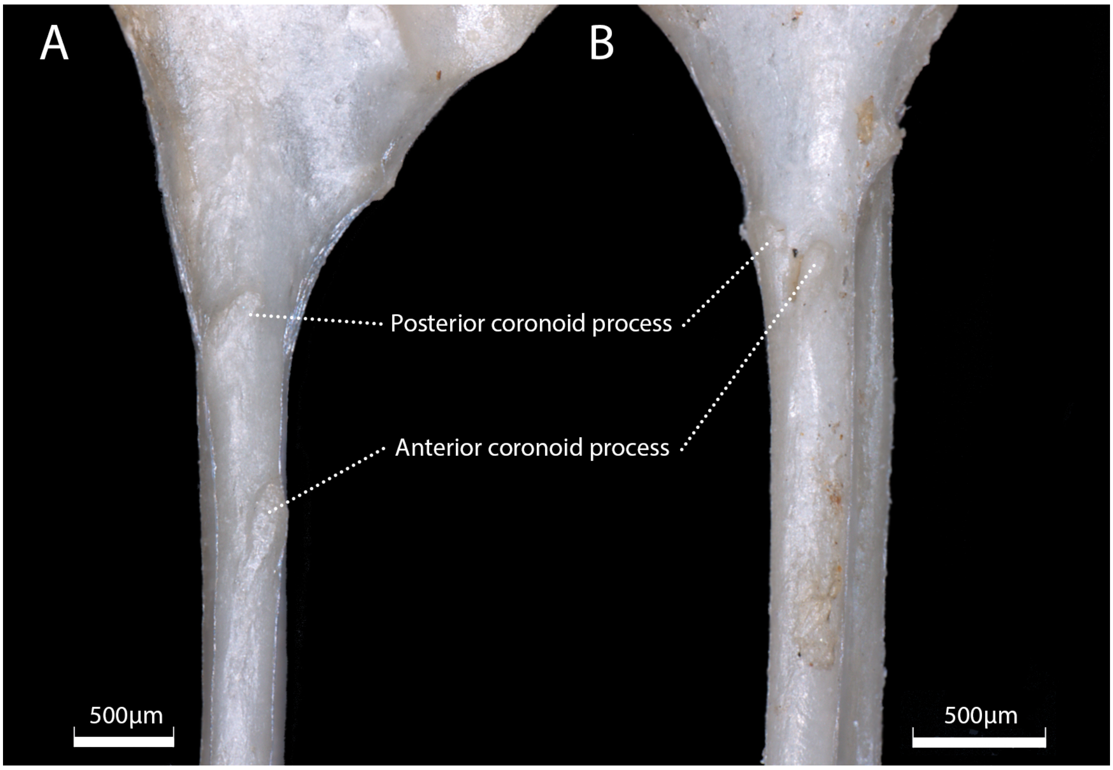

Figure 3. Dorsal partial view of the caudal part of the right mandibular ramus of *Elaenia parvirostris* (A; USNM 635911) and *Pseudocolopteryx sclateri* (B; USNM 227412) illustrating character 05 and its postulated states, respectively: anterior coronoid process not reaching the posterior coronoid process (state 0) *vs*. anterior coronoid process reaching the posterior coronoid process (state 1).

Character 06. Mandible, *pars caudalis*, pseudotemporal tubercle: present (0); absent (1).

The structure is absent or can appears only like a non-conspicuous mark in Rhynchocyclidae: Todirostrinae (*Todirostrum russatum* and *Hemitriccus margaritaceiventer*) and Oxyruncidae (*Oxyruncus cristatus*). In the rest of the species the pseudotemporal tubercle can be clearly identified.

Character 07. Mandible, *pars caudalis*, pseudotemporal tubercle, degree of development: weekly developed (0); well developed (1).

Well-developed pseudotemporal tubercle is similar in size (diameter and/or height) to the coronoid process. This condition can be observed in the analyzed species of the family Tityridae (*Tityra cayana* and *Pachyramphus polychopterus*) (Figure 4B). In most of the species, the pseudotemporal tubercle is conspicuous but clearly smaller than the coronoid process (Figures 1A-B, 3A-B, 4A). The character was coded as inapplicable in the species that lacks the structure (see character 06).

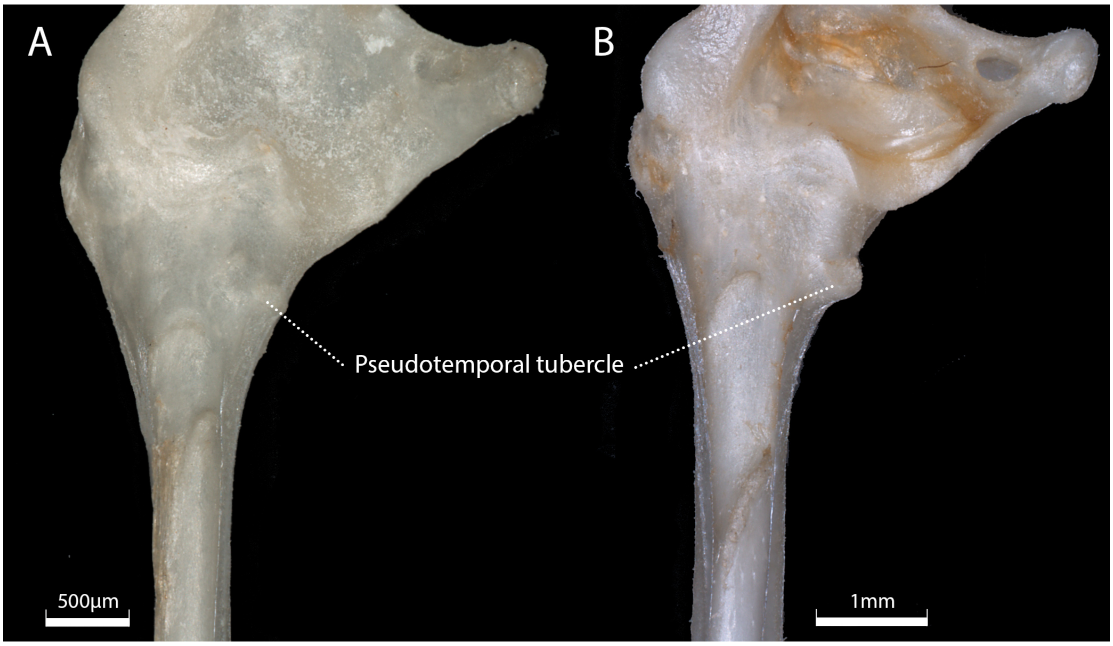

Figure 4. Dorsal partial view of the caudal part of the right mandibular ramus of *Myiopagis cotta* (A; USNM 502802) and *Pachyramphus polychopterus* (B; USNM 227412) illustrating character 06 and two of its postulated states, respectively: weekly developed pseudotemporal tubercle (state 0) *vs*. well developed pseudotemporal tubercle (state 1).

Character 08. Mandible, *pars caudalis*, pseudotemporal tubercle, position: caudal in the sagittal axis, inserted at the caudal enlargement of the ramus, and dorsal in the longitudinal axis (0); rostral in the sagittal axis, inserted closer to the mandibular ramus itself than of its caudal enlargement, and dorsal in the longitudinal axis (1); ventral in the longitudinal axis (2).

The position of the pseudotemporal tubercle varies both in sagittal/anteroposterior and longitudinal axes. Considering the sagittal axis, in most of the species the structure is situated in the intermediate part of the caudal enlargement of the ramus, being closer to the rostral margin of the medial cotyla than to rostral end of the ramus enlargement

(Figure 3A, 4A-B). In *Pseudocolopteryx*, *Serpophaga*, *Polystictus*, *Uromyias*, *Anairetes*, *Culicivora* and *Mecocerculus leucophrys* the pseudotemporal tubercle is closer to the rostral end of the caudal enlargement of the ramus (Figure 3B). In the longitudinal axis, the species that presents character states 0 and 1 have the structure situated within the dorsal half of the ramus. But in the analyzed species of Cotingidae (*Lipaugus vociferans* and *Pipreola whitelyi*) the tubercle clearly varies in its longitudinal position, being situated in the ventral part of the ramus. Inapplicable in the species that lacks the pseudotemporal tubercle (see character 06).

Character 09. Mandible, *pars caudalis*, caudal part of the ramus, height: smaller than the height at the lateral and caudal cotylas (0); plain in relation to the lateral and caudal cotylas (1).

In lateral or medial view, it is possible to identify a difference in the height of the mandibular ramus in its caudal portion. In the plesiomorphic state there is a strong gradual reduction of height towards the caudal limit of the mandible, so that the portion of the caudal end presents about half the height of the ramus in the position of the anterior coronoid process (Figure 5A). This condition can be observed in the root species, *Furnarius rufus*. In the apomorphic state, this height difference does not occur or is minimal, presenting the same or similar height comparing the medial-caudal portion of the ramus to its caudal end (Figure 5B).

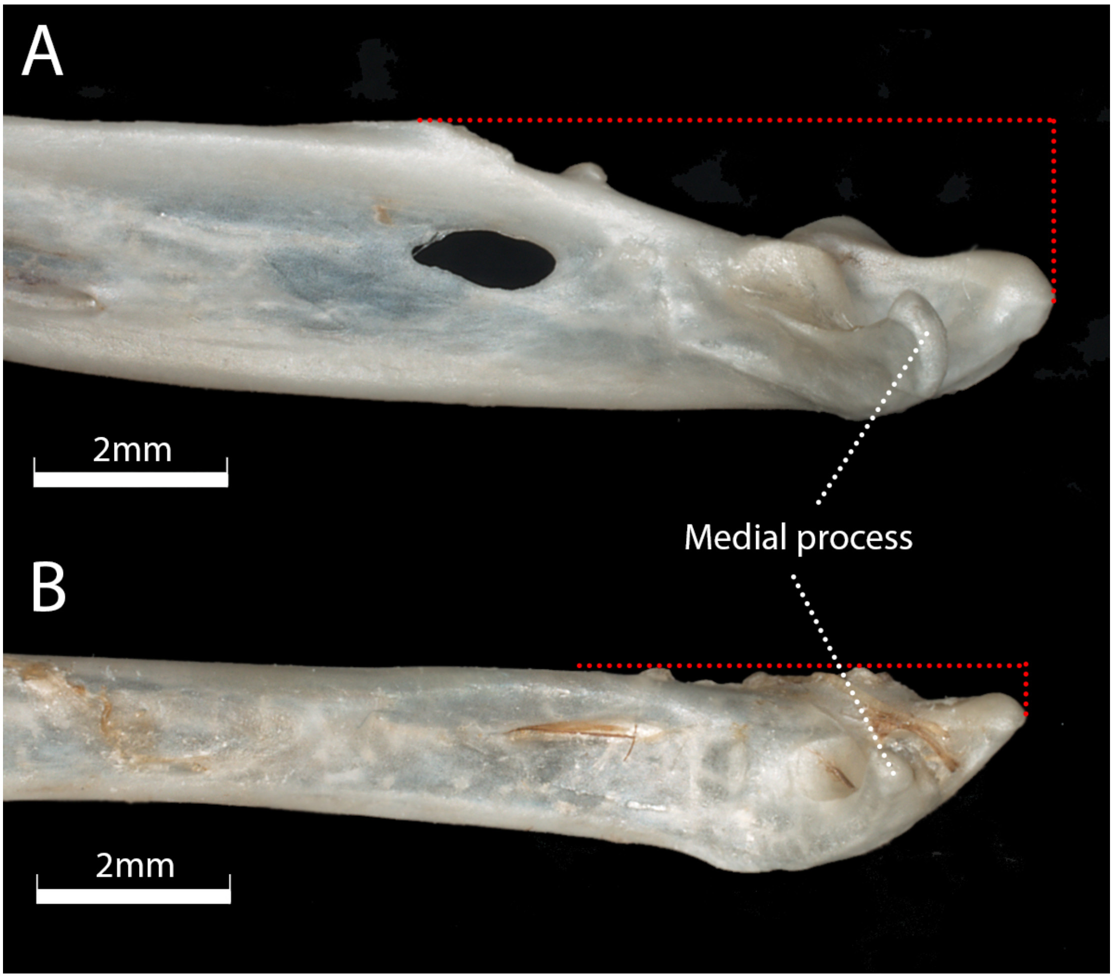

Figure 5. Medial view of the caudal part of the right mandibular ramus of *Furnarius rufus* (A; USNM 614681) and *Onychorhynchus coronatus* (B; USNM 637219) illustrating character 09 and its postulated states, respectively: smaller height at the caudal part (state 0) *vs*. plain caudal position in relation to the ramus. Red dotted lines used to emphasize the height differences.

Character 10. Mandible, *pars caudalis*, caudal cotyla, shape: nearly plain in relation to the ramus axis (0); dorsally oriented (1).

In the analyzed species of Onychorhynchidae (*Onychorhynchus coronatus* and *Myiobius barbatus*) the caudal cotyla is diagonal, facing posteromedially. In the caudal view, it results in a smaller angle with the medial process (higher in the other species), and the caudal cotyla is medial to the ramus axis (lateral in the others). In lateral view, the caudal cotyla is markedly higher than the lateral cotyla (Figure 6B), whereas in the other species the structure is almost flat (Figure 6A).

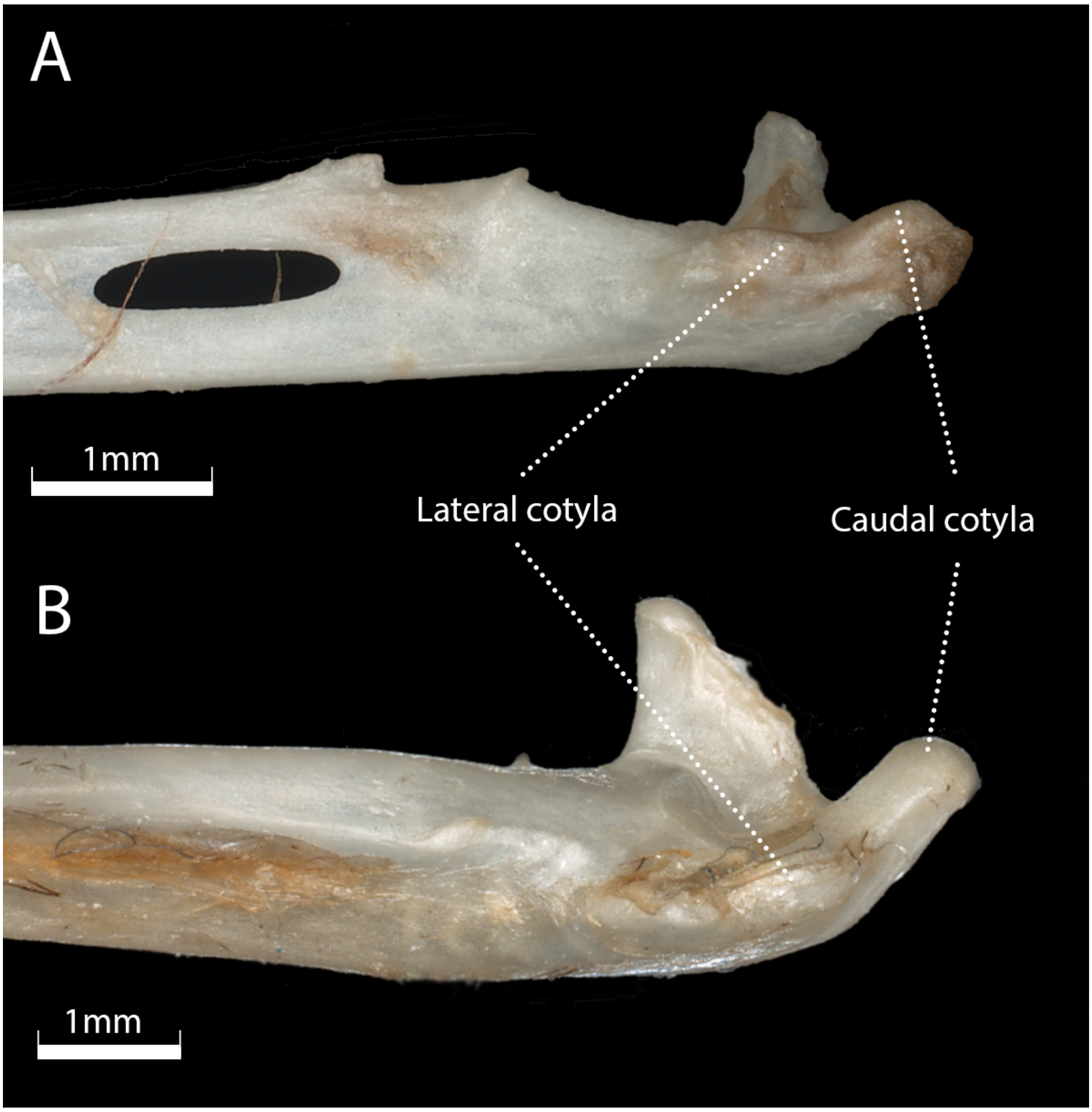

Figure 6. Lateral view of the caudal part of the left mandibular ramus of *Camptostoma obsoletum* (A; USNM 502491) and *Onychorhynchus coronatus* (B; USNM 637219) illustrating character 10 and its postulated states, respectively: plain caudal cotyla (state 0) *vs*. dorsomedially twisted caudal cotyla (state 1).

Character 11. Mandible, *pars caudalis*, bone narrowing between the caudal and lateral cotylas: present (0); absent (1).

In *Furnarius rufus*, there is a thinning between the caudal cotyla and the lateral cotyla, so that the bone in that portion is half the width of the referred cotylas (Figure 7A). In other species, the narrowing does not exist (Figure 7B), or if there is a slight reduction of the width in this portion it never approaches the half in relation to the width of the caudal and lateral cotylas.

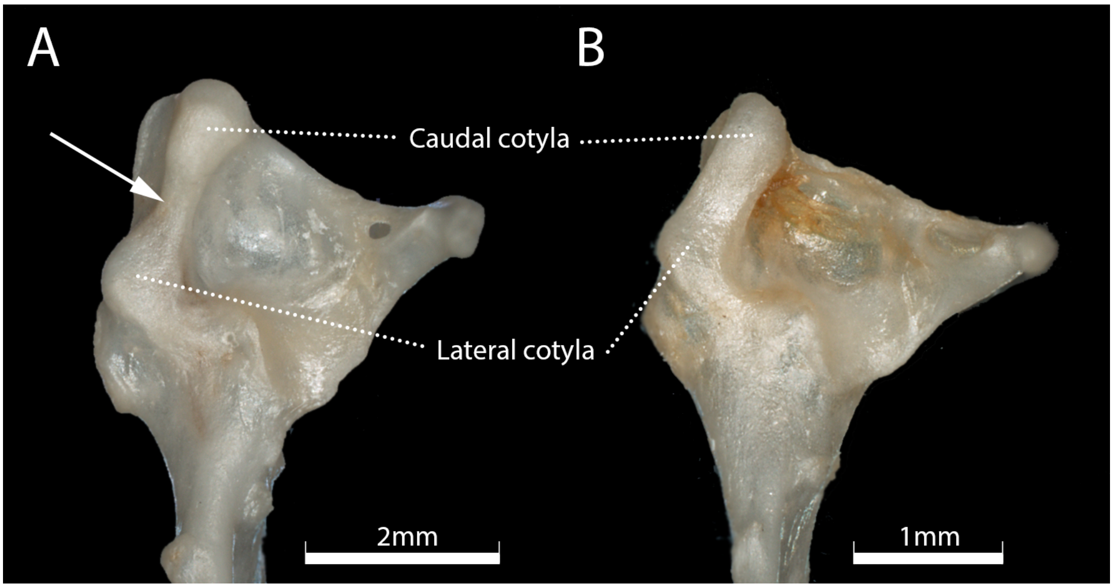

Figure 7. Dorsal view of the caudal part of the right mandibular ramus of *Furnarius rufus* (A; USNM 614681) and *Phaeomyias murina* (B; USNM 500565) illustrating character 11 and its postulated states, respectively: presence of a bone narrowing between the caudal and lateral cotylas (state 0) *vs*. absence of the bone narrowing (state 1). White arrow indicates the condition of the state 0.

Character 12. Mandible, *pars caudalis*, lateral cotyla, shape: dorsoventrally plain (0); dorsomedially twisted (1).

In *Platyrinchus mystaceus* and *Neopipo cinnamomea*, the lateral cotyla is dorsomedially oriented, joining and forming a wall with the intercotylar crest (Figure 8B). Consequently, the intercotylar sulcus is absent. In medial view, the lateral cotyla appears higher than the caudal cotyla. In the other species, the lateral cotyla is dorsoventrally flatter and the intercotylar sulcus can be identified (Figure 8A).

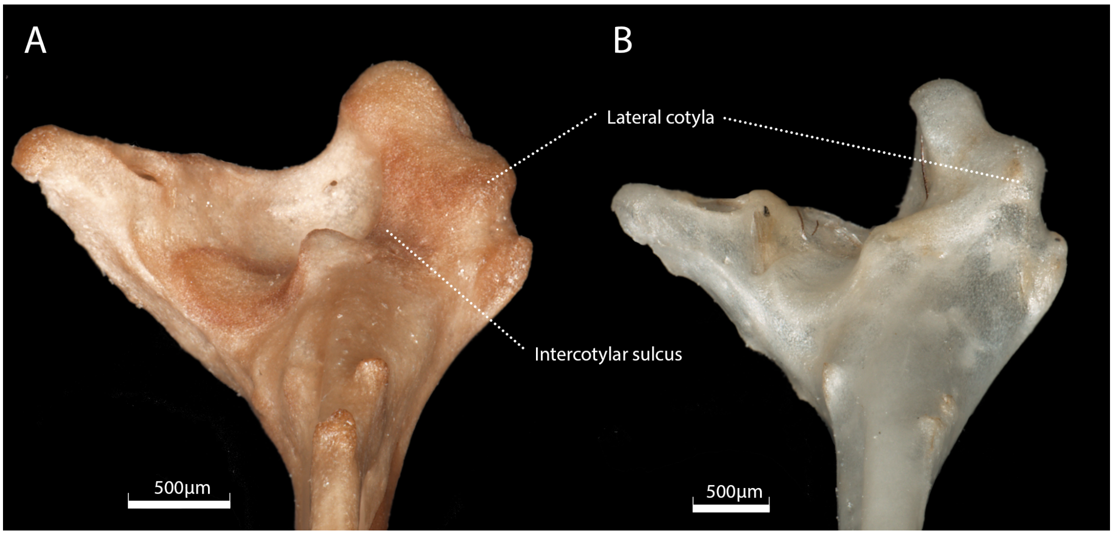

Figure 8. Anterodorsal view of the caudal part of the left mandibular ramus of *Zimmerius parvus* (A; USNM 343855) and *Platyrinchus mystaceus* (B; USNM 556422) illustrating character 12 and its postulated states, respectively: dorsoventrally plain lateral cotyla (state 0) *vs*. dorsomedially twisted lateral cotyla (state 1).

Character 13. Mandible, *pars caudalis*, medial cotyla, shape and size: medium size, proportional width-length relation (0); small, width lesser than length (1); large, width wider than length (2).

The state 2, in which the species presents a wide medial cotyla, was identified in Tityridae (*Tiryra cayana* and *Pachyramphus polychopterus*) and *Pitangus* *sulphuratus* (Figure 4B). A small medial cotyla, longer in length than in width (state 1), was coded only for *Pipreola whitelyi*. Most of the species presents an intermediate condition, in which the medial cotyla have similar width and length (Figure 7A-B), being the plesiomorphic state of the character.

Character 14. Mandible, *pars caudalis*, *fossa caudalis*, caudal wall, degree of development: well developed (0); weekly developed/reduced (1).

The bone wall that forms the *fossa caudalis* in the posterior end of the mandible bonds the caudal cotyla with the medial process. That caudal wall is weekly developed and almost completely opened in *Platyrinchus mystaceus* (Figure 9B) and partially opened in *Hirundinea ferruginea*, *Neopipo cinnamomea* and Cotingidae (*Lipaugus vociferans* and *Pipreola whitelyi*). In the remaining species the caudal wall is well developed and closed (Figure 9A).

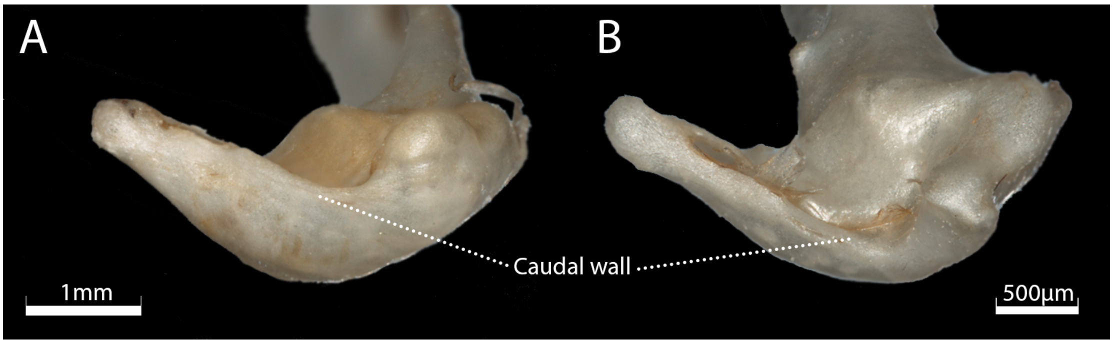

Figure 9. Caudal view of the caudal part of the right mandibular ramus of *Elaenia flavogaster* (A; USNM 492275) and *Platyrinchus mystaceus* (B; USNM 556422) illustrating character 14 and its postulated states, respectively: well developed caudal wall (state 0) *vs*. weekly developed (opened) caudal wall (state 1).

Character 15. Mandible, *pars caudalis*, lateral process, degree of development: weekly developed (0); well developed/prominent (1).

A prominent lateral process of the mandible was observed in *Serpophaga*, *Mecocerculus leucophrys*, *Anairetes*, *Uromyias*, *Pseudocolopteryx*, *Polystictus* and *Culicivora* (Figure 10B). In these species that lateral inflation can be easily identified also in ventral or lateral views, forming an angle with the caudal part of the lateral margin of the *incisura retroarticularis*. In the remaining species the structure is totally absent or appears poorly developed (Figure 10A).

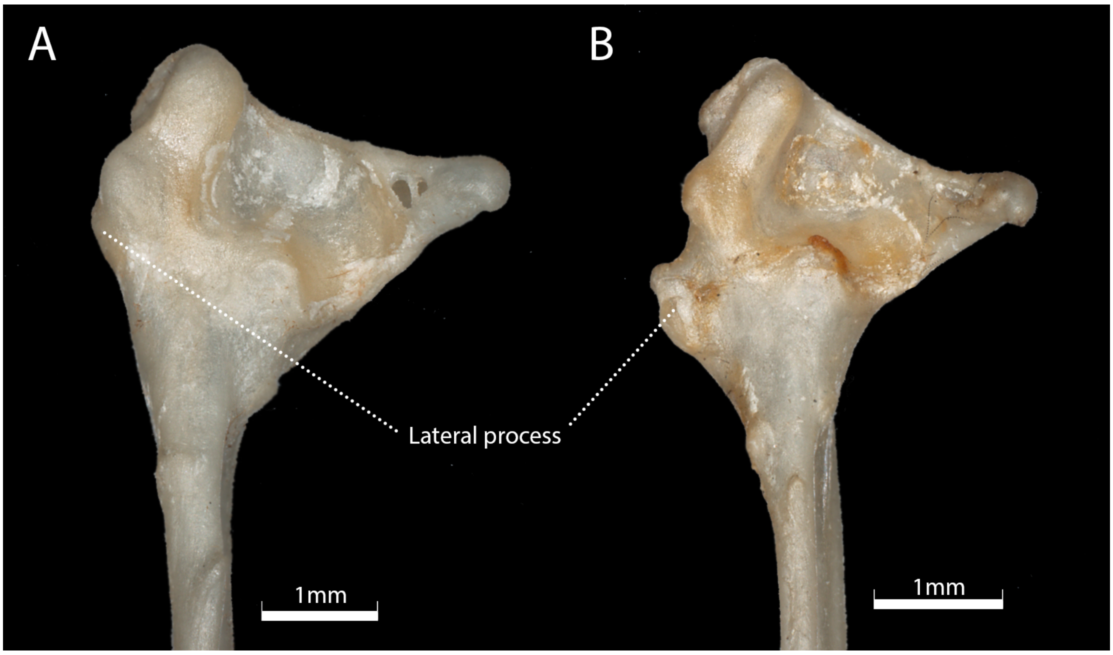

Figure 10. Dorsal view of the caudal part of the right mandibular ramus of *Elaenia martinica* (A; USNM 487918) and *Mecocerculus leucophrys* (B; USNM 428279) illustrating character 15 and its postulated states, respectively: weekly developed lateral process (state 0) *vs*. well developed lateral process (state 1).

Character 16. Mandible, *pars caudalis*, medial process at the medial tip, size/shape: enlarged width, flat (0); reduced width, rounded or acuminate (1).

In *Furnarius rufus*, *Tachuris rubrigastra* and part of *Serpophaga* (*S. nigricans* and *S. cinerea*) the medial end of the medial process is dorsoventrally flattened (Figure 5A, 11A), whereas in the other species the tip of the medial process is rounded or acuminate presenting a smaller width (Figure 5B, 11B).

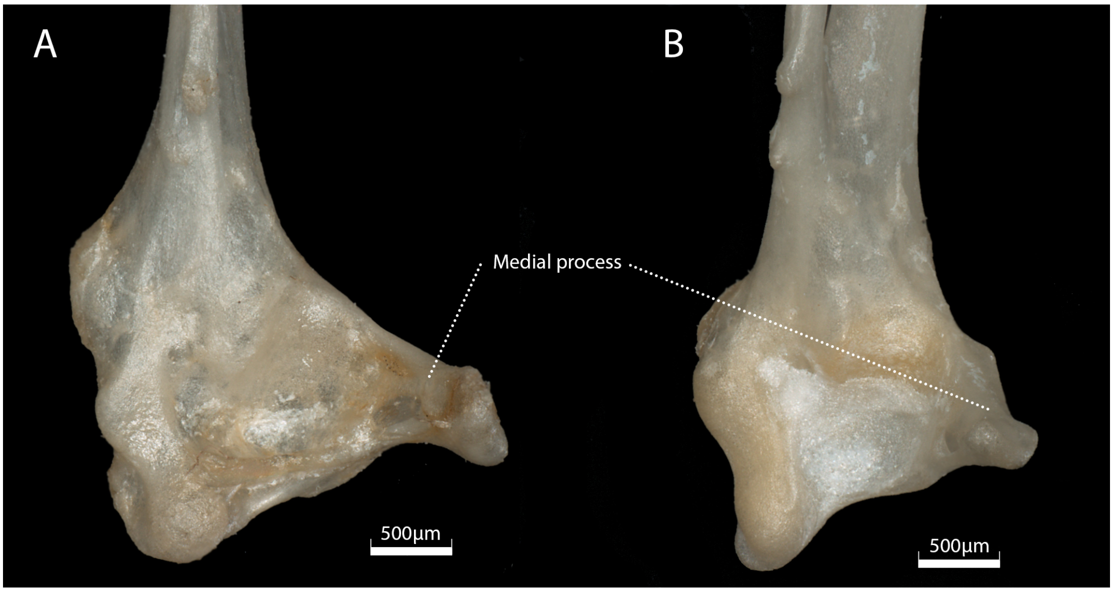

Figure 11. Dorsal view of the caudal part of the left mandibular ramus of *Tachuris rubrigastra* (A; USNM 614704) and *Zimmerius minimus* (B; USNM 344215) illustrating character 16 and its postulated states, respectively: flat medial process tip (state 0) *vs*. rounded medial process tip (state 1).

Character 17. Mandible, *pars caudalis*, articular end, protuberance below the caudal cotyla: present (0); absent (1).

In the species that presents the plesiomorphic state of the character, in lateral view the caudal cotyla can be clearly distinguished from a bony mass forming a protuberance below it (Figure 6A). In some species it can be observed also in dorsal view, slightly lateral or posterior in relation to the caudal cotyla. The structure was not considered homologous to the retroarticular process (see character 19) because of its reduced development degree, form and for not being a true postarticular process (in general its extension is the same as the caudal cotyla). The apomorphic state, the absence of the protuberance, was observed in *Onychorhynchus coronatus* (Figure 6B), *Piprites chloris*, Pipridae (*Chiroxiphia caudata* and *Xenopipo atronitens*) and Cotingidae (*Lipaugus vociferans* and *Pipreola whitelyi*).

Character 18. Mandible, *pars caudalis*, articular end, protuberance below the caudal cotyla, size and shape: small (0); large, inflated and laterally oriented (1).

In ventral or ventromedial view the apomorphic state is represented by an inflated and laterally oriented protuberance (Figure 12B). This condition was observed in *Mecocerculus* (except *M. leucophrys*), *Camptostoma*, *Ornithion* and *Phyllomyias* (except *P. fasciatus*). In dorsal view some species with the plesiomorphic state shows a visible lateral margin, which is just a small fold not the considered inflation. So in the rest of the species the protuberance is small and is not laterally inflated in ventral view (Figure 12A). Inapplicable for the species that lacks the protuberance below the caudal cotyla (see character 17).

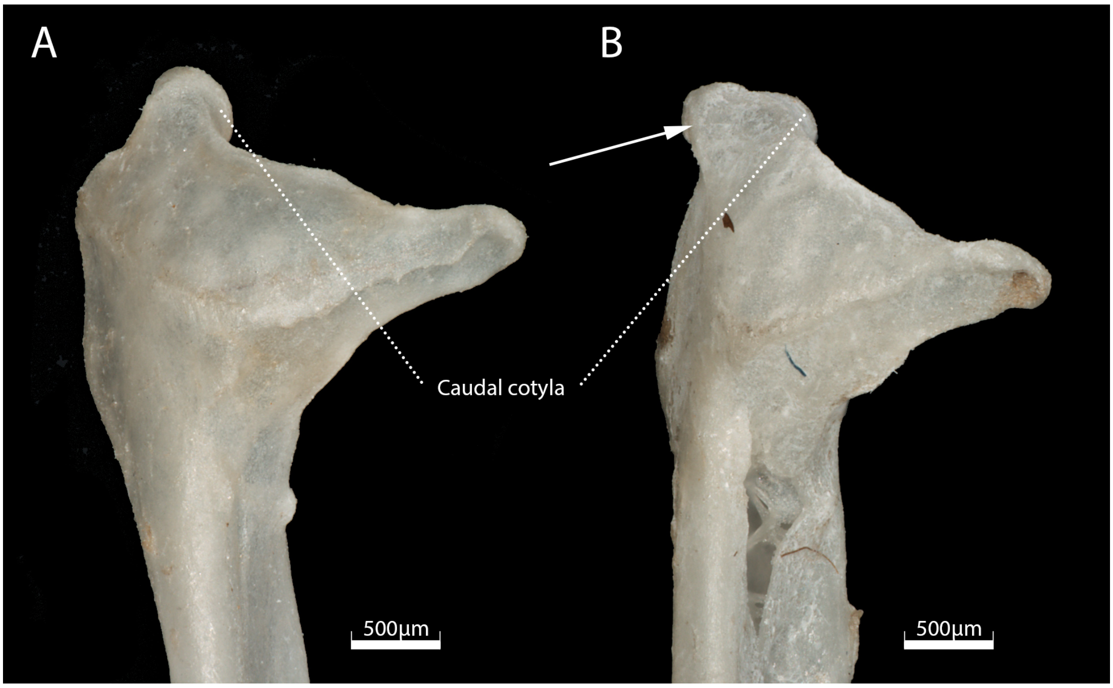

Figure 12. Ventromedial view of the caudal part of the left mandibular ramus of *Myiopagis viridicata* (A; USNM 555998) and *Mecocerculus minor* (B; USNM 560008) illustrating character 18 and its postulated states, respectively: small protuberance below the caudal cotyla (state 0) *vs*. inflated and laterally oriented protuberance (state 1). White arrow indicates the condition of the state 1.

Character 19. Mandible, *pars caudalis*, retroarticular process: absent or vestigial (0); present and prominent (1).

Only *Oxyruncus cristatus* presents a process clearly differentiated and prolonging caudally from the caudal cotyla (Figure 13; also see Figure 5F in Warter 1976). In the rest of the species the structure is absent, or there are a bony mass below the caudal cotyla which was not identified as a retroarticular process (see characters 17 and 18).

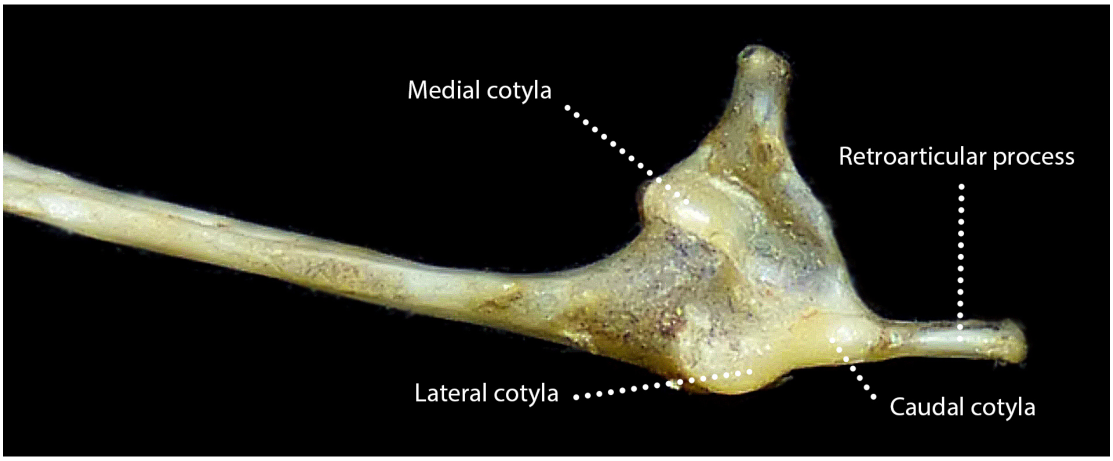

Figure 13. Dorsal view of the caudal part of the left mandibular ramus of *Oxyrunchus cristatus* (AMNH 410) illustrating state 1 of the character 19: prominent retroarticular process *vs*. absent or vestigial retroarticular process (state 0; illustrated in Figures 1, 5, 6, 7, 8, 10, 11).

Character 20. Mandible, *pars caudalis*, medial process, *foramen pneumaticum articulare*: present (0); absent (1).

The apomorphic state was observed only in the examined specimens of *Onychorhyncus coronatus* (Figure 6B).

Character 21. Mandible, *pars caudalis*, medial process, *foramen pneumaticum articulare*, size: small (0); large (1).

The medial process foramen was considered small when the minor diameter of the foramen (generally the diameter at the sagittal axis) was lesser than 1/3 of the medial process width in the position of the medial margin of the foramen. Only the root species *Furnarius rufus* and the outgroup species *Oxyrunchus cristatus* was coded with the plesiomorphic state of the character (Figure 14A). The remaining species have a large medial process foramen (more or equal than 1/3 of the utilized measure; Figure 14B-C). Inapplicable in the species that lacks the foramen (see character 20).

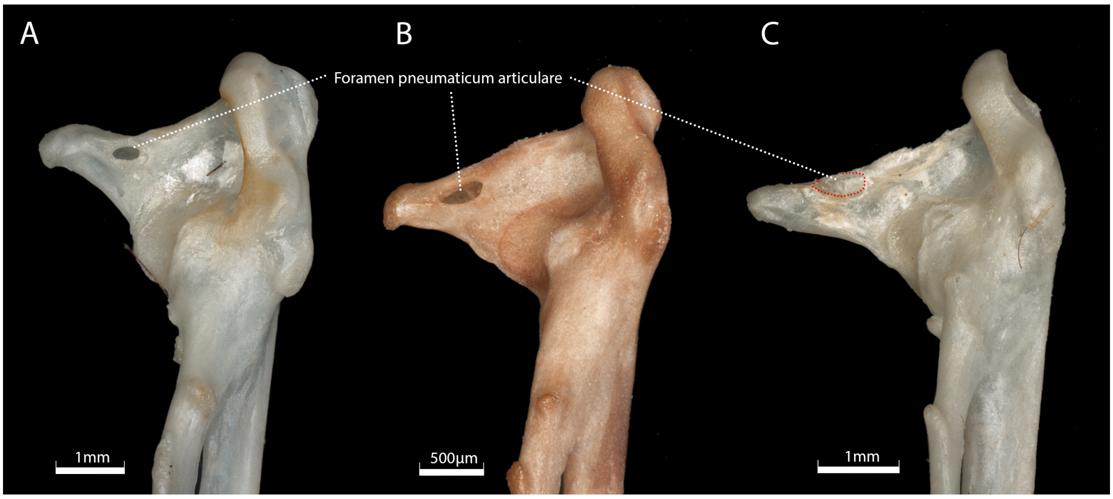

Figure 14. Dorsolateral view of the caudal part of the left mandibular ramus of *Furnarius rufus* (A; USNM 614681), *Zimmerius parvus* (B; USNM 343855) and *Piprites chloris* (C; USNM 622076) illustrating characters 21 and 22 and its postulated states: Char. 21 - small *foramen pneumaticum articulare* (state 0; A) *vs*. large *foramen pneumaticum articulare* (state 1; B and C); Char. 22 - *foramen pneumaticum articulare* dorsally positioned (state 0; A and B) *vs*. *foramen pneumaticum articulare* caudally positioned (state 1; C; the foramen appears covered by connective tissue, the red dotted line indicates its limits).

Character 22. Mandible, *pars caudalis*, medial process, *foramen pneumaticum articulare*, position: dorsal (0); dorsocaudal (1).

In *Piprites chloris*, the *foramen pneumaticum articulare* is dorsocaudally oriented, reaching the caudal wall of the medial process (Figure 14C). In all the remaining species the foramen is dorsally positioned, never reaching the caudal limits of the mandible, and it is possible to identify the bony bar between the foramen and the caudal margin of the medial process (Figures 14A-B). In the species that lacks the foramen, the character was coded as inapplicable (see character 20).

Character 23. Mandible, *pars caudalis*, intercotylar tubercle, shape: slight curved in the frontal-vertical axes (0); with a small notch below the medial margin (1).

The apomorphic state was found in Pipridae (*Chiroxiphia caudata* and *Xenopipo atronitens*), which presents a slight notch below the medial margin of the intercotylar tubercle, better observed in an anteromedial perspective.

Character 24. Mandible, *pars caudalis*, intercotylar tubercle, concavity in the rostral border: absent (0); present (1).

The analyzed species of *Zimmerius* presents a conspicuous concavity in the rostral end of the intercotylar tubercle that also reaches the rostral limits of the medial cotyla (Figure 15A). In all the remaining genera the concavity is totally absent (Figure 15B-C).

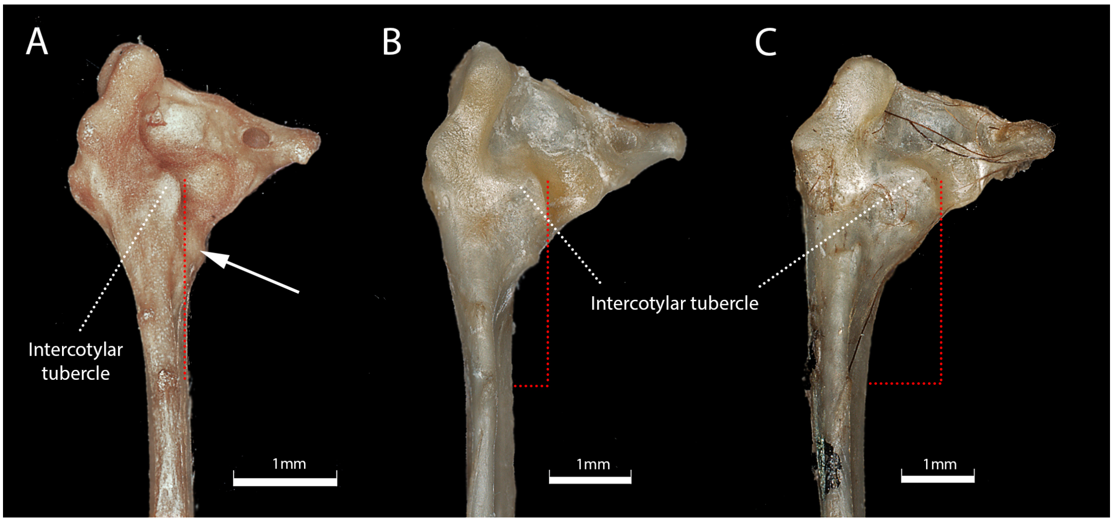

Figure 15. Dorsal view of the caudal part of the right mandibular ramus of *Zimmerius parvus* (A; USNM 343855), *Elaenia obscura* (B; USNM 347157) and *Xenopipo atronitens* (C; USNM 621075) illustrating characters 24 and 25 and its postulated states: Char. 24 - presence of a concavity rostral to the intercotylar tubercle (state 1; A; white arrow indicates the condition) *vs*. absence of the referred concavity (state 0; B and C); Char. 25 - intercotylar tubercle positioned in the same axis of the mandibular ramus (state 0; A) *vs*. slightly medial positioned (state 1; B) *vs*. medially positioned (state 2; C). Red dotted lines indicates the distances used to discretize the character 25 (intercotylar tubercle in relation to the mandibular ramus).

Character 25. Mandible, *pars caudalis*, intercotylar tubercle, position: at the same axis of the mandibular ramus (0); intermediate, slightly medial in relation to the mandibular ramus (1); medial in relation to the mandibular ramus (2).

The plesiomorphic state was observed in most of the species, that presents the anterior limits of the intercotylar tubercle on the same axis of the mandibular ramus (Figure 15A). The state 2 was identified in the examined species of Pipridae (*Chiroxiphia caudata* and *Xenopipo atronitens*), Cotingidae (*Lipaugus vociferans* and *Pipreola* *whitelyi*) and part of *Elaenia* (*E. gigas* and *E. strepera*), in which the intercotylar tubercle margin is medially situated in relation to the mandibular ramus, distant from the ramus more than its width (Figure 15C). The position of the tubercle can be directly associated with the general form and proportions of the caudal head of the mandible (lateromedial wider in these taxa, especially on that of the outgroup). An intermediate stage was also identified, including *Elaenia* (except *E. gigas* and *E. strepera*), *Myiopagis*, *Ornithion inerme*, *Oxyrunchus cristatus*, Tityridae (*Tityra cayana* and *Pachyramphus polychopterus*) and Tyrannidae: Tyranninae (*Pitangus sulphuratus* and *Myiozetetes cayanensis*). In these species the position of the intercotylar tubercle is not the same in relation to the mandibular ramus axis, but the distance between the considered position and the mandibular ramus is smaller than the width of the ramus (Figure 15B). The discretized character stages can also be associated with the position of the medial cotyla, so that the position of the medial cotyla was not included as a character.

Character 26. Mandible, *pars caudalis*, intercotylar sulcus: present (0); absent (1).

Most of the species presents the intercotylar sulcus, somewhat varying in development degrees (*e.g.* well developed in *Onychorhynchus coronatus*). The apomorphic state was identified in *Ornithion* and *Camptostoma*.

Character 27. Mandible, *pars caudalis*, ramus at the caudal end, configuration: distinction between the angular and articular bones well defined (0); differentiation between the angular and articular bones poorly defined (1).

The plesiomorphy was found only in the root species, *Furnarius rufus*, which have a marked differentiation between the angular and articular bones (Figure 16A). In the remaining species the differentiation of those bones in that portion of the mandibular ramus is not possible, being internally fused and totally covered by the bony corpus (Figure 16B).

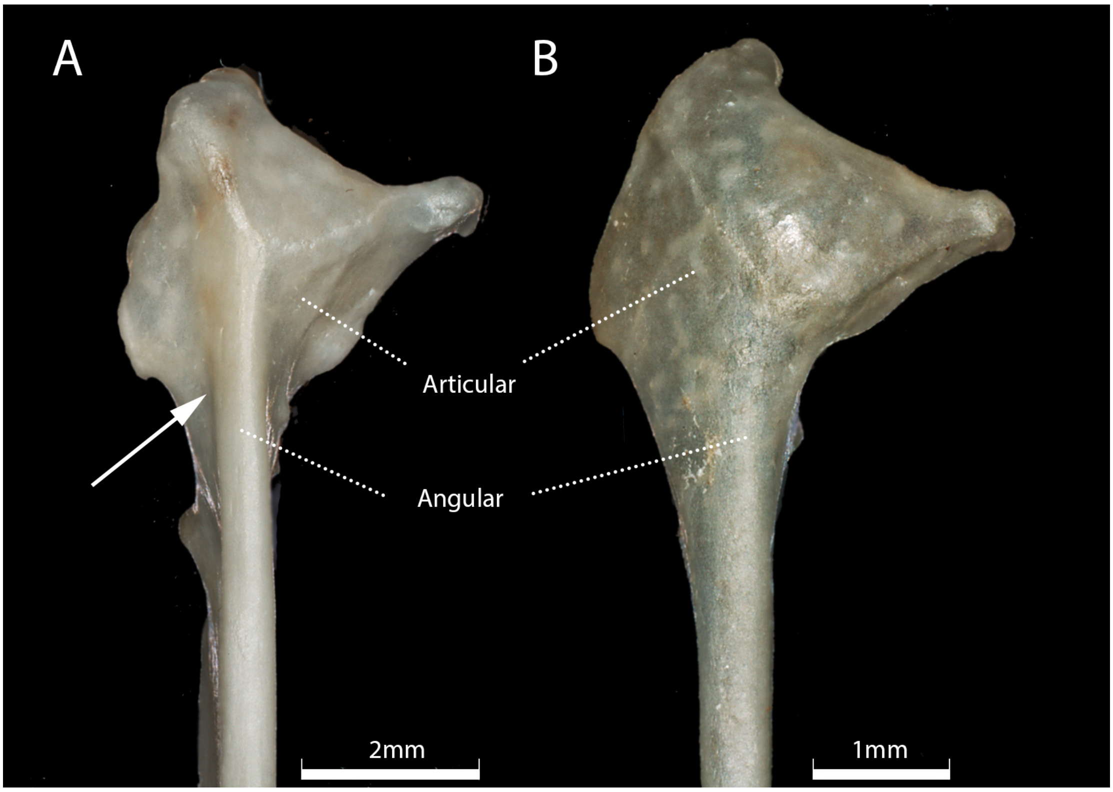

Figure 16. Ventral view of the caudal part of the left mandibular ramus of *Furnarius rufus* (A; USNM 614681) and *Myiobius barbatus* (B; USNM 632573) illustrating character 27 and its postulated states, respectively: well differentiated angular and articular bones (state 0) *vs*. poorly differentiated angular and articular bones (state 1). White arrow indicates the position of the junction of the referred bones and the condition of the plesiomorphic state.

Character 29. Mandible, *pars caudalis*, ramus at the caudal end, ventromedial arching: absent, almost straight ramus (0); slight (1); sharp (2).

Most of the analyzed species presents a slightly arched ramus at its caudal end just near to the articular head of the mandible (state 1; Figure 17B). But in the root species - *Furnarius rufus* - and in *Onychorhynchus*, *Myiobius*, *Sublegatus*, *Corythopis*, *Polystictus*, part of *Serpohaga* (*S. subcristata*, *S. munda*, *S. hypoleuca*) and *Suiriri suiriri* the arching is absent or at least non conspicuous, and the ramus seems straight in medial view (Figure 17C). The state 2, a well-arched ramus, was observed only in *Elaenia gigas* and *E. strepera* (Figure 17A). The character states are better observed and comparable in a medial or especially dorsomedial view.

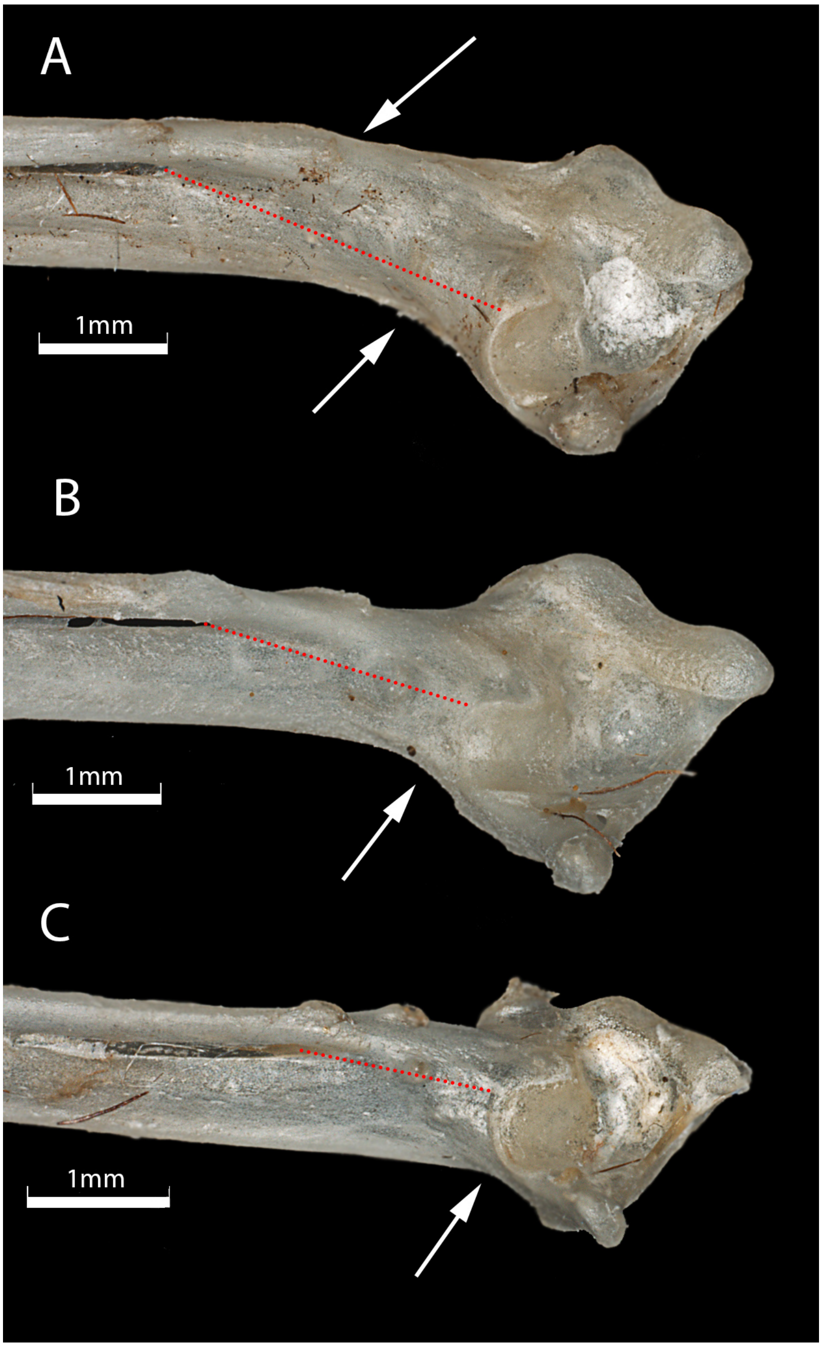

Figure 17. Dorsomedial view of the caudal part of the right mandibular ramus of *Elaenia strepera* (A; USNM 645291), *Myiopagis subplacens* (B; USNM 64388) and *Polystictus pectoralis* (C; USNM 622325) illustrating characters 29 and 32 and its postulated states: Char. 29 - sharply arched ramus (state 2; A) *vs*. slightly arched ramus (state 1; B) *vs*. straight ramus (state 0; C). The white arrows indicate the positions where the variation is better viewed. Char. 32 - rostrally positioned

mandibular fenestra (state 0; A and B) *vs*. caudally positioned mandibular fenestra (state 1; C). Red dotted lines indicate the distances used to discretize the character 32 (see notation). The pictures were taken with the exact same angle.

Character 30. Mandible, *pars caudalis*, mandibular fenestra, degree of development: well developed (0); poorly developed (1).

The apomorphic state is present in Onychorhynchidae (*Onychorhynchus coronatus* and *Myiobius barbatus*), *Pipreola whitelyi* and Pipridae (*Chiroxiphia caudata* and *Xenopipo atronitens*). There are some degrees of variation in *C. caudata* but most of the analyzed specimens better fitted this state. In these species the mandibular fenestra is not opened (can appears just as a shallow concavity) or is absent (Figures 5B, 6B). In the rest of the species the mandibular fenestra is opened and conspicuous (Figures 5A, 6A).

Character 31. Mandible, *pars caudalis*, mandibular fenestra, vertical position: dorsal (0); central (1).

The majority of the analyzed species presented the mandibular fenestra positioned at the dorsal half of the mandibular ramus (Figure 17) or at least closely to the dorsal margin (Figure 5A, 7A). Only *Lipaugus vociferans* (Cotingidae) showed a mandibular fenestra centrally positioned in the vertical axis. The character was considered inapplicable for the species that lacks structure or have it poorly developed or vestigial (see character 30).

Character 32. Mandible, *pars caudalis*, mandibular fenestra, horizontal position: caudal (0); rostral (1).

The position of the mandibular fenestra in the sagittal axis was measured according to the distance to the anterior margin of the medial cotyla (red dotted lines in Figure 17). Two character states were identified: the plesiomorphic state in which the considered distance is lesser or similar to the ramus height on that position (Figures 5A, 17C), observed in *Furnarius rufus* and in *Polystictus* and part of *Serpophaga* (*S. hypoleuca*, *S. munda*, *S. subcristata*). On those species, generally the caudal margin of the mandibular fenestra coincides or appears caudal in relation to the anterior coronoid process. And the apomorphic condition in which the used distance is higher than the ramus height (6A, 17 A and B), observed in most of the analyzed species. The character was inserted as inapplicable for the species that lacks a conspicuous mandibular fenestra (see character 30).

Character 33. Mandible, *pars caudalis*, mandibular fenestra, size, height: small (0); high (1).

Mandibular fenestra with small height - smaller than the height of the ramus' dorsal bar - was identified in *Furnarius rufus*, *Hirundinea ferruginea*, *Todirostrum russatum*, *Elaenia gigas*, *E. ridleyana*, *E. strepera*, *Myiopagis cotta*, *M. subplacens* and *Polystictus pectoralis* (Figure 17). The remaining species presents the mandibular fenestra with higher height (Figure 6A). Coded as inapplicable for the species that lacks the structure (see character 30).

Character 34. Mandible, *pars caudalis*, mandibular fenestra, size, width: shorter (0); longer (1). than the ramus height.

The plesiomorphic state was observed in *Furnarius rufus*, *Lipaugus vociferans*, *Pachyramphus polychopterus*, *Piprites chloris*, *Hirundinea ferruginea* and part of *Elaenia* (*E. gigas* and *E. ridleyana*), which presents a mandibular fenestra shorter than the ramus height on the same position (Figure 5A). In the rest of the species the fenestra width is longer than the ramus height (Figure 6A), or equivalent. Inapplicable in the species that lacks the mandibular fenestra (see character 30).

Character 35. Mandible, *pars intermedia*, *fossa aditus*, size/shape: shallow (0); deep (1).

The majority of the species presents the *fossa aditus* with a deep depression, and the plesiomorphic condition was found in *Furnarius rufus*, Onychorhynchidae (*Onychorhynchus coronatus* and *Myiobius barbatus*) and *Hirundinea ferruginea*.

Character 36. Mandible, *pars intermedia*, lateral fossa: present (0); absent (1).

Absence of the lateral fossa in the intermediate part of the mandible, the apomorphic state of the character, was observed in *Chiroxiphia*, *Xenopipo*, *Platyrinchus*, *Neopipo*, *Todirostrum*, *Tachuris* and *Myiobius*. In the remaining species (ingroup and part of outgroup including the root taxon) the lateral fossa is conspicuous.

Character 37. Mandible, *pars intermedia*, mandibular angle: present (0); absent (1).

The mandibular angle, situated between the intermediate and symphysial regions of the mandible, was not observed only in *Tachuris rubrigastra* (Tachurisidae).

Character 38. Mandible, *pars intermedia*, mandibular angle, difference in width between the caudal and rostral portions of the rami: absent, or not marked (0); present, well marked (1).

In the analyzed species representing Tyrannidae: Hirundineinae (*Hirundinea ferruginea* and *Myiotriccus ornatus*) and in *Sublegatus modestus*, the ramus width in the portions anterior and posterior in relation to the mandibular angle is markedly different (Figure 18A). In the rest of the species the ramus width on those portions are similar or at least the difference is slighter (Figure 18B).

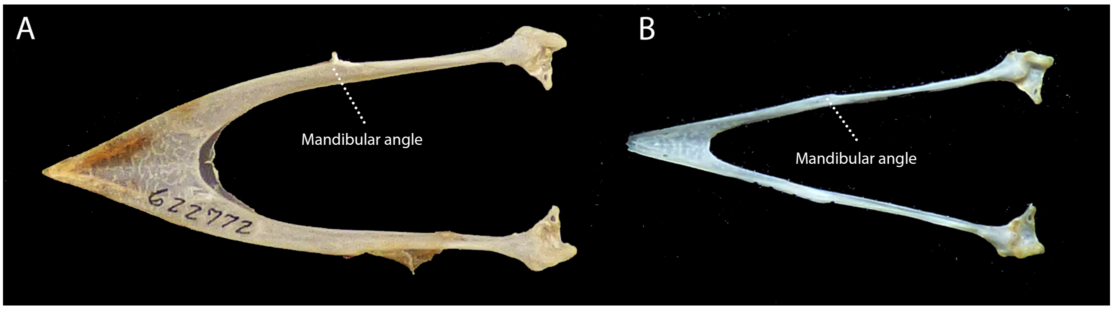

Figure 18. Dorsal view of the mandible of *Hirundinea ferruginea* (A; USNM 622772) and *Stigmatura napensis* (B; USNM 491716) illustrating character 38 and its postulated states, respectively: marked difference in ramus width between anterior and posterior parts (state 1) *vs*. similar width in anterior and posterior parts of the ramus (state 0). Not scaled.

Character 39. Mandible, *pars symphysialis*, mandibular symphysis, neurovascular foramina: present (0); absent (1).

The series of small neurovascular foramina varies in degrees of conspicuousness, but was not observed in part of the outgroup including *Onychorhynchus*, *Hemitriccus*, *Todirostrum*, *Phylloscartes*, *Corythopis*, *Pseudotriccus*, *Hirundinea* and *Myiotriccus*. In the remaining species the foramina can be identified.

Character 40. Mandible, *pars symphysialis*, mandibular symphysis, size, lenght: short, occupying less than 30% of the ramus (0); long, occupying more than 30% of the ramus (1).

All the ingroup and part of the outgroup (e.g. *Pipreola* and Pipridae) presents the symphysial region occupying less than 30% of the ramus length (Figure 18B), generally around 20% or even less (about 15% in *Elaenia strepera*). The apomorphic state, a long symphyseal region, was identified in *Hirundinea* (Figure 18A), *Myiotriccus*, *Todirostrum*, *Lipaugus*, *Pyrocephalus*, *Pitangus* and the ingroup species *Nesotriccus ridgwayi*.

Character 41. Mandible, *pars symphysialis*, mandibular symphysis, caudal margin, shape: rounded (0); straight, forming an angle with the ramus (1).

The apomorphic state was identified in *Inezia* and part of *Mecocerculus* (*M. stictopterus*, *M. poecilocercus* and *M. hellmayri*) (Figure 19A). The remaining species presents the caudal margin of the symphysis round shaped (Figure 19B).

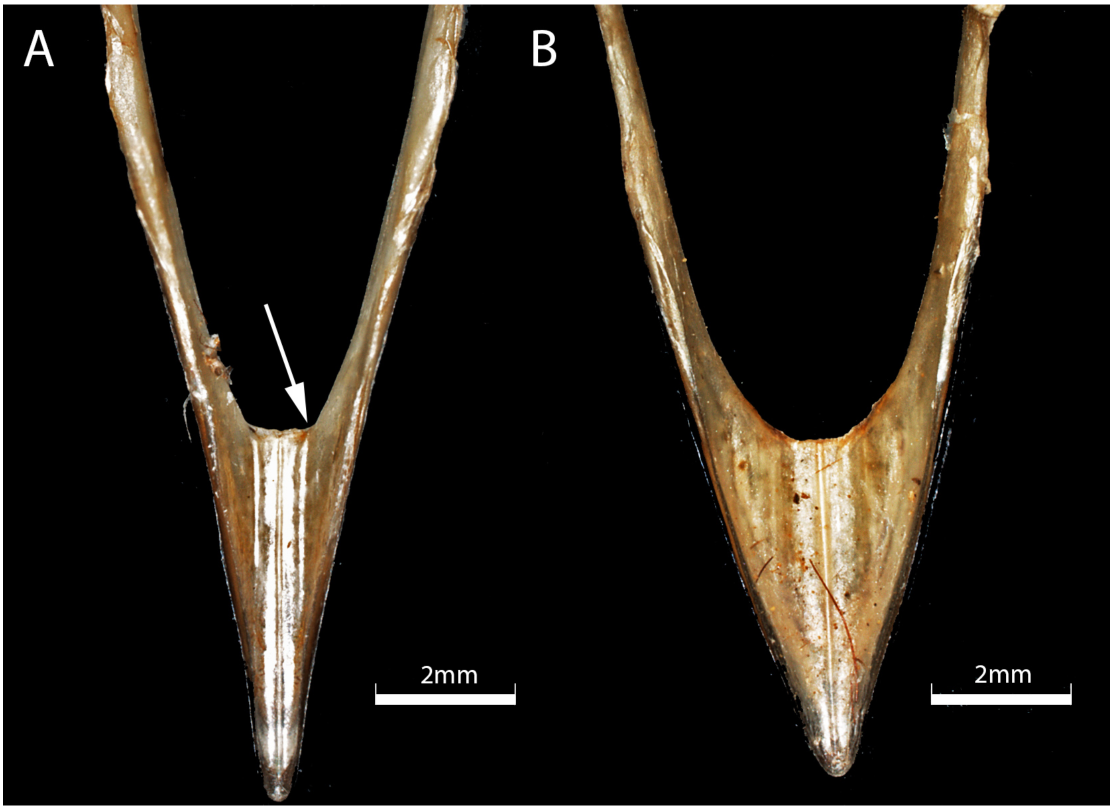

Figure 19. Dorsal partial view of the mandible of *Mecocerculus stictopterus* (A; LSU 170468) and *Culicivora caudacuta* (B; LSU 151790) illustrating character 41 and its postulated states, respectively: straight margin in the caudal part of the mandibular symphysis (state 1) *vs*. rounded margin in the caudal part of the mandibular symphysis (state 0). White arrow indicates the condition of the state 1.

Character 42. Mandible, distance between the rami: short, less than 50% of the ramus length (0); long, more than 50% of the ramus length (1).

The apomorphic condition, a larger angulation between the mandible rostral tip and the caudal ends of the rami (or the distance between the rami measured between the caudal cotylas), is present in species with large gape widths: *Chiroxiphia caudata* and *Xenopipo atronitens* (Pipridae), *Lipaugus vociferans* and *Pipreola whitelyi* (Cotingidae), *Oxyruncus cristatus* (Oxyruncidae), *Piprites chloris* (Pipritidae) and part of *Elaenia* (*E. strepera*, *E. pelzelni*, *E. flavogaster*, *E. obscura*, *E. dayi* and *E. gigas*) (Figures 20A-B). The plesiomorphic state was coded for species that have the referred distance smaller than 50% of the ramus length (Figure 20C).

Figure 20. Dorsal view of the mandible of *Elaenia strepera* (A; USNM 645291), *Piprites chloris* (B; USNM 622076) and *Anairetes parulus* (C; FMNH 376886) illustrating characters 42 and 43 and its postulated states: Char. 42 - long distance between the rami (state 1; A and B) *vs*. short distance between the rami (state 0; C). Char. 43 - curved mandibular ramus (state 1; A) *vs*. straight mandibular ramus (state 0; B and C). Red dotted lines indicate the distances used in the character 42 (see notation). Not scaled.

Character 43. Mandible, rami, shape in dorsal view: straight (0); curved (1).

Most of the species present the ramus as a straight line in dorsal view (Figure 18B, 20B-C), while in *Pipreola*, *Xenopipo*, *Chiroxiphia*, *Hirundinea*, *Myiotriccus*, *Oxyruncus* and *Elaenia strepera* a slight or pronounced curvature can be observed (Figures 18A, 20A).

Quadrate (44-52)

Character 44. Quadrate, mandibular process, caudal condyle, degree of development: well developed (0); poorly developed (1).

In the species that present the apomorphic state (*Platyrinchus mystaceus* and *Neopipo cinnamomea*), the caudal condyle is poorly developed so its caudal margin appears rostrally positioned in relation to the caudal margin of the *cotyla quadratojugalis* in a ventral view (Figure 21B). In the remaining species, the caudal condyle limit is caudal in relation to the *cotyla quadratojugalis* (Figure 21A).

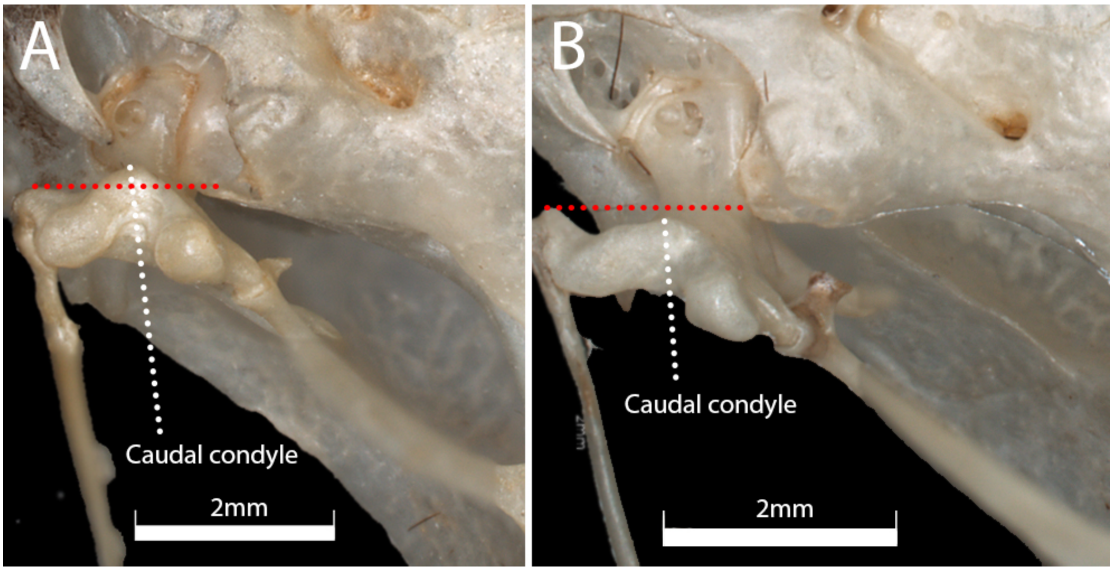

Figure 21. Ventral view of the left quadrate of *Zimmerius cinereicapillus* (A; FMNH 315849) and *Platyrinchus mystaceus* (B; USNM 556422) illustrating character 44 and its postulated states, respectively: well developed caudal condyle of the mandibular process of the quadrate (state 0) *vs*. poorly developed caudal condyle of the mandibular process of the quadrate (state 1). Red dotted lines indicates the position of

the caudal condyle in relation to the caudal margin of the *cotyla quadratojugalis* (the left end of the line; see notation).

Character 45. Quadrate, mandibular process, lateral condyle, *cotyla quadratojugalis*, shape: parallel in relation to the frontal axis (0); caudally curved (1).

In *Platyrinchus mystaceus*, the *cotyla quadratojugalis*, which is the root of the lateral condyle of the mandibular process of the quadrate, presents a caudal twist (Figure 21B), representing the apomorphic condition of the character. In the rest of the species the *cotyla quadratojugalis* is parallel in relation to the frontal/lateromedial axis (Figure 21A), or appears just slightly curved.

Character 46. Quadrate, mandibular process, lateral condyle, size: long (0); short (1).

In most of the species the lateral condyle of the mandibular process of the quadrate partially covers the dorsal end of the jugal arch (Figure 21A). The apomorphy was observed in *Elaenia gigas*, *E. pelzelni* and *E. strepera*, in which the lateral condyle not covers the jugal arch and not reaches the medial margin of the *cotyla quadratojugalis* (Figure 22).

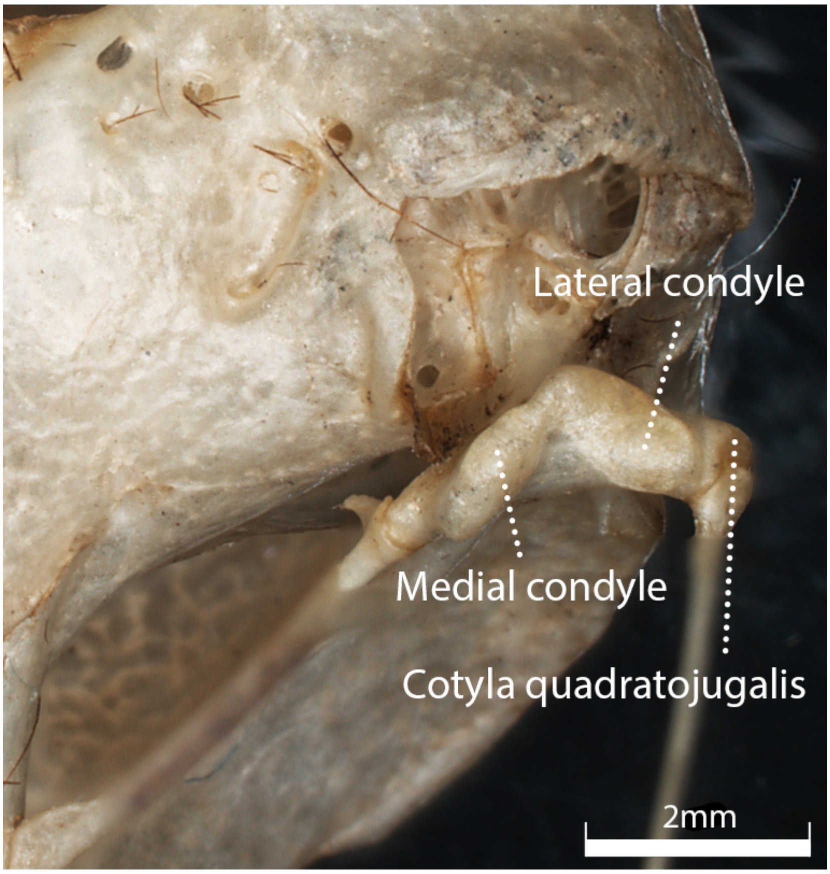

Figure 22. Ventral view of the right quadrate of *Elaenia strepera* (USNM 645291) illustrating the apomorphic state of the character 46: short lateral condyle of the mandibular process of the quadrate, not reaching the medial margin of the *cotyla quadratojugalis* and not partially covering the jugal arch.

Character 47. Quadrate, mandibular process, medial condyle, size: short (0); long (1).

A long medial condyle of the mandibular process of the quadrate, representing the apomorphic condition of the character, was observed in *Elaenia strepera*, *Pipreola whitelyi* and *Lipaugus vociferans* (Figure 22). On those species the length is twice the width. The plesiomorphic state is represented by a medial condyle with similar length and width, generally drop-shaped (Figure 21A and B).

Character 48. Quadrate, otic process, shape/orientation: linear with the caudal condyle (0); linear with the medial condyle (1).

In Cotingidae (represented by *Pipreola whitelyi* and *Lipaugus vociferans*) the otic process of the quadrate appears linear in relation to the medial condyle of the mandibular process (Figure 23B) instead of linear with the caudal condyle like in most of the analyzed species (Figure 23A). In the species that present the apomorphic condition, the quadrate laterally exceeds the lateral limits of the neurocranium.

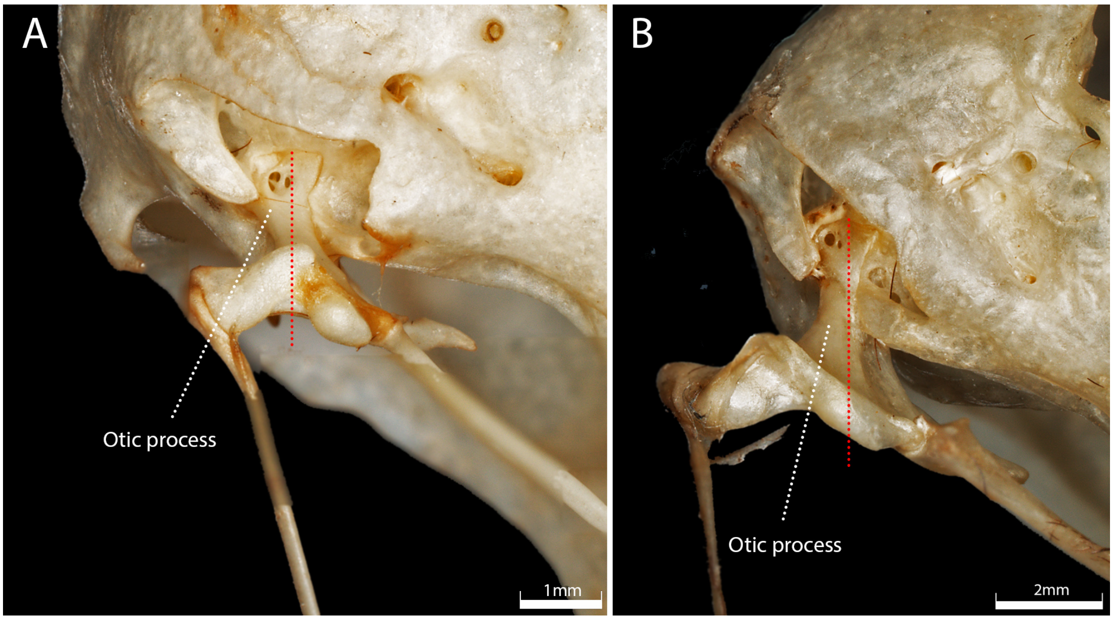

Figure 23. Ventral view of the left quadrate of *Pseudotriccus pelzelni* (A; USNM 560009) and *Pipreola whitelyi* (B; USNM 622783) illustrating character 48 and its postulated states, respectively: otic process of the quadrate linear with the caudal condyle (state 0) *vs*. otic process of the quadrate linear with the medial condyle (state 1). Red dotted lines indicates the lines used to orientate and discretize the character.

Character 49. Quadrate, orbital process, orientation: dorsal (0); dorsorostral (1); rostral (2).

Two of the three states of the character 49 are well distributed within the analyzed specimens: species of the genera *Anairetes*, *Uromyias*, *Pseudocolopteryx*, *Mecocerculus*, *Capsiempis*, *Phaeomyias*, *Polystictus*, *Culicivora*, *Pseudelaenia*, part of *Phyllomyias* (*P. plumbeiceps*, *P. virescens* and *P. fasciatus*), *Serpophaga* and *Furnarius* present the orbital process slightly curved and dorsally oriented (Figure 24A), representing the plesiomorphic condition of the character. The state 1, in which the process is oriented between the vertical and sagittal axes (dorsal and rostral orientation; "diagonal" in lateral view), was observed in *Elaenia*, *Myiopagis*, *Tyrannulus*, *Euscarthmus*, *Camptostoma*, *Ornithion*, part of *Phyllomyias* (*P. burmeisteri*, *P. nigrocapillus*, *P. uropygialis* and *P. cinereiceps*), *Suiriri*, *Stigmatura*, *Inezia*, *Zimmerius* and most of the outgroup (Figure 24B). And two robust species of the outgroup (*Oxyruncus cristatus* and *Lipaugus vociferans*) shows the orbital process of the quadrate in a rostral orientation (Figure 24C).

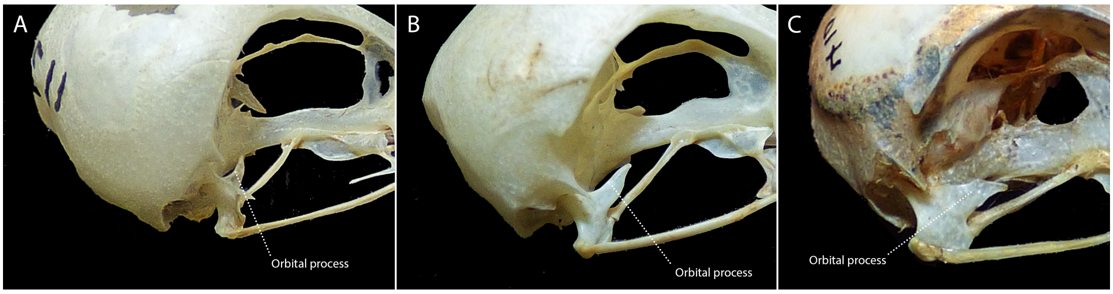

Figure 24. Lateral partial view of the cranium in the position of the right quadrate of *Anairetes reguloides* (A; LSU 113685), *Elaenia martinica* (B; USNM 487918) and *Oxyruncus cristatus* (C; AMNH 410) illustrating character 49 and its postulated

states, respectively: dorsally oriented orbital process (state 0) *vs*. dorsorostrally oriented orbital process (state 1) *vs*. rostrally oriented orbital process. Not scaled.

Character 50. Quadrate, orbital process, size: short (0); long, lengthier than half of the pterygoid (1).

Part of *Elaenia* (*E. gigas*, *E. dayi*, *E. obscura* and *E. flavogaster*) and Pipridae (*Chiroxiphia caudata* and *Xenopipo atronitens*) shows a long orbital process, longer than half of the pterygoid length. In the remaining ingroup and outgroup species the structure possess a smaller length, or is similar in size to half of the pterygoid. The character is better viewed in a caudoventral perspective.

Character 51. Quadrate, *corpus*, size, width: narrow (0); wide (1).

The robust species *Oxyruncus cristatus* (Oxyruncidae) and *Lipaugus vociferans* (Cotingidae) present a wide quadrate *corpus* (Figure 24C), contrasting with the narrow *corpus* found in the rest of the species (Figure 24A and B). The discretization of the character can be clearly recognizable in a lateral or laterofrontal view.

Character 52. Quadrate, otic process, pneumatic foramen: present (0); absent (1).

The two representative species of Onychorhynchidae analyzed (*Onychorhynchus coronatus* and *Myiobius barbatus*) lack any conspicuous foramina in the otic process of the quadrate. In the remaining groups the pneumatic foramen, as a single large foramen or a series of small foramina, can be easily observed in a ventral or posteroventral view.

Cranium (53-144)

Character 53. Cranium, occipital region, occipital condyle, subcondylar fossa, configuration/extension: limited to the anterior half of the occipital condyle (0); extended to both anterior and posterior halves of the occipital condyle (1).

Oxyruncus cristatus (Oxyruncidae) presents an extended subcondylar fossa, which is under the entire occipital condyle *corpus*, so none free part of the condyle can be observed. All the remaining species shows the occipital condyle with a free part in its posterior half (the subcondylar fossa is just under the anterior half of the condyle).

Character 54. Cranium, occipital region, basioccipital, parasphenoidal lamina, size/extension: short (0); long (1).

In *Mecocerculus* (except *M. leucophrys*) the basioccipital region is longer than in the remaining species, a difference that can be observed comparing the distances between the occipital condyle and the rostral margin of the lamina (a measure representing the basioccipital length) *vs*. the occipital condyle to the posterior limit of the cranium (so representing the length of the foramen magnum plus the supraoccipital), in ventral view. A long basioccipital represents the apomorphy (Figure 25A). In the plesiomorphic condition the basioccipital length is shorter than the occipital condyle-supraoccipital distance, or shows similar length (Figure 25B).

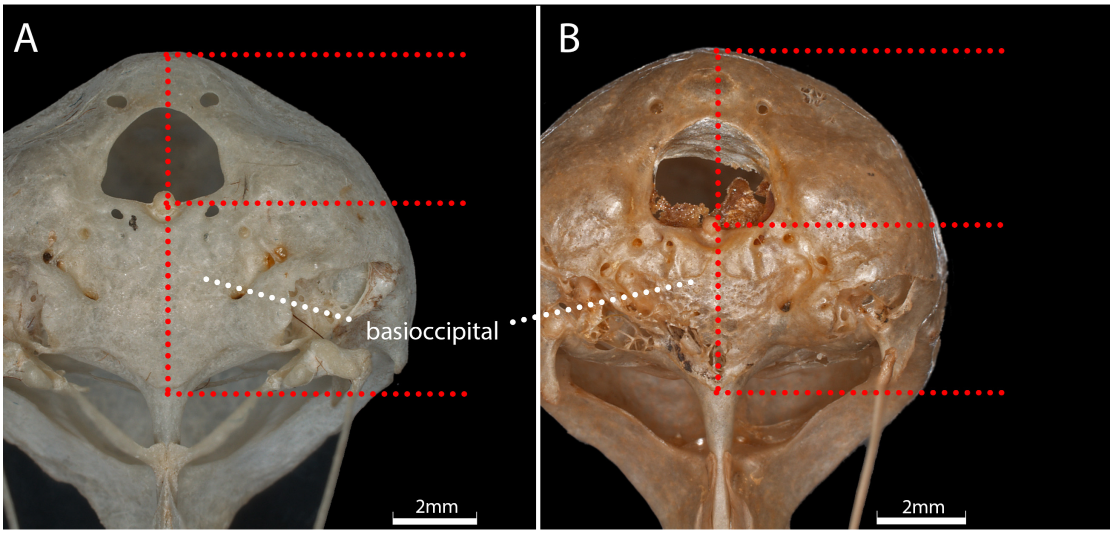

Figure 25. Ventral partial view of the cranium of *Mecocerculus minor* (A; USNM 560008) and *Ornithion inerme* (B; USNM 491501) illustrating character 54 and its postulated states, respectively: long basioccipital (state 1) *vs*. short basioccipital (state 0). Red dotted lines indicates the distances used to discretize the character (see notation). The photos were taken from the same angle.

Character 55. Cranium, occipital region, transverse nuchal crest, degree of development: absent or weakly marked (0); well marked (1).

In *Oxyruncus* and *Hirundinea*, the transverse nuchal crest was clearly identified and is well defined, while in the remaining species the structure is absent or barely identified.

Character 56. Cranium, occipital region, supraoccipital, *prominentia cerebellaris*, degree of development: weekly developed (0); well developed (1).

In most species, the *prominentia cerebellaris* is distinguishable, although it is poorly developed (Figure 25A) or even almost imperceptible (Figure 25B). In *Onychorhynchus coronatus* (Figure 26), *Piprites chloris*, *Lipaugus vociferans* and *Pipreola whitelyi*, on the other hand, the structure is clearly more robust, generally more acuminate (usually rounded or dome-shaped in the species that present the plesiomorphic condition).

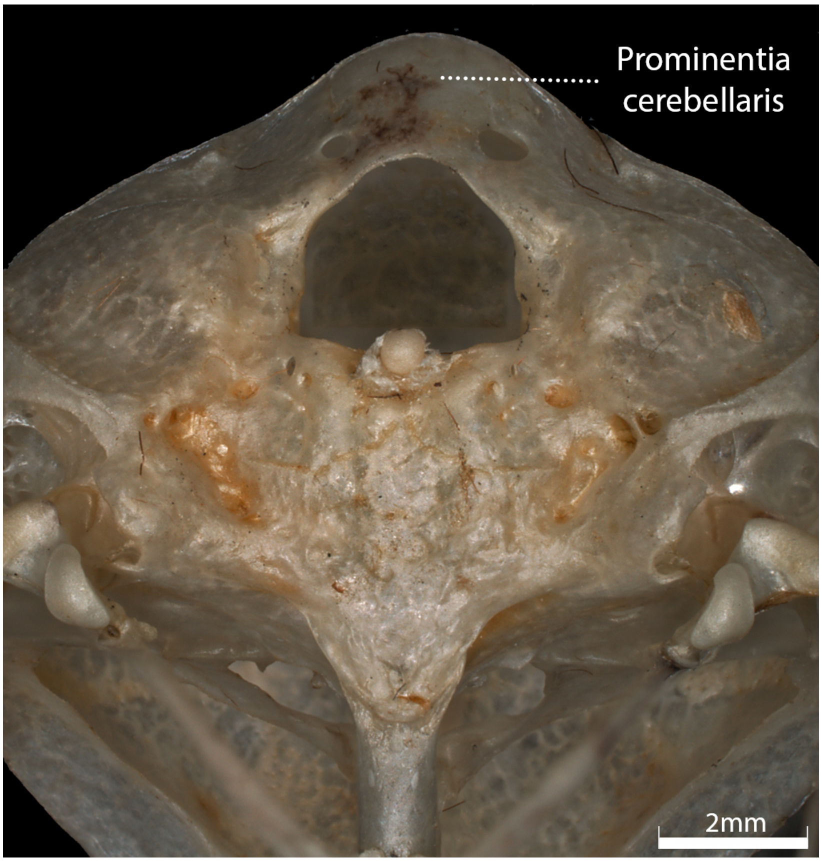

Figure 26. Ventral partial view of the cranium of *Onychorhynchus coronatus* (USNM 562365) illustrating the apomorphic state of the character 56: well developed *prominentia cerebellaris*.

Character 57. Cranium, occipital region, *foramina nervi hypoglossi*, number: more than one (0); one (1).

Most of the analyzed species present two or three hypoglossal nerve foramina, which vary subtly in size and position (Figure 27A). In general the foramen that is closest to the anterior margin of the foramen magnum ("h1" in Mayr 2017) is the largest and most conspicuous. In some species of the outgroup (*Hemitriccus*, *Myiobius*, *Onychorhynchus Myiophobus*, *Pyrocephalus*, *Corythopis*, *Hirundinea*, *Xenopipo*, *Chiroxiphia*, *Oxyruncus*), part of *Myiopagis* (*M. cotta*, *M. flavivertex* and *M. subplacens*), *Elaenia strepera* and *Mecocerculus poecilocercus*, however, only h1 was identified (Figure 27B). No species lacks this foramen, whose homology was verified mainly based on its position, but sometimes it appears vestigial. Inspection of these structures requires adequate magnification and illumination, and especially the use of specimens whose preparation has left no remains of tissue covering the foramens.

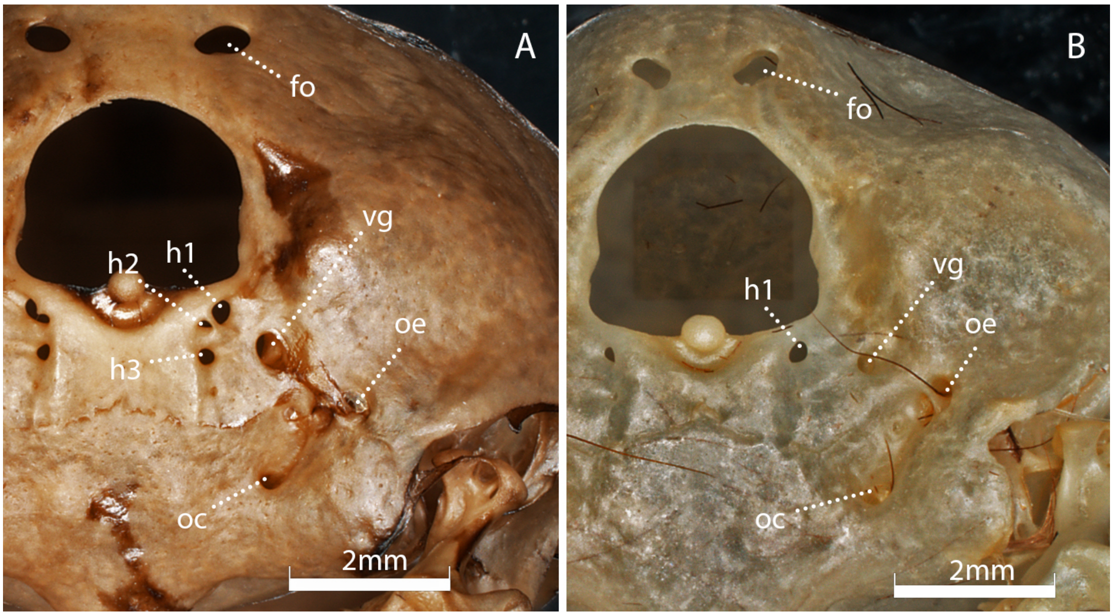

Figure 27. Ventral partial view of the cranium of *Zimmerius chrysops* (A; USNM 428800) and *Myiophobus fasciatus* (B; USNM 639312) illustrating character 57 and its postulated states, respectively: more than one hypoglossal nerve foramina (state 0) *vs*. one hypoglossal nerve foramen (state 1). h1, h2, h3 = hypoglossal nerve foramina (see notation); vg = *foramen nervi vagi*; oc = *ostium canalis carotici*; oe = *ostium canalis ophthalmicus externus*; fo = *fonticulus occipitalis*.

Character 58. Cranium, occipital region, *foramen nervi vagi*, degree of development: well developed (0); absent or poorly developed (1).

The apomorphic condition was observed in part of the outgroup including Pipridae (*Xenopipo atronitens* and *Chiroxiphia caudata*) and *Todirostrum russatum*. In other species, the referred foramen can be clearly identified (Figure 27), even though it varies in size.

Character 59. Cranium, occipital region, *ostium canalis carotici*, position: close to the *ostium canalis ophthalmicus externus* (0); distant from the *ostium canalis ophthalmicus externus* (1).

In most species, including the root species, the *ostium canalis carotici* is closer to or similar in distance to the *ostium canalis ophthalmicus externus* than the distance from this to the *foramen nervi vagi* (Figure 27A). In *Myiophobus*, *Muscigralla*, *Pipreola*, *Lipaugus* and *Piprites*, this distance is greater (Figure 27B).

Character 60. Cranium, occipital region, *ostium canalis ophthalmicus externus*, position: close to the posteromedial margin of the *ala parasphenoidalis* (0); distant from the posteromedial margin of the *ala parasphenoidalis* (1).

In *Myiopagis subplacens* and *M. gaimardii*, the *ostium canalis ophthalmicus externus* is more distant from the posteromedial margin of the *ala parasphenoidalis* than to the *foramen nervi vagi*.

Character 61. Cranium, occipital region, *fonticulus occipitalis*, position: lateral (0); medial (1).

In all of the ingroup species the position of each of the *fonticulus occipitalis* coincides with the lateral margins of the foramen magnum (Figure 27A), so they are more distant from each other. In all of the outgroup species (except for the root species, *Furnarius rufus*), the *fonticuli* are medial in relation to the lateral margin of the foramen magnum (Figure 27B), so closer to each other.

Character 62. Cranium, parashpenoidal lamina, rostral margin/parasphenoidal rostrum, shape: round and wide (0); acuminate and narrow (1).

The apomorphy, a more acuminate parasphenoidal rostrum (Figure 28B), was found in part of *Mecocerculus* (*M. calopterus*, *M. stictopterus*, *M. hellmayri* and *M. poecilocercus*) and part of *Phyllomyias* (*P. plumbeiceps*, *P. virescens*). The remaining species present a rounded and wider parasphenoidal rostrum (Figure 28A).

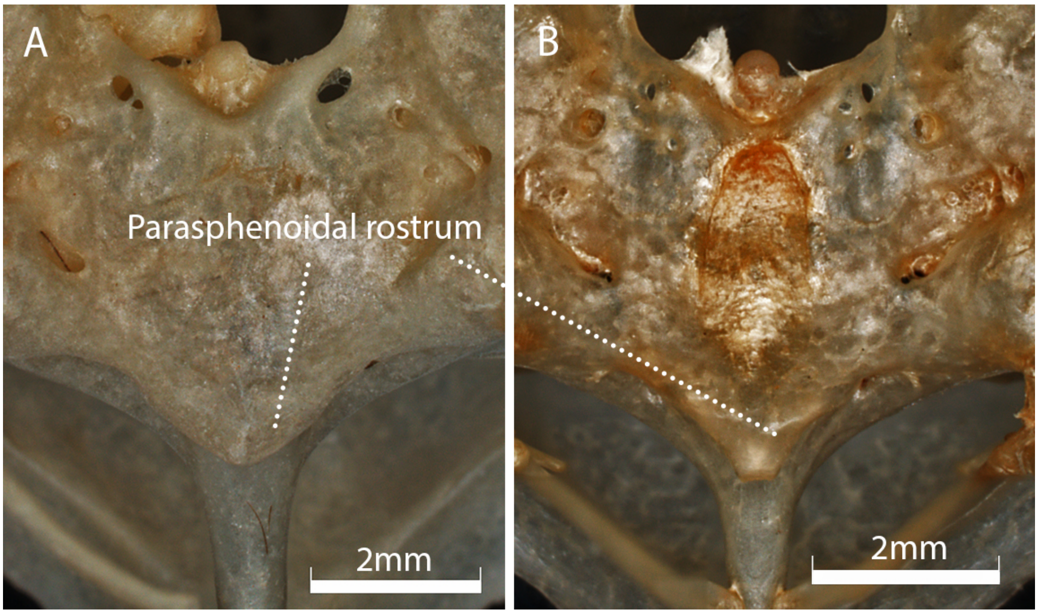

Figure 28. Ventral partial view of the cranium of *Myiopagis cotta* (A; USNM 502802) and *Phyllomyias plumbeiceps* (B; LSU 129957) illustrating character 62 and its postulated states, respectively: rounded parasphenoidal rostrum (state 0) *vs*. acuminate parasphenoidal rostrum (state 1).

Character 63. Cranium, occipital region, basioccipital, basioccipital process/*ala parasphenoidalis*, posterolateral indentation: absent (0); present (1).

Among the examined species, part of the outgroup representatives (*Myiophobus*, *Sublegatus*, *Pyrocephalus*, *Phylloscartes*, *Pseudotriccus*, *Muscigralla*, *Hirundinea*, *Myiotriccus*, *Myiobius*, *Onychorhynchus*, *Todirostrum*) and some taxa of the ingroup (*Anairetes* spp., *Uromyias* spp., *Capsiempis flaveola*, *Elaenia pelzelni*, *E. spectabilis*, *Phaeomyias murina*, *Nesotriccus ridgwayi*) show a curved indentation in the posterior and lateral portions of the *ala parasphenoidalis* (Figures 27B and 29). In the species that present the plesiomorphic state the indentation is absent, and the *ala parasphenoidalis* form an almost straight angle with the parasphenoidal lateral process (Figure 27A).

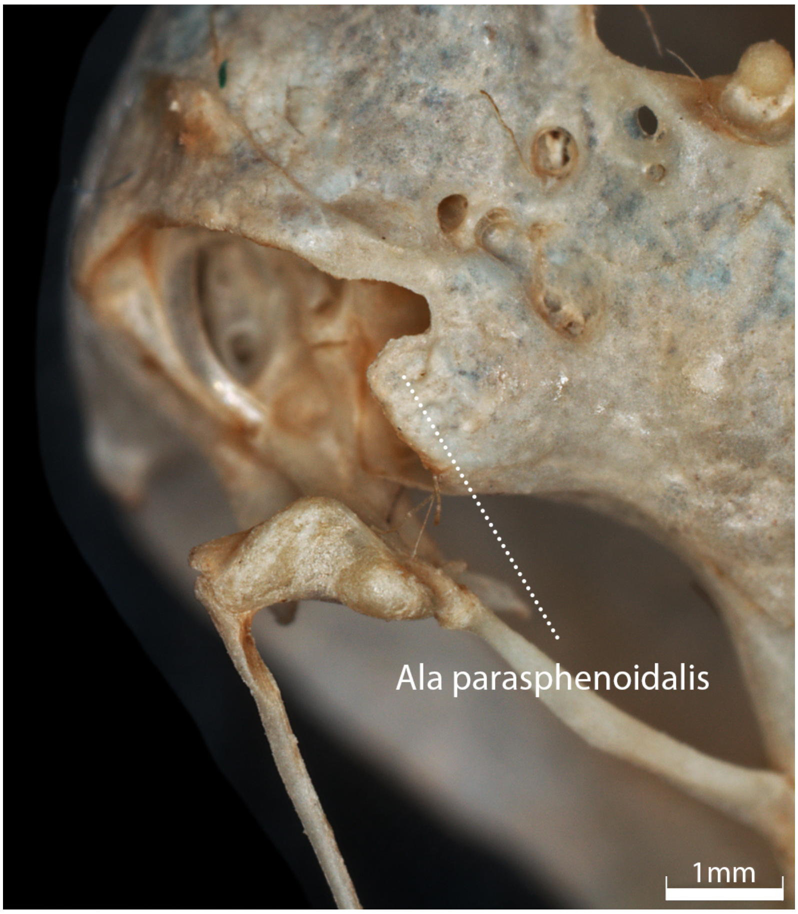

Figure 29. Ventral partial view of the cranium of *Sublegatus modestus* (USNM 620773) illustrating the apomorphic state of the character 63: presence of a posteromedial indentation in the *ala parasphenoidalis*.

Character 64. Cranium, occipital region, basioccipital, basioccipital process/*ala parasphenoidalis*, shape: plain or laterally convex and wide (0); with a narrow and acuminate process (1).

In *Uromyias agilis* and *U. agraphia* there is a narrow and acuminate process in the lateral margin of the *ala parasphenoidalis* (Figure 30). In other species, the lateral margin is flat or convex, never forming a narrow process as in *Uromyias* (Figures 21, 22, 23, 25, 27, 29).

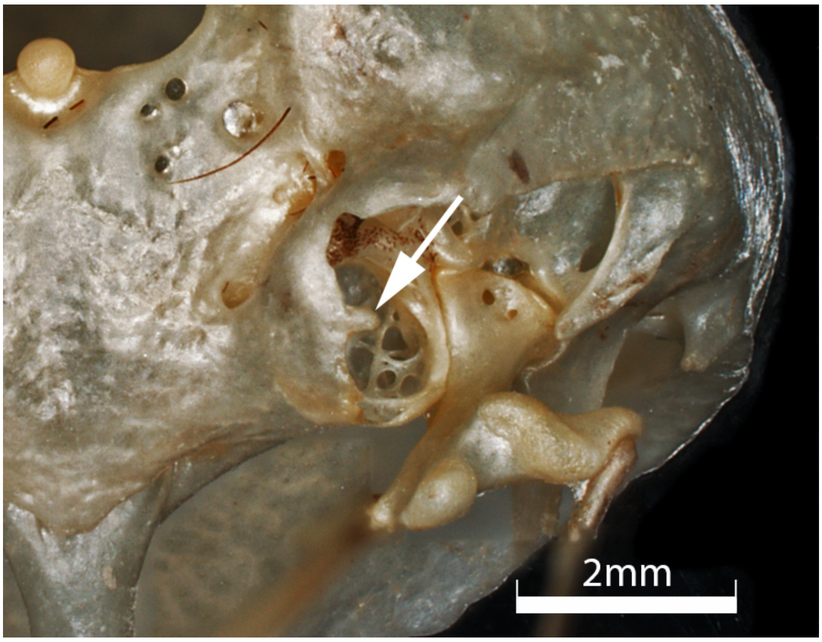

Figure 30. Ventral partial view of the cranium of *Uromyias agilis* (USNM 614866) illustrating the apomorphic condition of the character 64: presence of a lateral process in the *ala parasphenoidalis* (indicated by the arrow).

Character 65. Cranium, occipital region, exoccipital, parasphenoidal process, anterior margin, shape: rounded, diagonal in relation to the frontal axis (0); straight, transversal in relation to the frontal axis (1).

In the majority of the analyzed species the anterior margin of the parasphenoidal process is diagonal in relation to the frontal axis, resulting in a rounded/concave shape in ventral view (Figures 23 and 29), sometimes with a fold in its mid part (Figure 22). In *Anairetes*, *Uromyias*, *Serpophaga*, *Culicivora*, *Pseudocolopteryx* and *Mecocerculus* (except *M. minor*), the referred margin is almost straight, and perpendicular in relation to the frontal axis, thus forming a right angle with the *ala parasphenoidalis* (Figure 30).

Character 66. Cranium, occipital region, exoccipital, parasphenoidal process, anterior margin, frontal extension: not covering the otic process of the quadrate (0); completely covering the otic process of the quadrate (1).

In all species the otic process of the quadrate can be clearly observed in ventral view (Figures 21, 22, 23, 27A, 30), but in *Oxyruncus cristatus* the anterior margin of the parasphenoidal process extends over it.

Character 67. Cranium, occipital region, exoccipital, paraoccipital process, small process in the anterior margin: absent (0); present (1).

In the analyzed representatives of Rhynchocyclidae: Pipromorphinae (*Pseudotriccus pelzelni*, *Phylloscartes ventralis* and *Corythopis torquatus*) and in two ingroup species (*Zimmerius chrysops* and *Z. minimus*) a process is observed in the anterior margin of the paraoccipital process, just below the temporal fossa, between the paraoccipital process and the suprameatic process (Figure 31B).

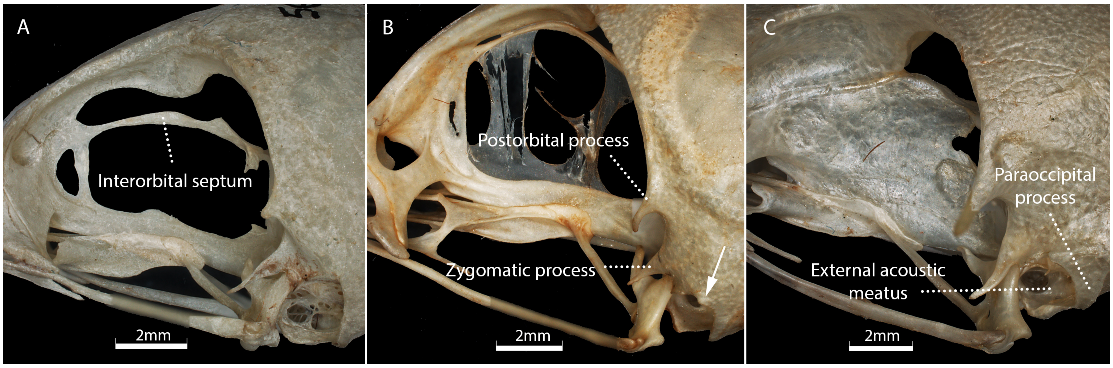

Figure 31. Lateral partial view of the left side of the cranium of *Mecocerculus minor* (A; USNM 560008), *Pseudotriccus pelzelni* (B; USNM 560009) and *Onychorhynchus coronatus* (C; USNM 562365) illustrating characters 67 and 69 and its postulated states: Char. 67 - presence of a process in the anterior margin of the paraoccipital process (state 1; B, indicated by the arrow) *vs*. absence of a process in the anterior margin of the paraoccipital process (state 0; A and C); Char. 69 - elliptical external acoustic meatus (state 1; A and B) *vs*. rounded external acoustic meatus (state 0; C).

Character 68. Cranium, occipital region, exoccipital, paraoccipital process, degree of development: well developed, conspicuous (0); poorly developed (1).

In *Tachuris rubrigastra* and *Pachyramphus polychopterus* the paraoccipital process is weekly developed, almost inconspicuous in lateral view.

Character 69. Cranium, squamosal region, external acoustic meatus, shape: rounded (0); elliptical (1).

The entire ingroup and part of the outgroup (*Lipaugus*, *Pipreola*, *Tityra*, *Oxyruncus*, *Todirostrum*, *Phylloscartes*, *Pseudotriccus*, *Corythopis*, *Hirundinea*, *Myiotriccus*) shows an oval-shaped external acoustic meatus (Figure 31A and B). The apomorphic state, a meatus with a more rounded shape, can be observed in the remaining outgroup taxa (Figure 31C).

Character 70. Cranium, squamosal region, external acoustic meatus, suprameatic process: present (0); absent/inconspicuous (1).

A conspicuous suprameatic process, located dorsally in relation to the external acoustic meatus and bellow the base of the zygomatic process, is present in all species of the ingroup genera *Elaenia*, *Myiopagis*, *Suiriri*, and *Tyrannulus*, and in the outgroup representatives of Cotingidae (*Lipaugus vociferans* and *Pipreola whitelyi*), Tityridae (*Tityra cayana* and *Pachyramphus polychopterus*), Platyrinchidae (*Platyrinchus mystaceus* and *Neopipo cinnamomea*), Tachurisidae (*Tachuris rubrigastra*), Rynchocyclidae: Pipromorphinae (*Corythopis torquatus*, *Pseudotriccus pelzelni*, *Phylloscartes ventralis*), Tyrannidae: Tyranninae (*Pitangus sulphuratus* and *Myiozetetes cayanensis*), and Tyrannidae: Fluvicolinae (*Sublegatus modestus*, *Pyrocephalus rubinus*, *Myiophobus fasciatus*). The process varies slightly in size among the species, with *Lipaugus* being the most conspicuous case (Figure 32). The structure was completely lost in the rest of the ingroup (the remaining Elaeniini and all the Euscarthmini) and in the rest of the outgroup representing Onychorhynchidae, Tyrannidae: Hirundineinae and Muscigrallinae, Rhynchocyclidae: Todirostrinae, Pipritidae and Pipridae (Figures 31A and C).

Figure 32. Laterofrontal partial view of the right side of the cranium of *Lipaugus vociferans* (USNM 562337) illustrating the plesiomorphic condition of the character 70: presence of a conspicuous suprameatic process (indicated by the arrow).

Character 71. Cranium, temporal region, temporal fossa: present (0); absent (1).

The presence of concavity in the temporal region is more represented in the outgroup, although it is completely absent in *Todirostrum*, *Hemitriccus*, *Platyrinchus*, *Neopipo*, *Tachuris*, *Phylloscartes*, and *Xenopipo*. Within the ingroup, it can be observed only in *Elaenia dayi*, *E. pelzelni* and *E. martinica* (Figure 24B), although it is less evident than in outgroup species such as *Oxyruncus cristatus* (Figure 24C).

Character 72. Cranium, temporal region, temporal fossa, degree of development/depth: weekly developed, shallow (0); well developed, deep (1).

In robust outgroup species such as those belonging to the genera *Lipaugus*, *Onychorhynchus*, *Pachyramphus*, *Tityra*, *Oxyruncus*, *Chiroxiphia*, *Pitangus* and *Hirundinea*, the temporal fossa is deep. The character was coded as inapplicable for the taxa that lacks the structure (see character 69).

Character 73. Cranium, temporal/parietal region, temporal fossa, extension/length: limited to the temporal/lateral region (0); reaching the nuchal region (1).

In all analyzed species the temporal fossa is limited to the temporal region, but in *Oxyruncus cristatus* and *Pipreola whitelyi* the concavity reaches the nuchal region.

Character 74. Cranium, squamosal region, zygomatic process, size in lateral view: medium-sized, almost reaching the anterior limit of the quadrate (0); short, not reaching the central part of the quadrate *corpus* (1); long, exceeding the anterior limit of the *corpus* of the quadrate (2).

Most of the species examined present state 2, a long zygomatic process. In lateral view, the tip of the process exceeds the *corpus* of the quadrate (or the base of the orbital process) (Figure 31), and in some species it almost reaches the jugal bar. However in *Elaenia*, *Myiopagis*, *Tyrannulus*, *Phaeomyias*, *Nesotriccus*, *Camptostoma*, *Ornithion*, part of *Phyllomyias* (*P. burmeisteri*, *P. uropygialis*, *P. nigrocapillus* and *P. cinereiceps*), *Xenopipo*, *Chiroxiphia*, *Todirostrum*, *Hemitriccus* and in the root species *Furnarius rufus*, the tip of the process almost reaches the anterior limit of the quadrate, or slightly reaches, not exceeding. In *Lipaugus*, *Pipreola* and *Oxyruncus* the process is very short, not reaching half of the *corpus* of the quadrate (Figure 32).

Character 75. Cranium, squamosal region, zygomatic process, shape in dorsofrontal view: filiform or acuminate (0); dorsoventrally flattened and wide with rounded edge (1); bifurcated or with the tip flattened or concave (2).

In none of the analyzed species the zygomatic process is fused to the postorbital process as occurs in some groups of passerines of the Furnariida parvorder such as Rhinocryptidae, Thamnophilidae and Formicariidae (Galvão and Gonzaga 2011, Maurício *et al* 2012). On the other hand, the structure is quite variable in form, so that three states were identified from this variation in a dorsofrontal perspective, namely:

filiform or acuminate in most of the species including the root species (Figures 33A and 32); wide and with rounded edge in *Stigmatura*, part of *Elaenia* (*E. dayi*, *E. obscura*/*sordida*, *E. flavogaster*), *Pachyramphus*, *Tityra* (Figure 33B); bifurcated or with flat or concave edge in part of *Anairetes* (*A. flavirostris* and *A. parulus*), part of *Mecocerculus* (*M. hellmayri*, *M. calopterus*, *M. stictopterus* and *M. poecilocercus*), part of *Elaenia* (*E. fallax* and *E. martinica*), *Euscarthmus*, *Capsiempis*, *Phaeomyias*, *Nesotriccus*, *Pseudelaenia*, *Phyllomyias fasciatus*, *Knipolegus*, *Pitangus* and *Myiozetetes* (Figure 33C). These states reflect the general patterns found, even if some minor variation can be found within each of the states considered. The analysis of delicate structures such as this, for example the thin tip of the zygomatic process, is performed more reliably on cleared and stained specimens, where the tips and small processes remain in their original shape (Franz and Zusi *in prep.*).

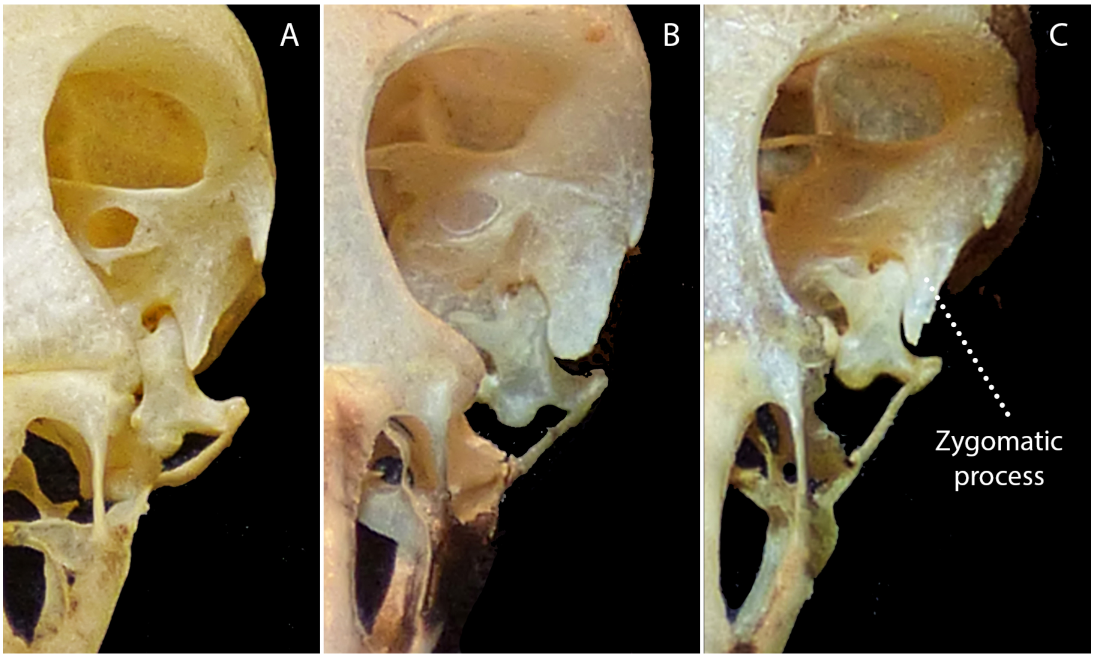

Figure 33. Dorsofrontal partial view of the left side of the cranium of *Corythopis torquatus* (A; YPM 106312), *Stigmatura budytoides* (B; AMNH 26902) and

Anairetes flavirostris (C; USNM 7318) illustrating character 75 and its postulated states, respectively: acuminate zygomatic process (state 0) *vs*. rounded zygomatic process (state 1) *vs*. bifurcated zygomatic process (state 2). Not scaled.

Character 76. Cranium, squamosal region, postorbital process, degree of development/size: nearly absent (0); short, poorly developed (1); long, well developed (2).

In *Lipaugus*, *Pipreola*, *Piprites*, *Chiroxiphia*, *Xenopipo* and *Furnarius* the postorbital process (squamosal process *sensu* Posso and Donatelli 2007) is almost absent (Figures 34A and 32), configuring the plesiomorphic condition. Most of the species present a conspicuous although small/short postorbital process (Figures 34B and 31A), and in *Onychorhynchus*, *Myiobius*, *Hirundinea*, *Myiotriccus*, *Corythopis*, *Phylloscartes* and *Pseudotriccus* the process have a longest projection (Figures 31B and C).

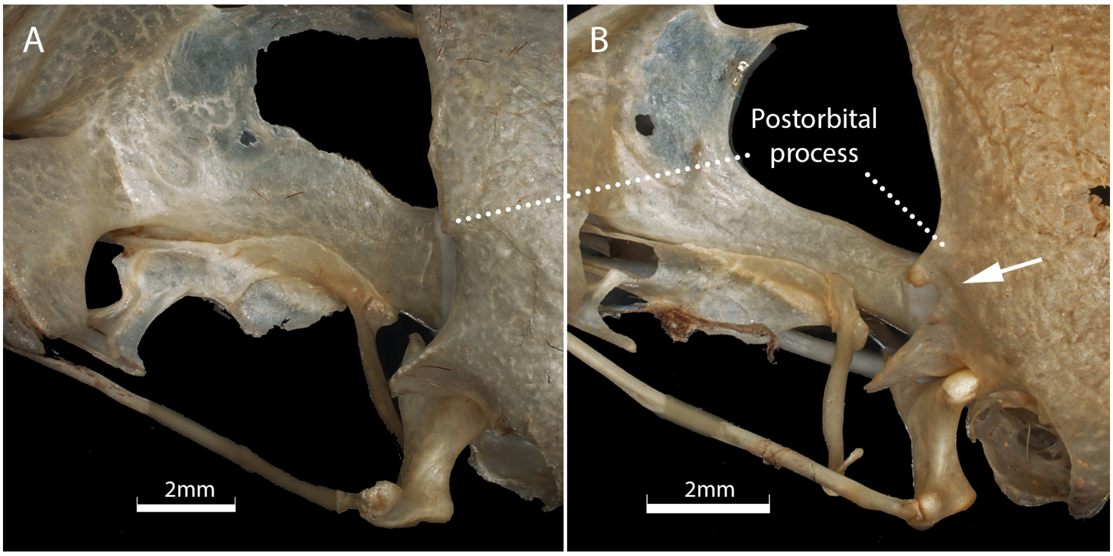

Figure 34. Posterolateral partial view of the left side of the cranium of *Piprites chloris* (A; USNM 622076) and *Stigmatura napensis* (B; USNM 491716) illustrating

characters 76 and 79 and its postulated states: Char. 76 - almost absent postorbital process (state 0; A) *vs*. short postorbital process (state 1; B); Char. 79 - presence of an edge in the squamosal bone (state 1; B) *vs*. absence of an edge in the squamosal bone (state 0; A). White arrow indicates the apomorphic condition of the character 79.

Character 77. Cranium, squamosal region, postorbital process, shape: right triangle (0); hook, ventrally curved (1); laterally twisted (2).

Most of the analyzed species present postorbital process in the form of a short and wide triangular flap resembling a simple straight triangle, in a lateral perspective (Figures 31A and C). In *Pseudotriccus pelzelni*, the aforementioned process is sharpened and ventrally twisted towards the zygomatic process (Figure 31B). In part of the representatives of the genus *Elaenia* (*E. dayi*, *E. obscura* and *E. flavogaster*), the postorbital process is twisted laterally, which is better visualized in frontal view. Inapplicable for the species coded with the plesiomorphic state of the character 76.

Character 78. Cranium, squamosal region, postorbital process, position: close to the zygomatic process (0); distant from the zygomatic process (1).

In general the position of the postorbital process is the same in the studied species, being at a distance of the zygomatic process that is shorter the width of the *corpus* of the quadrate, in lateral view (Figure 34A). The apomorphic condition was observed in *Elaenia* spp. and *Oxyruncus cristatus*, in which the postorbital process is distant from the zygomatic process (Figure 34B).

Character 79. Cranium, squamosal region, edge/indentation in the squamosal at the base of the zygomatic process: absent (0); present (1).

In *Stigmatura*, *Euscarthmus*, *Inezia*, *Mecocerculus* (except *M. leugophrys*), part of *Phyllomyias* (*P. plumbeiceps*, *P. virescens*, *P. burmeisteri*, *P. cinereiceps*, *P. uropygialis*, *P. nigrocapillus*, *P. zeledoni*), *Ornithion*, and *Camptostoma* there's a conspicuous edge in the squamosal bone near the base of the zygomatic process (Figure 34B).

Character 80. Cranium, frontal, medial ridge: present (0); absent (1).

(Lanyon 1984; "Char." 02)

All of the ingroup species and most of the outgroup taxa present a conspicuous frontal ridge (Figure 32), slightly varying in depth. The feature was not identified in *Onychorhynchus*, *Myiobius*, *Platyrinchus*, and *Tachuris*, so representing the apomorphy.

Character 81. Cranium, frontal, medial ridge, depth: shallow (0); deep (1).

Within the species with a conspicuous medial ridge in the frontal, most of it shows a shallow depression (Figure 32). But the ridge is markedly deep in *Pipreola*, *Pachyramphus*, *Hirundinea*, *Knipolegus*, *Pyrocephalus*, and *Sublegatus*. Character coded as inapplicable for the species that lack the depression (see character 80).

Character 82. Cranium, frontal, rostral inflation: absent (0); present (1).

The apomorphic condition, an inflation in the frontal in its rostral portion, was observed in *Lipaugus*, *Oxyruncus*, *Chiroxiphia*, *Xenopipo*, *Onychorhynchus*, and *Myiobius* (Figure 32).

Character 83. Cranium, frontal, size/width: narrow (0); intermediate (1); wide (2).

In species coded with the plesiomorphic state, the width of the frontal is similar to the width of the nasal opening, in dorsal view (Figure 35A), therefore greatly reduced. It includes species of the genera *Furnarius*, *Phylloscartes*, *Pseudotriccus*, *Todirostrum*, *Hemitriccus*, *Euscarthmus*, *Capsiempis*, *Culicivora*, *Uromyias*, *Anairetes*, *Mecocerculus*, *Stigmatura*, and *Inezia*. The wider condition was found in *Oxyruncus*, *Onychorhynchus*, *Chiroxiphia*, *Xenopipo*, *Pitangus*, *Myiozetetes*, and *Ornithion*. In these species, the width of the frontal bone corresponds to about half the width of the skull, in dorsal view (Figure 35C). The intermediate state includes species in which the frontal is approximately 1/3 of the width of the skull (Figure 35B).

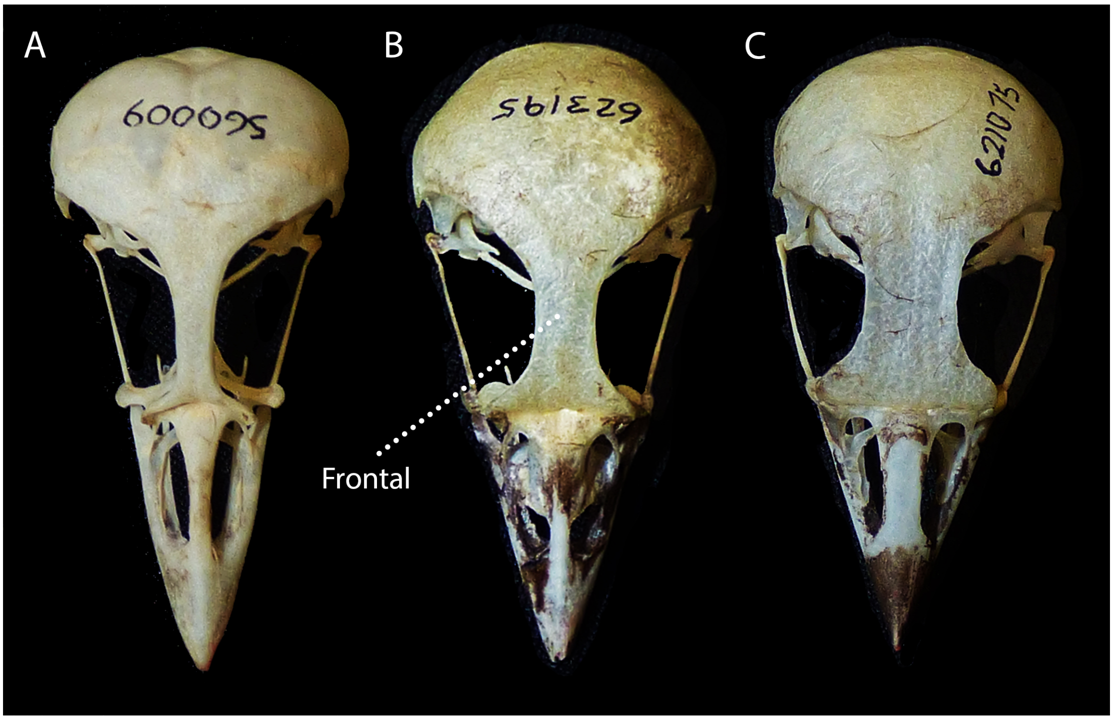

Figure 35. Dorsal view of the cranium of *Pseudotriccus pelzelni* (A; USNM 560009), *Myiopagis flavivertex* (B; USNM 623195) and *Xenopipo atronitens* (C; USNM 621075) illustrating character 83 and its postulated states, respectively: narrow frontal (state 0; A) *vs*. medium-sized frontal (state 1; B) *vs*. wide frontal (state 2; C). Not scaled.

Character 84. Cranium, frontal/lacrimal, lacrimal process, degree of development: weekly developed (0); well developed (1).

A well-projected and conspicuous lacrimal process was identified in *Elaenia*, *Suiriri*, *Myiopagis*, *Piprites*, *Oxyruncus*, *Pipreola*, *Lipaugus*, *Xenopipo* (Figure 35C), *Chiroxiphia*, *Onychorhynchus*, *Myiobius*, *Phylloscartes*, *Knipolegus*, *Pyrocephalus*, *Pitangus*, *Myiozetetes*, and *Sublegatus*.

Character 85. Cranium, frontal/lacrimal, lacrimal process, shape: accompanies the curvature of the orbit (0); interrupts the curvature of the orbit and protrudes dorsolaterally, forming an angle (1).

In *Elaenia dayi*, *E. gigas*, *Suiriri burmeisteri*, *Oxyruncus cristatus*, *Piprites chloris*, *Onychorhynchus coronatus*, and *Myiobius barbatus* the lacrimal process forms an angle in relation to the curvature of the orbit in the position of the suture between the frontal and lacrimal bones (Figure 36). In the remaining species the lacrimal process projects laterally fitting the line of the curvature of the orbit (Figure 35).

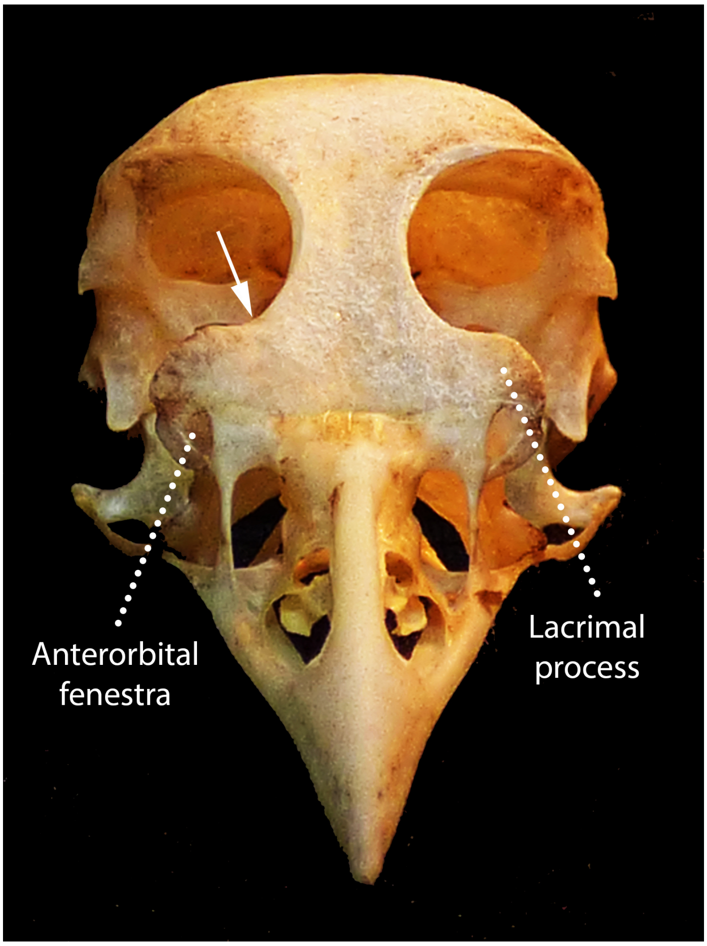

Figure 36. Dorsofrontal view of the cranium of *Elaenia dayi* (AMNH 22226) illustrating the apomorphic condition of the character 85: presence of an angulation between the lacrimal process and the curvature of the orbit (indicated by the arrow).

Character 86. Cranium, frontal/lacrimal, lacrimal process, lateral projection: surpass the jugal bar (0); reaches and not exceeds the jugal bar (1); not reaches the jugal bar (2).

In most of the examined specimens the lateral projection of the lacrimal process just reaches the jugal bar in dorsal view (Figure 37B), representing the state 1. In the root species and in *Ornithion*, part of *Phyllomyias* (*P. nigrocapillus* and *P. burmeisteri*), *Phaeomyias*, *Tyrannulus*, part of *Zimmerius* (*Z. cinereicapillus*, *Z. chrysops*, *Z. minimus*, *Z. bolivianus*), *Elaenia dayi*, *Oxyruncus* and *Piprites* the projection exceeds the lateral margin of the jugal bar (Figure 37A), so corresponding to the plesiomorphy. In *Inezia*, *Culicivora*, *Uromyias*, *Myiophobus*, *Todirostrum*, *Muscigralla*, *Myiotriccus*, and *Hirundinea* the projection does not reach the jugal bar (Figure 37C). The narrower projections were found in the Hirundineinae representatives (*Hirundinea ferruginea* and *Myiotriccus ornatus*).

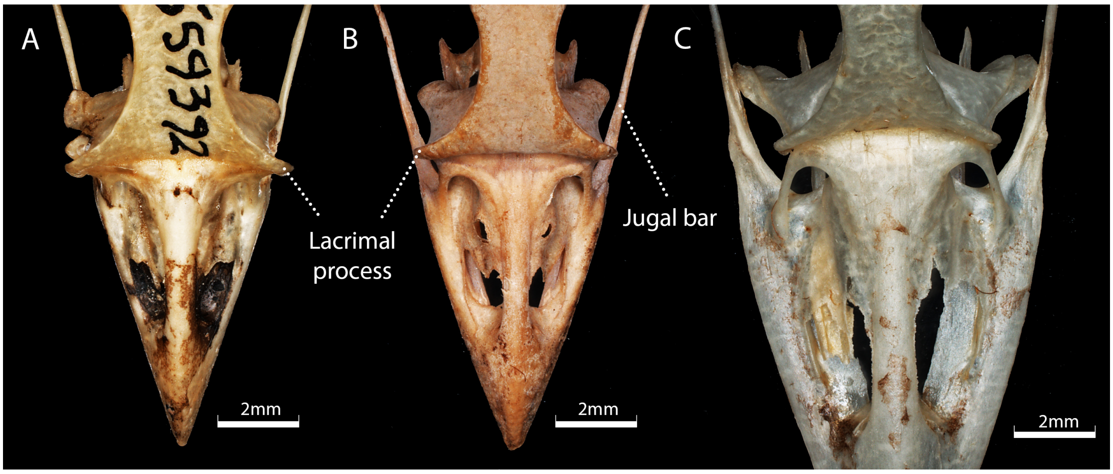

Figure 37. Dorsal view of the cranium of *Pseudotriccus pelzelni* (A; USNM 560009), *Myiopagis flavivertex* (B; USNM 623195) and *Xenopipo atronitens* (C; USNM 621075) illustrating character 83 and its postulated states, respectively: narrow frontal (state 0) *vs*. medium-sized frontal (state 1) *vs*. wide frontal (state 2). Not scaled.

Character 87. Cranium, frontal, rostral limit at the fusion with the nasal (craniofacial flexor zone), shape in dorsal view: concave (0); straight (1).

Most of the species shows a straight rostral limit of the frontal at the fusion with the nasal (Figure 37B), including the root species, *Furnarius rufus*. But *Myiopagis* (except *M. subplacens* and *M. gaimardii*), *Ornithion*, *Mecocerculus* (except *M. minor* and *M. leucophrys*), part of *Phyllomyias* (*P. plumbeiceps*, *P. nigrocapillus*, *P. cinereiceps*, *P. burmeisteri*, *P. zeledoni*), *Pseudocolopteryx*, part of *Serpophaga* (*S. cinerea* and *S. nigricans*), *Tyrannulus*, *Phaeomyias*, *Nesotriccus*, part of *Zimmerius* (*Z. cinereicapillus*, *Z. minimus*, *Z. chrysops*, *Z. acer*), part of *Elaenia* (*E. dayi*, *E. obscura*, *E. flavogaster*), *Sublegatus*, *Pseudotriccus*, *Hirundinea*, and *Todirostrum* have a rostrocaudal curvature in the frontal, granting a concave shape in dorsal view (Figures 37A and C).

Character 88. Cranium, parietal region, temporal crest in dorsal view: inconspicuous (0); conspicuous (1).

In *Pseudotriccus pelzelni*, *Corythopis torquatus*, *Oxyruncus cristatus*, and *Pipreola whitelyi* the temporal crest in its medial portion can be clearly observed in dorsal view (Figure 35A), representing an apomorphy.

Character 89. Cranium, lacrimal, anterorbital fenestra: absent (0); present (1).

A conspicuous anterorbital fenestra was found only in *Elaenia dayi* and *E. spectabilis*, representing the apomorphic condition of a neomorphic character (Figure 36).

Character 90. Cranium, lacrimal, orbital process, degree of development/shape: reduced (0); enlarged, with a semicircular or acuminate lateral projection or at least wider compared to the middle portion of the lacrimal (1).

The lacrimal in most of the analyzed species present a lateral or laterofrontal enlargement in the orbital process, where it contacts the lacrimal process of the frontal (Figure 38B). A reduced orbital process, with none lateral inflation, was found in *Anairetes*, *Culicivora*, *Serpophaga*, *Polystictus*, *Pseudocolopteryx*, *Myiophobus*, *Myiotriccus*, *Oxyruncus* and *Furnarius* (Figure 38A).

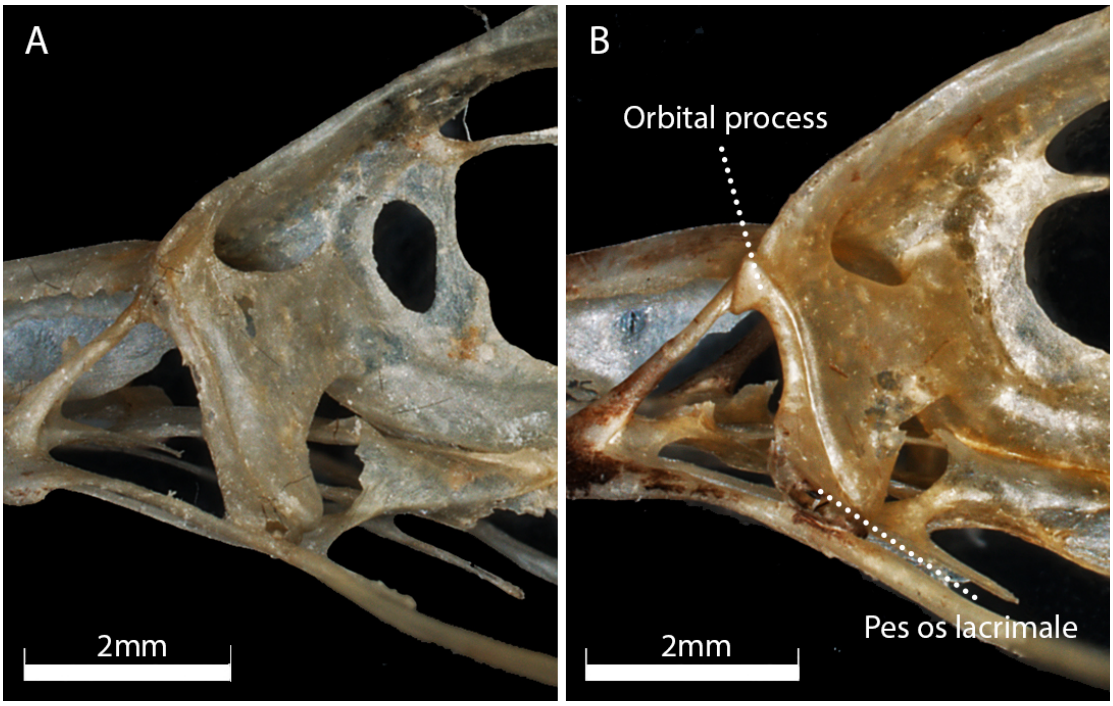

Figure 38. Lateral partial view of the left side of the cranium of *Serpophaga munda* (A; FMNH 335182) and *Inezia inornata* (B; FMNH 334478) illustrating character 90 and its postulated states, respectively: not expanded orbital process of the lacrimal (state 0) *vs*. expanded orbital process of the lacrimal (state 1).

Character 91. Cranium, lacrimal, *pes os lacrimale*, lateral inflation: absent (0); present (1).

The majority of the analyzed species present a lateral inflation in the *pes os lacrimale* (Figure 38B), but in part of *Serpophaga* (*S. hypoleuca*, *S. subcristata* and *S. munda*), *Polystictus*, and in the root species the inflation is completely absent and the proximal portion of the lacrimal appears straight, with a similar width compared to the orbital process and the general *corpus* of the lacrimal (Figure 38A).

Character 92. Cranium, lacrimal, *pes os lacrimale*, shape in ventral view/contact with the jugal bar: caudorostrally elongated or globular, in contact with the jugal bar in its intermediate portion (0); laterally expanded, in contact with the jugal bar in its medial portion (1); medially expanded, in contact with the jugal bar in its lateral portion (2).

In most of the species the *pes os lacrimale* contact the jugal bar in its intermediate portion (Figure 39A). In *Pseudotriccus pelzelni* and *Phylloscartes ventralis* the structure is expanded laterally, contacting the jugal bar in its medial portion (Figure 39B). And in *Myiopagis viridicata* the *pes os lacrimale* appears medially expanded, being in contact with the jugal bar in its lateral portion (Figure 39C). Considered inapplicable in the root species, in which the structure is not differentiated from the ectethmoid (completely fused; see character 93).

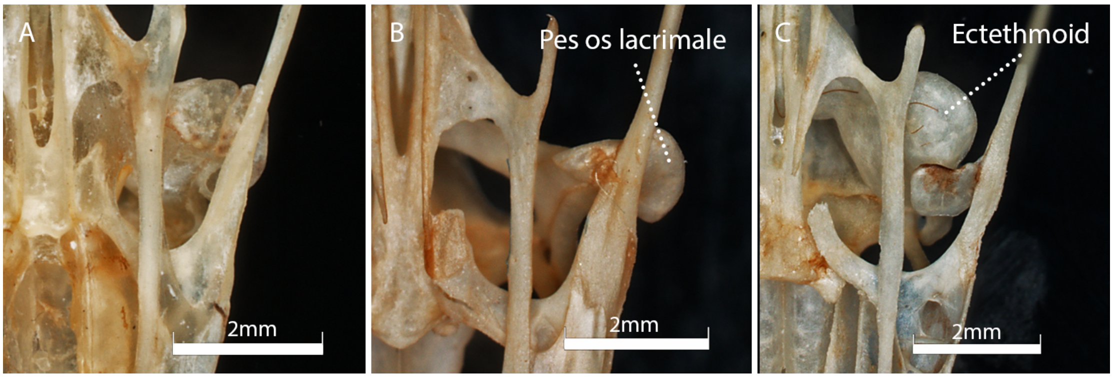

Figure 39. Ventral partial view of the right side of the cranium of *Zimmerius minimus* (A; USNM 344215), *Pseudotriccus pelzelni* (B; USNM 560009), and *Myiopagis viridicata* (C; USNM 555998) illustrating character 92 and its postulated states, respectively: *pes os lacrimale* contacting the jugal bar in its intermediate portion (state 0) *vs*. *pes os lacrimale* contacting the jugal bar in its medial portion (state 1) *vs*. *pes os lacrimale* contacting the jugal bar in its lateral portion (state 2).

Character 93. Cranium, lacrimal and ectethmoid, fusion: complete (0); incomplete/superficial (1); absent/unfused (2).

In the root species, *Furnarius rufus*, the ectethmoid is completely fused with the lacrimal. In the outgroup species of the genera *Myiobius*, *Tachuris*, *Xenopipo*, and *Chiroxiphia* the ectethmoid is just partially fused. And in the remaining taxa the two bones are clearly distinguished so the fusion is absent (Figure 38).

Character 94. Cranium, ectethmoid, position in relation to the *pes os lacrimale* in ventral view: medial (0); caudal (1); rostral (2).

The ectethmoid is medially positioned in most of the species (Figures 38A and B), but in *Onychorhynchus coronatus* it is positioned rostrally in relation to the *pes os lacrimale*, and in *Myiopagis viridicata*, *Elaenia dayi*, *E. flavogaster*, and *E. obscura* its position is more caudal (Figure 38C). In the species that shows the two bones completely fused (*Furnarius rufus*), the state was coded as inapplicable.

Character 95. Cranium, ectethmoid, thickness: laminar (0); inflated (1); extremely inflated (2).

Furnarius, *Pitangus*, *Myiozetetes*, *Pseudotriccus*, and *Myiophobus* representatives have ectethmoid with reduced thickness, laminar aspect in lateral view. The rest of the outgroup and all the ingroup presents ectethmoid inflated. And all species of the genus *Myiopagis* have the ectethmoid particularly greatly inflated (Figure 39C).

Character 96. Cranium, orbit, orbitonasal lateral foramen, shape: compressed (0); rounded (1); elliptical (2).

The plesiomorphic condition, an orbitonasal lateral foramen dorsoventrally compressed, is present only in the root species, *Furnarius rufus*, in *Piprites chloris* and in the analyzed species of the genus *Anairetes*, *Stigmatura*, *Mecocerculus leucophrys*, and part of *Phyllomyias* (*P. uropygialis* and *P. nigrocapillus*) (Figure 40A). State 1, an orbitonasal lateral foramen with a rounded shape, was observed in *Pitangus sulphuratus*, *Myiozetetes cayanensis*, *Platyrinchus mystaceus*, *Neopipo cinnamomea*, and *Tachuris rubrigastra* (Figure 40B). State 2 occurs in most of the species, and represents a foramen with elliptic, elongated, oval, or irregular shape (Figure 40C).

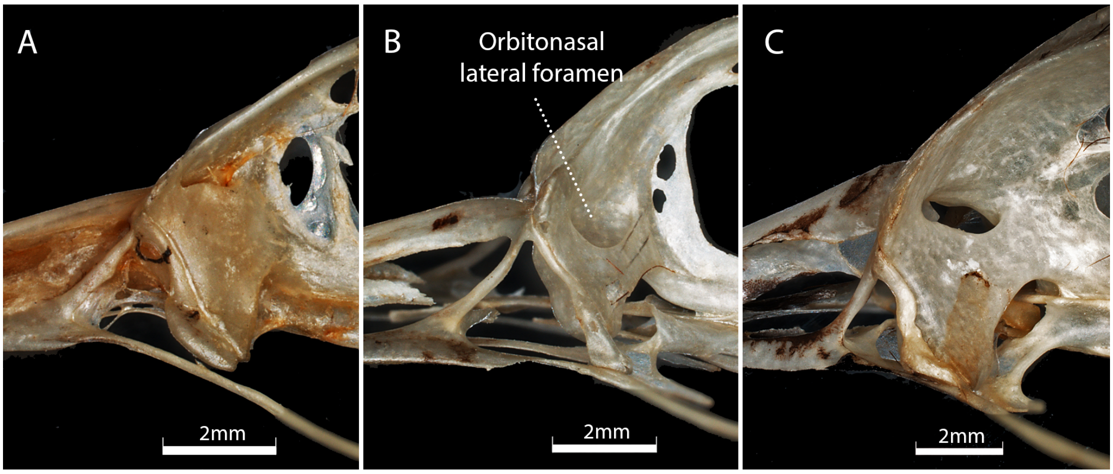

Figure 40. Lateral partial view of the left side of the cranium of *Anairetes parulus* (A; USNM 227803), *Platyrinchus mystaceus* (B; USNM 622252), and *Xenopipo atronitens* (C; USNM 621075) illustrating character 96 and its postulated states, respectively: compressed orbitonasal lateral foramen (state 0) *vs*. rounded orbitonasal lateral foramen (state 1) *vs*. elongated orbitonasal lateral foramen (state 2).

Character 97. Cranium, orbit, orbitonasal lateral foramen, configuration: one foramen (0); vestige of two foramina (1).

In *Zimmerius* spp., there is an incomplete separation in two foramina.

Character 98. Cranium, orbit, orbitonasal lateral foramen, degree of development/size: poorly developed, reduced (0); enlarged (1).

In *Onychorhynchus coronatus*, *Myiobius barbatus*, and *Pseudotriccus pelzelni*, the orbitonasal lateral foramen is so enlarged that the lateral margin almost reaches laterally the lacrimal. In dorsal view, just in *M. barbatus* and *P. pelzelni* the foramen can be observed (in *O. coronatus* the frontal is sufficiently wide and covers it).

Character 99. Cranium, orbit, orbitonasal foramen: absent (0); present (1).

The apormophic state, presence of the orbitonasal foramen, can be observed in *Serpophaga*, *Anairetes*, *Uromyias*, *Pseudocolopteryx*, *Polystictus*, *Culicivora*, *Mecocerculus leucophrys*, *Stigmatura*, *Euscarthmus*, *Pseudotriccus*, and *Platyrinchus* (Figures 40A and B).

Character 100. Cranium, orbit, orbitonasal foramen, size: reduced (0); enlarged (1).

Comparing the species that present the orbitonasal foramen, it is large and conspicuous just in *Anairetes*, *Uromyias*, *Serpophaga*, *Pseudocolopteryx*, and

Polystictus (Figure 40A). Considered inapplicable for the species that lacks the referred foramen (see character 99).

Character 101. Cranium, orbit, optic foramen, size: small (0); large (1).

In *Uromyias*, *Stigmatura*, *Euscarthmus*, *Inezia*, *Pseudotriccus*, *Corythopis*, *Phylloscartes*, *Todirostrum*, *Hemitriccus*, *Platyrinchus*, *Neopipo*, and *Tachuris* the interorbital bar is displaced closer to the dorsal limit of the orbital opening, and the interorbital septum is poorly ossified rostrally and ventrally, so that the gap relative to the optic foramen is increased in relation to the other taxa compared (Figure 41A and B), representing the plesiomorphic condition of the character.

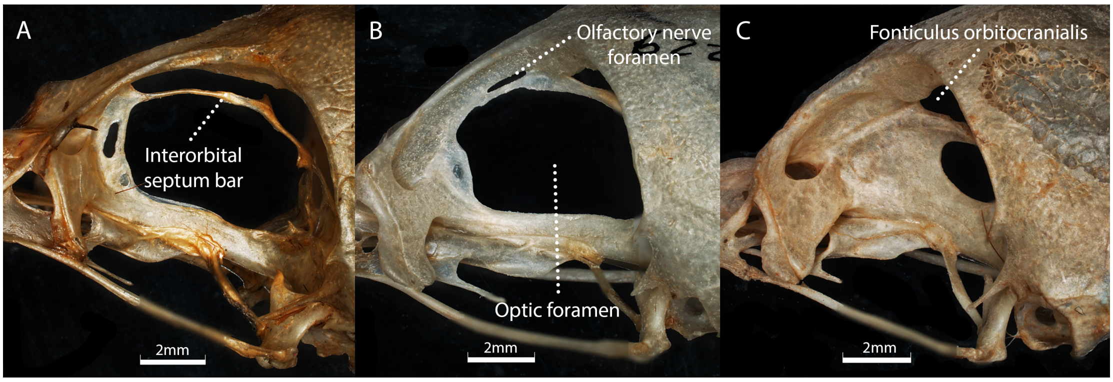

Figure 41. Lateral partial view of the left side of the cranium of *Uromyias agraphia* (A; LSU 90080), *Todirostrum russatum* (B; USNM 622765), and *Sublegatus modestus* (C; USNM 620773) illustrating character 101 and its postulated states, respectively: enlarged optic foramen (A and B; state 1) *vs*. reduced optic foramen (C; state 0).

Character 102. Cranium, orbit, interorbital septum bar, position/configuration: not reaching the dorsal portion of the interorbital septum (0); touching the dorsal portion of the interorbital septum (1).

In *Suiriri suiriri* (excluding *S. s. burmeisteri*, here treated as a separate species), *Pseudotriccus pelzelni*, *Corythopis torquatus*, *Phylloscartes ventralis*, *Todirostrum russatum*, *Hemitriccus margaritaceiventer*, *Platyrinchus mystaceus*, *Neopipo cinnamomea*, *Tachuris rubrigastra*, *Onychorhynchus coronatus*, *Oxyruncus cristatus*, *Pitangus sulphuratus*, and *Myiozetetes cayanensis* the interorbital septum bar reaches the dorsal portion of the interorbital septum (Figures 41B and C).

Character 103. Cranium, orbit, olfactory nerve foramen: present and reduced (0); present and well developed (1); absent (2).

Most of the analyzed taxa present a well-developed olfactory nerve foramen, with no separation of it and the *fonticulus orbitocranialis* (Figure 41A). In *Pseudotriccus*, *Todirostrum*, *Hemitriccus*, *Platyrinchus*, *Neopipo*, and *Furnarius* the foramen is present but is reduced, as a result of the position of the interorbital septum bar (Figure 41B; also see characters 101 and 102). In *Suiriri suiriri*, *Corythopis*, *Phylloscartes*, *Tachuris*, *Oxyruncus*, *Pitangus*, *Myiozetetes*, *Sublegatus* and *Onychorhynchus* the interorbital septum is enlarged and well fused in its rostral half, so the foramen is absent (Figure 41C). Polymorphism (states 0 and 2) was observed in *Lipaugus*, *Pipreola*, *Tityra*, *Pachyramphus*, and *Myiobius*.

Character 104. Cranium, orbit, *fonticulus orbitocranialis*, degree of development: well developed (0); poorly developed, reduced (1).

In a frontal perspective, the analyzed species of *Suiriri* (*S. suiriri* and *S. burmeisteri*) and the outgroup representatives of *Pitangus*, *Myiozetetes*, *Myiophobus*, *Sublegatus*, *Pyrocephalus*, *Knipolegus*, *Hirundinea*, and *Tityra* present a poorly developed *fonticulus orbitocranialis*, not reaching the lateral margin of the cranium as in the remaining species, in which it approaches the postorbital process.

Character 105. Cranium, maxilla, premaxilla, size, width: half or less than the width of the cranium (0); wider than half the width of the cranium (1).

Within the two states identified there is a certain variation, but generally in species included in the plesiomorphic state the width of the premaxilla at its caudal base is similar or smaller than the width of the cranium in its larger portion (Figures 42A, C and D). In species where the apomorphic condition has been identified, the width of the premaxilla base is not only greater than half the width of the cranium, as is almost similar (Figure 42B). Apomorphy is present in *Hirundinea*, *Myiobius*, *Onychorhynchus*, *Myiotriccus*, *Lipaugus*, *Pitangus*, *Sublegatus*, *Myiophobus* and in the ingroup *Suiriri* species.

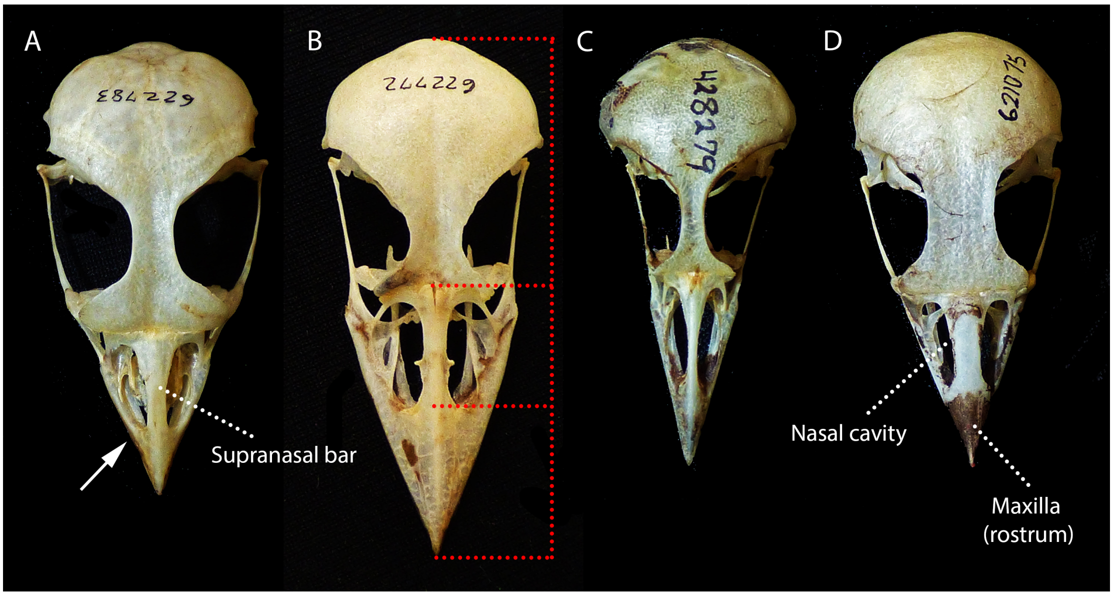

Figure 42. Dorsal view of the cranium of *Pipreola whitelyi* (A; USNM 622783), *Hirundinea ferruginea* (B; USNM 622772), *Mecocerculus leucophrys* (C; USNM 428279), and *Xenopipo atronitens* (D; USNM 621075) illustrating character 105 and its postulated states, respectively: narrow premaxilla (A, C and D; state 0) *vs*. wide premaxilla (B; state 1). Red doted lines indicate the measures mentioned in the text (next characters). Not scaled.

Character 106. Cranium, maxilla, premaxilla, size, length: longer than the rest of the cranium (0); equivalent to the rest of the cranium (1); shorter than the rest of the cranium (2).

The plesiomorphic condition was observed only in the root species, *Furnarius rufus*, and in *Onychorhynchus coronatus* and *Nesotriccus ridgwayi*. In most of the analyzed species the length of the premaxilla is smaller than the rest of the cranium (Figures 42A, D, 35). In *Pseudocolopteryx*, *Suiriri*, *Corythopis*, *Hirundinea*, *Myiobius*, *Lipaugus*, *Hemitriccus*, *Muscigralla*, *Pitangus*, and *Todirostrum* the length of the premaxilla is similar to the length of the rest of the cranium, so occupying approximately 50% of the cranium total length (Figures 42B and C).

Character 107. Cranium, maxilla, premaxilla, lateral curvature: absent (0); present (1).

In *Pipreola*, *Chiroxiphia*, *Todirostrum*, *Onychorhynchus*, *Myiotriccus*, *Pitangus*, *Sublegatus*, *Myiophobus*, and *Elaenia strepera* the lateral margin of the premaxilla presents a subtle curvature (Figure 42A, indicated by the white arrow), which is absent in the remaining species (Figures 42B, C and D).

Character 108. Cranium, maxilla, premaxilla, supranasal bar (*pila supranasalis*), size, width: narrow (0); wide (1).

In *Oxyruncus*, *Xenopipo* and *Tityra* the supranasal bar has similar width or is wider than the nasal cavity in the same portion (Figure 42D), representing the apomorphic condition. This character can be also described considering the distances between the nares.

Character 109. Cranium, maxilla, premaxilla, supranasal bar (*pila supranasalis*), extension: narrow (“pseudoschizorhiny”**) (0); wide (1).**

In *Furnarius rufus* the *pila supranasalis* extends besides the *zona flexoria craniofacialis*, corresponding to the “pseudoschizorhinal” form of “rhiny” (Feduccia 1967, 1973), contrasting with the “holorhinal” pattern observed in the other taxa.

Character 110. Cranium, maxilla, premaxilla, rostrum, size/extension: similar or greater than the nasal cavity length (0); shorter than the nasal cavity length (1).

Most of the analyzed species present a premaxillar rostrum shorter than the nasal cavity (Figures 42A, C and D). In *Furnarius*, *Hirundinea*, *Oxyruncus*, *Corythopis*, *Onychorhynchus*, *Hemitriccus*, *Todirostrum*, *Muscigralla*, *Pitangus*, and *Myiozetetes* the rostrum is longer than the nasal cavity length or present similar size (Figure 42B).

Character 111. Cranium, maxilla, premaxilla, height: less than half of the cranium height (0); more than half of the cranium height (1).

Just in *Tityra cayana* and *Oxyruncus cristatus* the height of the premaxilla is greater than half of the cranium length, so representing the apomorphy.

Character 112. Cranium, maxilla, jugal bar, curvature: absent (0); present (1).

A slight curvature can be observed in *Oxyruncus*, *Pipreola*, *Sublegatus*, *Todirostrum*, and *Elaenia strepera* (Figures 43 and 41B).

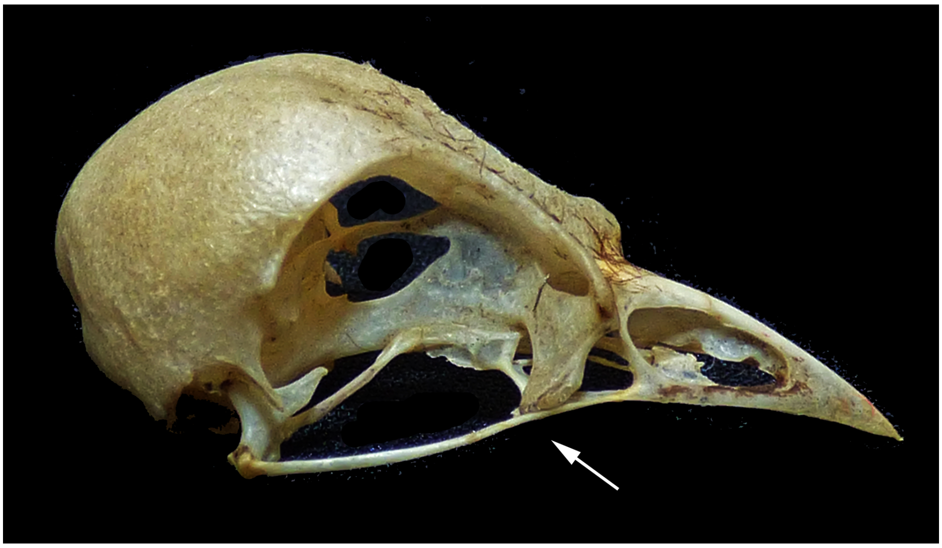

Figure 43. Lateral view of the right side of the cranium of *Elaenia strepera* (USNM 645291) illustrating the apomorphic state of the character 112: curved jugal arch (*vs*. straight jugal arch).

Character 113. Cranium, maxilla, premaxilla, nasal capsule, ossification/obliteration: absent, unossified (0); present, partially ossified (1); present, completely obliterated (2).

(Modified from Lanyon 1986; “Char.” 08)

The apomorphic form was divided into two clear coding states, with species that present a completely obliterated nasal capsule/cavity, including *Suiriri*, *Lipaugus*, *Sublegatus*, *Platyrinchus*, *Neopipo* (Figure 32); in addition to species in which obliteration is partial, occupying approximately half of the nasal capsule, as representatives of the genera *Myiobius*, *Pachyramphus*, *Tityra*, *Myiotriccus*, *Pipreola*, *Phylloscartes*, *Pyrocephalus*, part of *Elaenia* (*E. dayi*, *E. flavogaster* and *E. obscura*), *Zimmerius* (except *Z. cinereicapillus*), and part of *Myiopagis* (*M. flavivertex*, *M. viridicata*, *M. subplacens* and *M. gaimardii*). The plesiomorphic state includes species in which obliteration is completely absent (Figure 43).

Character 114. Cranium, maxilla, jugal bar, lateral expansion in the rostral end: absent (0); present (1).

A conspicuous lateral expansion was observed in the rostral portion of the jugal arch of *Myiobius barbatus* (Figure 44).

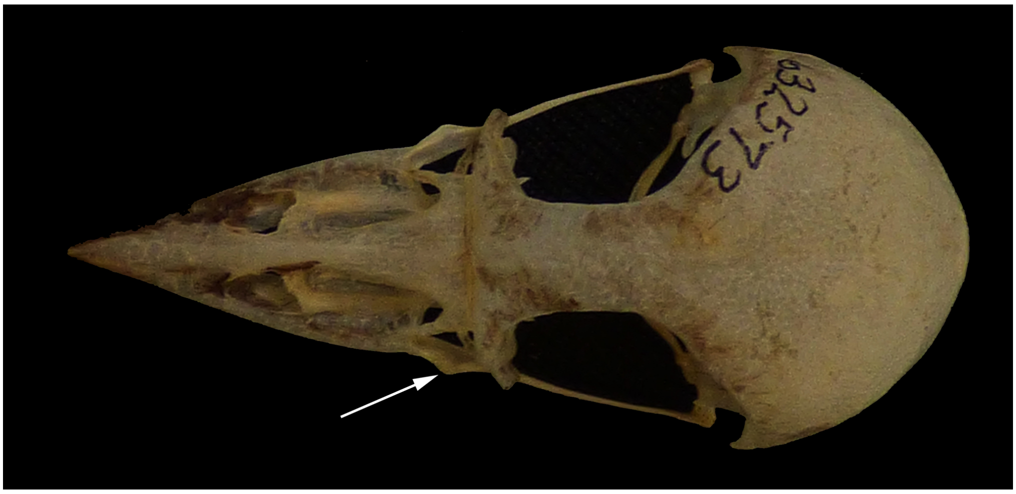

Figure 43. Dorsal view of the cranium of *Myiobius barbatus* (USNM 632573) illustrating the apomorphic state of the character 114: presence of a lateral expansion in the rostral portion of the jugal arch.

Character 115. Cranium, maxilla, premaxilla, nasal septum, ossification: absent, unossified (0); present, completely or partially ossified (1).

(Modified from Lanyon 1988; “Char.” G)

The plesiomorphic condition was found only in the root species, *Furnarius rufus*, and in *Tachuris rubrigastra*. The remaining taxa present at least a portion of the nasal septum ossified.

Character 116. Cranium, maxilla, premaxilla, nasal septum, degree of ossification: poorly ossified (0); completely ossified (1).

(Modified from Lanyon 1988; “Char.” G)

Partial ossification in the nasal septum was found in most of the analyzed species (Figure 44A), but within the ingroup the fully ossified nasal septum condition is common and well distributed (partial ossification of the nasal septum is especially well-defined in *Capsiempis flaveola*, *Phaeomyias murina*, *Nesotriccus ridgwayi*, *Phyllomyias fasciatus*, and *Stigmatura* spp.). Complete ossification can be observed in *Mecocerculus*, *Serpophaga*, *Euscarthmus*, *Culicivora*, *Pseudocolopteryx*, *Suiriri*, *Myiopagis*, *Tyrannulus*, *Uromyias*, *Elaenia*, *Camptostoma*, *Zimmerius*, *Myiobius*, *Tityra*, *Sublegatus*, *Myiophobus*, *Knipolegus*, *Phylloscartes*, *Muscigralla*, *Platyrinchus*, *Neopipo* (Figure 44B). Inapplicable in the species that lacks the nasal septum ossification (see character 115).

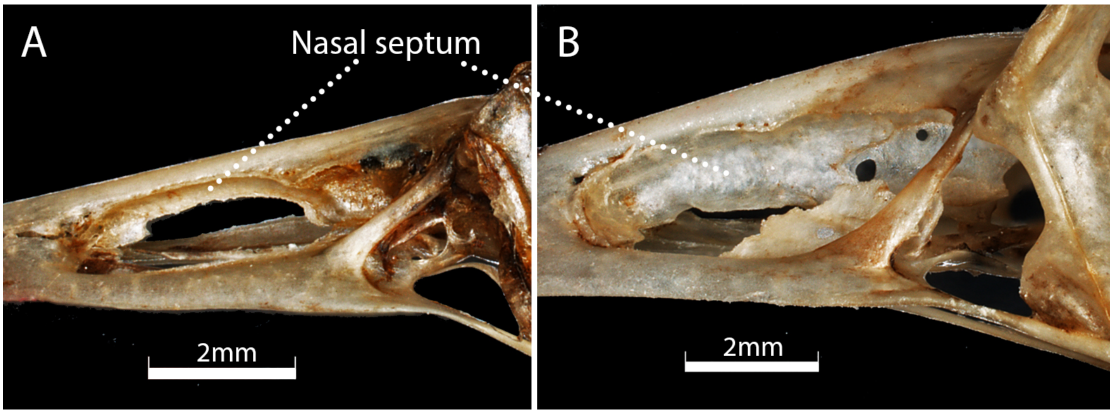

Figure 44. Lateral partial view of the left side of the cranium/premaxilla of *Stigmatura budytoides* (A; USNM 227781) and *Elaenia ridleyana* (B; USNM 491935) illustrating character 116 and its postulated states, respectively: partially ossified nasal septum *vs*. completely ossified nasal septum.

Character 117. Cranium, maxilla, premaxilla, nasal septum, transverse trabecular plate: absent (0); present (1).

(Modified from Lanyon 1988; "Char." A)

All the representatives of the ingroup, except *Myiopagis* species analyzed (Figure 45A), plus outgroup species belonging to the genera *Sublegatus*, *Myiophobus*, *Pseudotriccus*, *Corythopis*, *Phylloscartes*, and *Pyrocephalus* have a trabecular plate in the inferior margin of the nasal septum, representing a neomorphy (Figure 45B, C and D). The trabecula, as pointed out by Lanyon (1988), presents certain variation in shape and size.

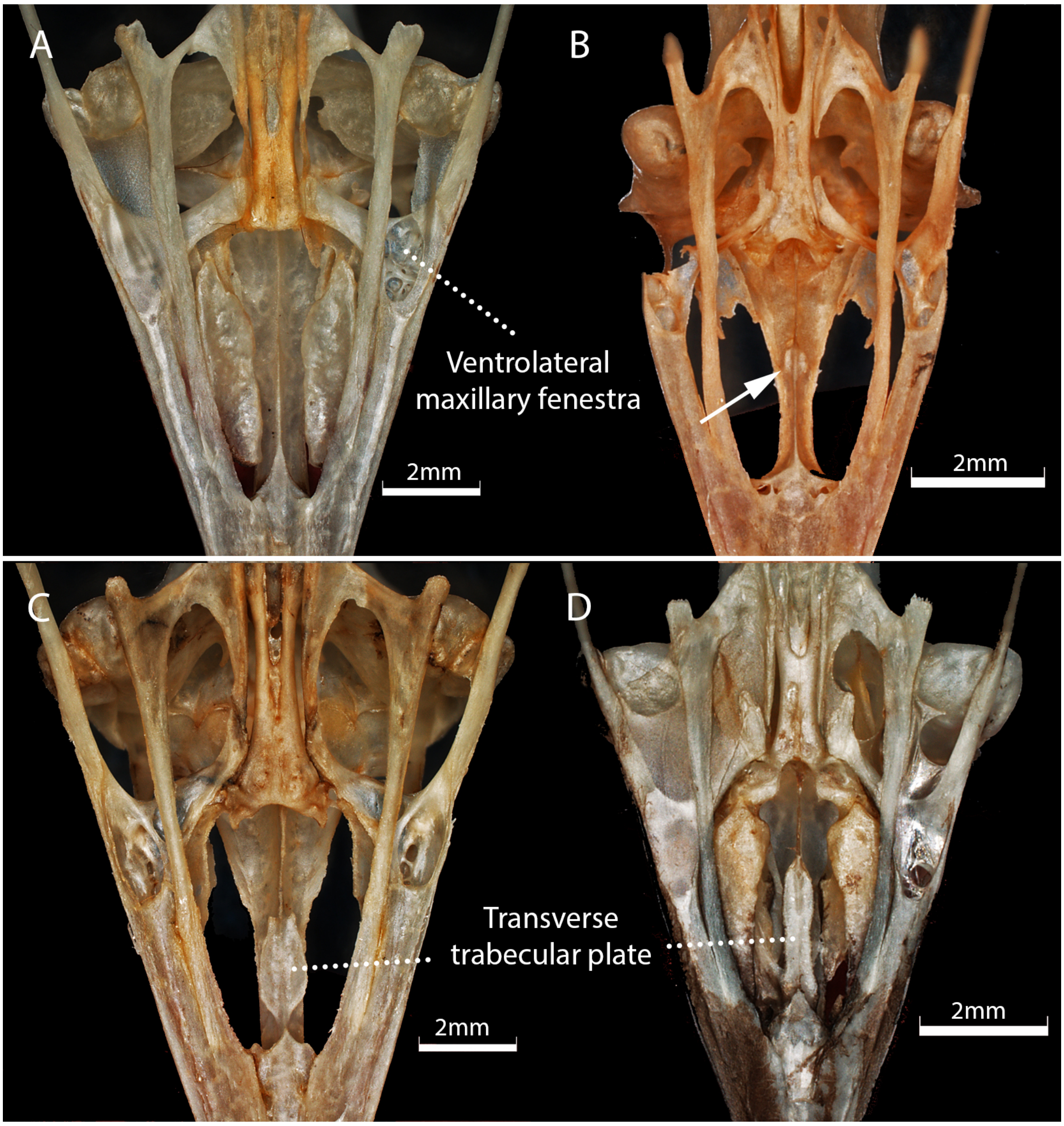

Figure 45. Ventral partial view of the cranium/palate of *Myiopagis subplacens* (A; USNM 643882), *Ornithion inerme* (B; USNM 491501), *Elaenia ridleyana* (C; USNM 491935), and *Zimmerius acer* (D; USNM 621784) illustrating character 117 and its postulated states, respectively: absent transverse trabecular plate (A, state 0) *vs*. present transverse trabecular plate (B; state 1).

Character 118. Cranium, maxilla, premaxilla, nasal septum, transverse trabecular plate, size, length: shorter than half of the nasal septum (0); longer than half of the nasal septum (1).

In *Zimmerius*, *Uromyias*, *Serpophaga*, *Phyllomyias*, *Suiriri*, *Pseudocolopteryx*, *Inezia*, *Mecocerculus*, *Culicivora*, *Euscarthmus*, *Polystictus*, *Sublegatus*, *Phylloscartes*, and *Corythopis* the transverse trabecular plate extends for more than half of the nasal septum (Figure 45D). Coded as inapplicable in the species that lacks the trabecula (see character 117).

Character 119. Cranium, maxilla, premaxilla, nasal septum, anterior notch: absent (0); present (1).

(Modified from Lanyon 1988; "Char." A)

Elaenia martinica, *E. fallax* and the outgroup representatives of Tyrannidae: Fluvicolinae (*Myiophobus*, *Sublegatus*, *Pyrocephalus*, *Knipolegus*) shows an anterior notch in the nasal septum (Figure 46), representing the apomorphic condition. Inapplicable in the taxa that lacks the nasal septum.

Figure 46. Lateral view of the right side of the cranium of *Elaenia martinica* (USNM 487918) illustrating the apomorphic state of the character 119: presence of an anterior notch in the nasal septum.

Character 120. Cranium, maxilla, premaxilla, nasal septum, additional transverse trabecular plate in the posterior portion of the nasal septum: absent (0); present (1).

(Modified from Lanyon 1988; "Char." D)

In addition to the transverse trabecular plate homologous to what is observed in the other species (see character 117), *Stigmatura* has a second trabecula, located posteriorly.

Character 121. Cranium, maxilla, premaxilla, nasal septum, transverse trabecular plate bulbous-shaped and short: absent (0); present (1).

In comparison with the other taxa, *Ornithion* presents a rather reduced transverse trabecular plate, with a bulbous shape (Figure 45B).

Character 122. Cranium, maxilla, premaxilla, nasal septum, transverse trabecular plate, shape: not laterally expanded (0); laterally expanded, reaching the supranasal bar lateral margin in ventral view (1).

In *Elaenia strepera*, *E. ridleyana*, *E. ruficeps*, *E. flavogaster*, *E. obscura*, *E. spectabilis* and *Sublegatus modestus* the transverse trabecular plate is laterally expanded, reaching the lateral margin of the *pila supranasalis* in ventral view (Figure 45C).

Character 123. Cranium, maxilla/palate, nasal, maxillary process, dorsal portion, size/width: wider than ventral portion, or with similar width (0); narrower than ventral portion (1).

In most of the analyzed species the dorsal portion of the maxillary process of the nasal is narrower in relation to the width of the ventral portion (Figure 44B). The plesiomorphy was identified in *Suiriri*, *Stigmatura*, *Mecocerculus leucophrys*, *Onychorhynchus*, *Xenopipo*, *Chiroxiphia*, *Myiobius*, *Pipreola*, *Hemitriccus*, *Lipaugus*, *Oxyruncus*, *Piprites*, *Tityra*, *Sublegatus*, *Phylloscartes*, *Corythopis*, *Knipolegus*, and *Furnarius* (Figure 44A).

Character 124. Cranium, premaxilla, nasal cavity, caudal margin, position: dorsal in relation to the culmen level (0); ventral in relation to the culmen level (1).

In the root taxon, *Furnarius rufus*, the caudal margin of the nasal capsule/cavity is dorsally positioned in relation to the culmen level.

Character 125. Cranium, palatine, transpalatine process, length: longer than the vomer width, or with similar length (0); shorter than vomer (1).

In most of the species the transpalatine process is lengthier compared to the width of the vomer (Figure 47A and C). The apomorphic condition can be observed in *Elaenia*, *Myiopagis*, *Suiriri*, *Tyrannulus*, part of *Zimmerius* (*Z. acer* and *Z. parvus*), *Phyllomyias nigrocapillus*, *Euscarthmus*, *Culicivora*, *Phaeomyias*, *Piprites*, *Xenopipo*, *Chiroxiphia*, *Lipaugus*, *Oxyruncus*, *Tityra*, *Pachyramphus*, *Pipreola*, *Muscigralla*, and *Myiobius* (Figure 47B).

Figure 47. Ventral partial view of the cranium/palate of *Mecocerculus stictopterus* (A; LSU 170468), *Elaenia strepera* (B; USNM 645291), and *Hirundinea ferruginea* (C; USNM 622772) illustrating character 125 and its postulated states, respectively: long transpalatine process (A and C, state 0) *vs*. short transpalatine process (B; state 1).

Character 126. Cranium, palatine, transpalatine process, shape: thin (0); spatulate, wide (1).

Wide and spatulate transpalatine process was observed in *Zimmerius*, *Suiriri*, *Tyrannulus*, *Myiopagis*, *Elaenia*, *Hirundinea*, *Platyrinchus*, *Lipaugus*, *Pipreola*, *Tityra*, *Pachyramphus*, *Piprites*, *Xenopipo*, and *Chiroxiphia* (Figure 47B and C), different from the slender process present in most of the taxa (Figure 47A).

Character 127. Cranium, palatine, transpalatine process, orientation: laterocaudal (0); caudal (1).

In *Hirundinea ferruginea* the transpalatine process is caudally oriented (Figure 47C), representing an apomorphy (in the remaining species it is laterally oriented).

Character 128. Cranium, palatine, rostral process: present (0); absent (1).

Piprites chloris lacks the rostral process of the palatine (Figure 48), which is conspicuous in the remaining species, although varying in degree of development (Figure 47).

Figure 48. Ventral partial view of the cranium of *Piprites chloris* (USNM 487918) illustrating the apomorphic state of the character 128: absence of the rostral process of the palatine (the arrow indicates the position).

Character 129. Cranium, palatine, maxillary process, width: narrow (0); wide (1).

Suiriri, *Elaenia*, *Myiopagis*, *Tyrannulus*, *Platyrinchus*, *Neopipo*, *Sublegatus*, *Xenopipo*, *Hirundinea*, *Myiotriccus*, *Onychorhynchus*, *Myiobius*, *Myiophobus*, *Pyrocephalus*, *Knipolegus*, *Chiroxiphia*, *Oxyruncus*, *Tityra*, *Pachyramphus* and *Piprites* present maxillary process of the palatine wider than the width of the jugal bar in its median portion (Figures 47B and 48).

Character 130. Cranium, palatine, *pars choanalis*, width: wider than the maxillary process (0); narrower than the maxillary process (1).

The majority of the studied skeletons possess *pars choanalis* of the palatine wider than the maxillary process (Figures 47 and 48), or with similar size. But in *Pseudelaenia leucospodia*, *Capsiempis flaveola*, *Phaeomyias murina*, *Phyllomyias fasciatus* and *Nesotriccus ridgwayi* and the structure is markedly narrower (Figure 49).

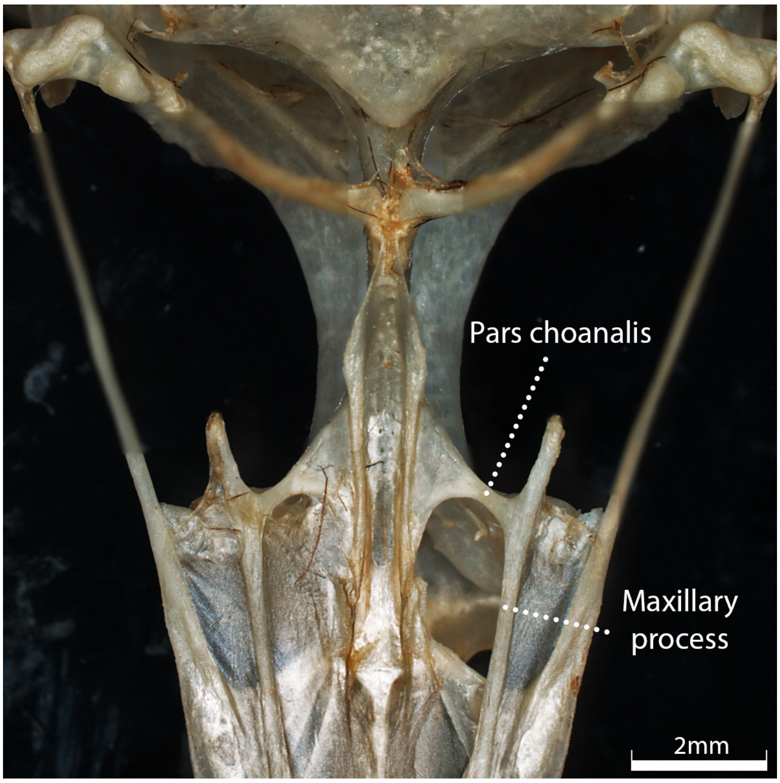

Figure 49. Ventral partial view of the cranium of *Pseudelaenia leucospodia* (USNM 643841) illustrating the apomorphic state of the character 130: narrow *pars choanalis* of the palatine.

Character 131. Cranium, palate, *fossa choanalis*, size/extension: length distinctly larger than width (0); width and length almost the same size (1).

In *Furnarius rufus* and *Tachuris rubrigastra* the length of the *fossa choanalis* is particularly larger than the width of the fossa.

Character 132. Cranium, palate/maxillar, ventrolateral maxillary fenestra: present (0); absent (1).

Representative species of the genera *Uromyias*, *Inezia*, *Tyrannulus*, *Platyrinchus*, *Piprites*, *Chiroxiphia*, and *Xenopipo* lack the ventrolateral maxillary fenestra, which is conspicuous in the remaining species and varies in the degree of development (Figure 45).

Character 133. Cranium, palatine, maxillary process, rostral end, shape: not expanded, with similar width to the caudal portion (0); laterally expanded (1).

In *Platyrinchus mystaceus*, *Neopipo cinnamomea*, *Onychorhynchus coronatus*, *Myiotriccus ornatus* and *Hirundinea ferruginea* the maxillary process of the palatine presents a strong enlargement in its rostral base (Figure 50). The remaining species presenting the plesiomorphic state shows a maxillary process with similar width between the rostral and caudal portions (Figure 45).

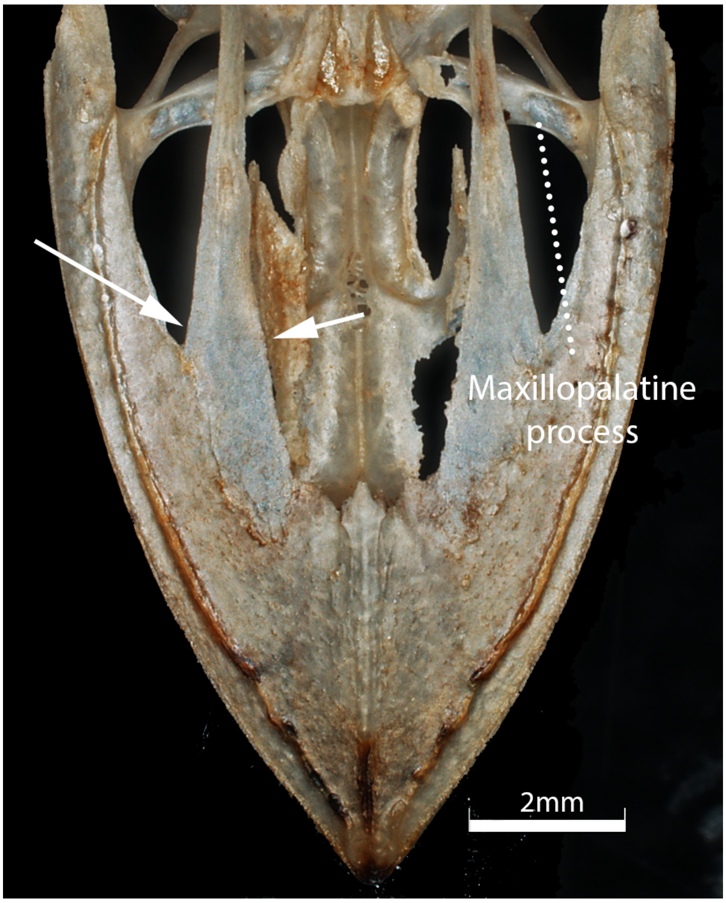

Figure 50. Ventral partial view of the cranium of *Platyrinchus mystaceus* (USNM 556422) illustrating the apomorphic state of the character 133: expanded rostral portion of the maxillary process of the palatine (indicate by the arrows).

Character 134. Cranium, maxilla/palate, maxillopalatine process, size, width in the median portion: not reduced (0); reduced (1).

Maxillopalatine process with a thin *corpus* in its intermediate portion was observed in part of *Phyllomyias* (*P. nigrocapillus*, *P. cinereiceps*, *P. uropygialis*, *P. zeledoni*, and *P. burmeisteri*), *Ornithion*, and *Camptostoma*, representing a neomorphy (Figure 51A).

Character 135. Cranium, maxilla/palate, maxillopalatine process, shape: rounded, medially contacting the vomer (0); spatulate (1); triangular, caudolaterally oriented (2); acuminate, caudally twisted (3); sharp, perfectly fitting the vomer lateral margin (4).

The maxillopalatine process is probably one of the most variable structures that was examined in the present study. But despite such variation, some clear patterns have been identified and seem unique at the genus level for some taxa. The states identified with regard to shape were: the plesiomorphic condition with rounded shape at the medial end, found in most of the terminals studied (state 0, Figure 51F); spatulate just in *Mecocerculus minor* (state 1, Figure 51E); triangular and caudolaterally oriented in all species of *Zimmerius* (state 2, Figure 51B); sharp and well attached to the lateral margin of the vomer in *Stigmatura* spp. and *Muscigralla* (state 4, Figure 51D); and caudally twisted in the two species of *Uromyias* (state 3, Figure 51C).

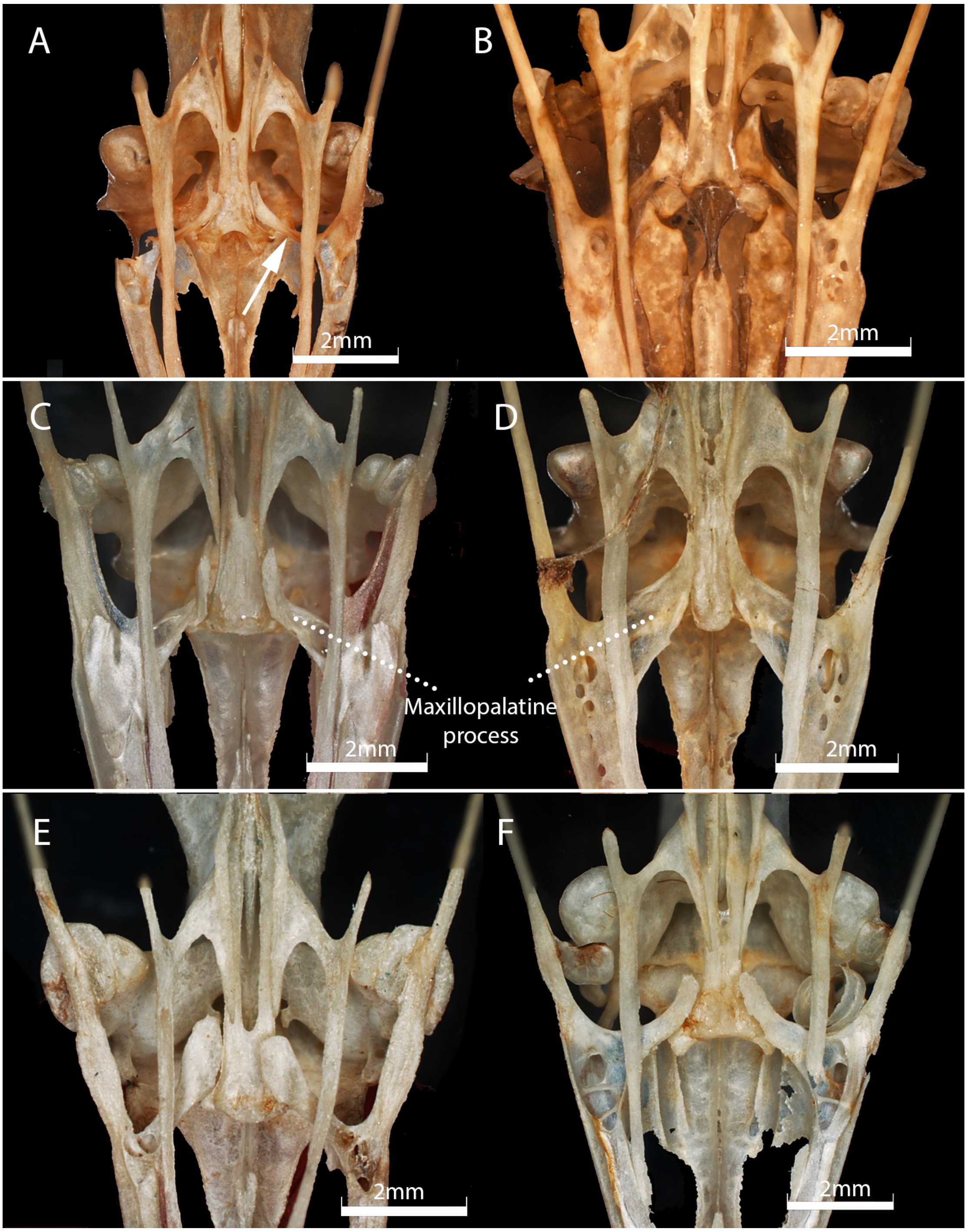

Figure 51. Ventral partial view of the cranium/palate of *Ornithion inerme* (A; USNM 491501), *Zimmerius chrysops* (B; USNM 428800), *Uromyias agilis* (C; USNM 614866), *Stigmatura napensis* (D; USNM 491716), *Mecocerculus minor* (E; USNM 560008), and *Myiopagis viridicata* (F; USNM 555998), illustrating characters 134 and 135 and its postulated states: Char. 134 - thin *corpus* of the maxillopalatine

process (A, indicated by the arrow) *vs*. not reduced (wide) maxillopalatine process (B-F). Char. 135 - maxillopalatine process shapes: round (A and F), triangular (B), twisted (C), sharp (D), spatulate (E).

Character 136. Cranium, maxilla/palate, maxillopalatine process, ventral fossa: absent (0); present (1).

A conspicuous fossa can be observed in a ventral perspective of the maxillopalatine process in *Sublegatus* and the representative taxa of Platyrinchidae, *Platyrinchus mystaceus* and *Neopipo cinnamomea* (Figure 50), which is totally absent in the rest of the groups (Figure 45).

Character 137. Cranium, maxilla/palate, vomer, mediorostral margin, shape: U-shaped, concave (0); flat (1); convex (2).

As expected, all species analyzed present the "aegithognathous" typical vomer. The morphological variation found is both in the mediorostral margin and in the lateral process (Warter's "horn"). The mediorostral margin can be flat (Figure 51C), a condition found in *Uromyias*, *Anairetes*, *Serpophaga*, *Culicivora*, *Polystictus*, *Inezia*, *Mecocerculus leucophrys*, *Pseudocolopteryx*, *Capsiempis*, *Phaeomyias*, *Nesotriccus*, *Pseudelaenia*, *Phyllomyias*, *Myiotriccus*, *Xenopipo*, *Corythopis*, *Knipolegus*, *Lipaugus*, *Pitangus*, *Myiozetetes*, and *Chiroxiphia*; concave, as in *Zimmerius*, *Tyrannulus*, *Suiriri*, *Ornithion*, *Euscarthmus*, *Camptostoma*, *Myiopagis*, *Elaenia*, *Myiobius*, *Myiophobus*, *Sublegatus*, *Todirostrum*, *Piprites*, *Oxyruncus* (Figures 51A, B and F); or convex, observed just in *Stigmatura*, *Mecocerculus minor*, *Phyllomyias nigrocapillus*, and *Pseudotriccus* (Figures 51D and E).

Character 138. Cranium, maxilla/palate, vomer, configuration: fused with the alinasal turbinals (compound vomer) (0); unfused with the alinasal turbinals (1).

Only in the root species, *Furnarius rufus* (Furnariidae), the ossified alinasal turbinals are fused to the vomer forming a "compound vomer".

Character 139. Cranium, maxilla/palate, vomer, vomerine "horn" (lateral process), shape/extension: wide lamina, conspicuous, more medially positioned (0); cylindrical/acuminate, reduced, positioned more laterally (1).

The pattern considered apomorphic reunites species with laterally positioned lateral processes/condyles in the *corpus* of vomer, reduced, and with acuminate form instead of laminar, and include those of the genera *Suiriri*, *Capsiempis*, *Pseudelaenia*, part of *Phyllomyias* (*P. fasciatus*), *Phaeomyias*, *Nesotriccus*, part of *Mecocerculus* (*M. leucophrys*), *Culicivora*, *Serpophaga*, *Pseudocolopteryx*, *Polystictus*, *Uromyias*, and *Anairetes* (Figure 51C).

Character 140. Cranium, palatine, ventral crest (*crista ventralis*), caudal notch: present (0); absent (1).

In *Furnarius rufus* the ventral crest of the palatine presents a caudal notch, conspicuous in ventral view.

Character 141. Cranium, maxilla/palate, vomer, choanal fossa, extension: caudal, not reaching the caudal limit of the maxillopalatine process (0); rostral, reaching the caudal limit of the maxillopalatine process (1).

In most of the studied species the rostral margin of the choanal fossa approaches more the mediorostral limit of the vomer, reaching or almost reaching the caudal tip of the maxillopalatine process in the sagittal axis (Figure 52A). In *Myiophobus*, *Sublegatus*, *Pyrocephalus*, *Knipolegus*, *Todirostrum*, *Hemitriccus*, *Pseudotriccus*, *Phylloscartes*, *Piprites*, *Onychorhynchus*, *Myiobius*, *Myiotriccus*, *Hirundinea*, *Chiroxiphia*, *Xenopipo*, *Pitangus*, *Myiozetetes*, *Oxyruncus*, *Tachuris*, *Lipaugus*, *Pipreola*, *Tityra*, *Pachyramphus*, and *Muscigralla* the rostral margin of the fossa is positioned more caudal, never reaching the maxillopalatine process (Figure 52B).

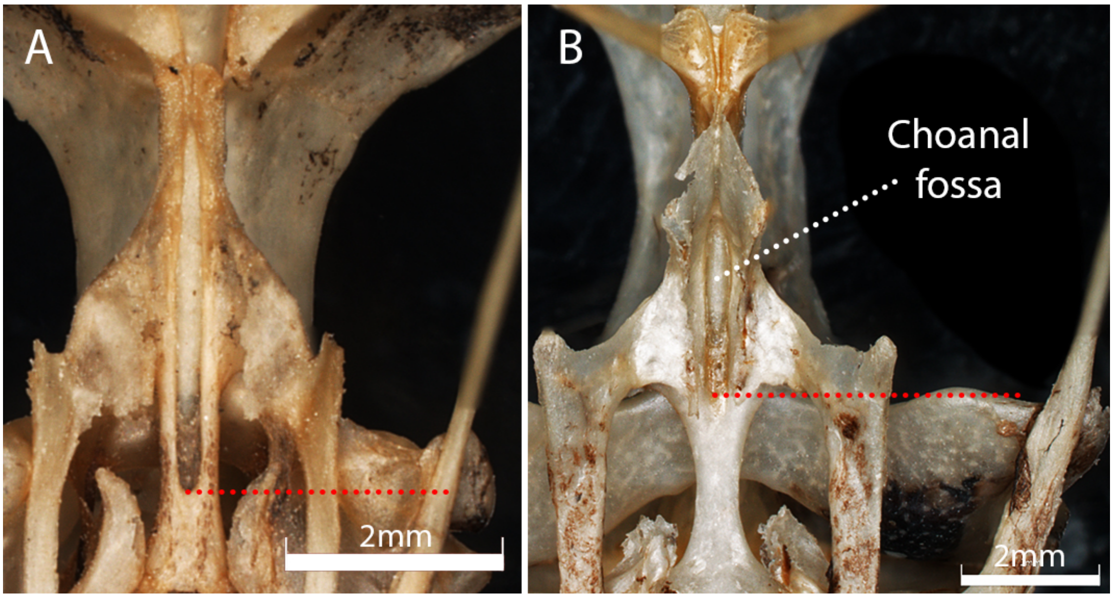

Figure 52. Ventral partial view of the cranium/palate of *Tyrannulus elatus* (A; USNM 559392) and *Piprites chloris* (B; USNM 622076) illustrating character 141 and its postulated states, respectively: rostral end of the choanal fossa rostrally positioned (A,

state 1) *vs*. rostral end of the choanal fossa caudally positioned (B; state 0). Red doted lines indicate the position of the rostral limit of the fossa choanalis.

Character 142. Cranium, palatine, pterygoid, curvature: absent, straight (0); present, curved (1).

The apomorphic condition, a curved pterygoid (Figures 53B and C), was observed in *Onychorhynchus*, *Myiobius*, *Piprites*, *Chiroxiphia*, *Xenopipo*, *Pitangus*, *Knipolegus*, *Pyrocephalus*, *Myiozetetes*, *Hirundinea*, *Myiotriccus*, *Sublegatus*, *Tachuris*, *Hemitriccus*, *Todirostrum*, *Muscigralla*, *Phylloscartes* and all the ingroup (except *Serpophaga cinerea* and *S. nigricans*).

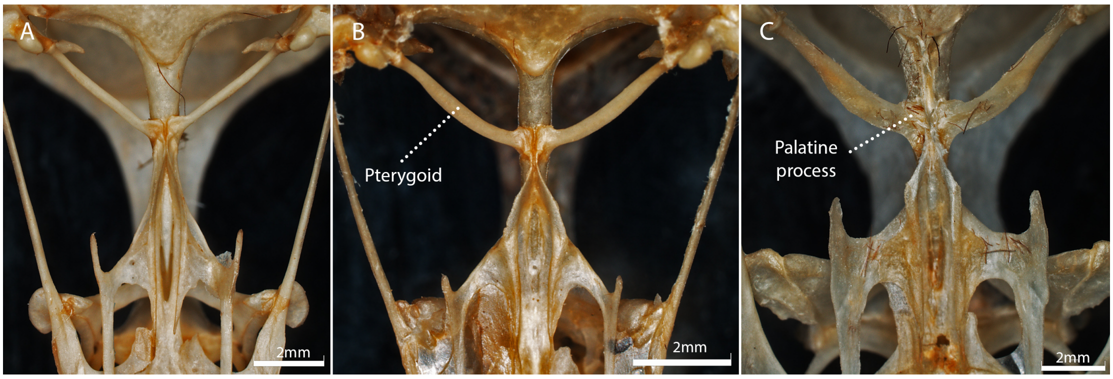

Figure 53. Ventral partial view of the cranium of *Pseudotriccus pelzelni* (A; USNM 560009), *Culicivora caudacuta* (B; LSU 151790), and *Hirundinea ferruginea* (C; USNM 622772) illustrating character 142 and its postulated states, respectively: straight pterygoid (A, state 0) *vs*. curved pterygoid (B and C; state 1).

Character 143. Cranium, palatine, pterygoid, width: rostrally wider (0); uniform (1).

In *Furnarius*, *Hirundinea*, *Xenopipo*, *Myiobius*, *Muscigralla*, and *Sublegatus* the width at the rostral portion of the pterygoid is larger compared to the caudal portion (Figure 53C), thus representing the plesiomorphy.

Character 144. Cranium, palatine, pterygoid, palatine process, size/degree of development: reduced, not dilated (0); enlarged, dilated (1).

The analyzed species representing *Pipreola*, *Myiobius*, *Todirostrum*, *Hemitriccus*, *Platyrinchus*, *Neopipo*, *Piprites*, and *Onychorhynchus* present a dilated palatine process of the pterygoid (Figure 53C), distinguishing from the reduced process of the remaining taxa (Figures 53A and B).

Postcranium (145-151)

Character 145. Synsacrum, intratransversal foramina, degree of development: present, conspicuous (0); absent, or strongly reduced/fused (1).

In the outgroup species *Chiroxiphia caudata*, *Xenopipo atronitens*, *Hemitriccus margaritaceiventer*, *Oxyruncus cristatus*, and *Lipaugus vociferans*, the synsacrum intratransversal foramina are strongly reduced (fused) or even absent (Figure 54B). In all the remaining taxa the foramina are conspicuous (Figure 54A).

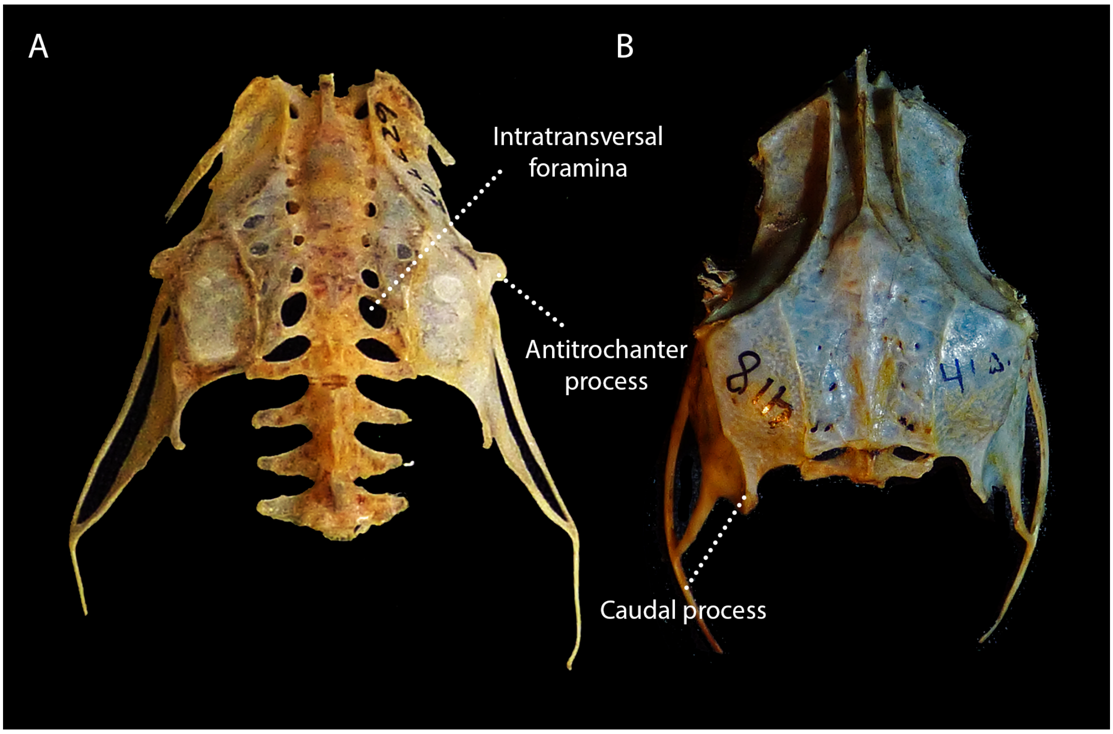

Figure 54. Dorsal view of the synsacrum of *Hirundinea ferruginea* (A; USNM 622772), and *Oxyruncus cristatus* (B; AMNH 410) illustrating character 145 and its postulated states, respectively: conspicuous intratransversal foramina (A, state 0) *vs*. inconspicuous intratransversal foramina (B; state 1). Not scaled.

Character 146. Synsacrum, caudal process, configuration: free from the *scapus ischii* (0); laterally fused with the *scapus ischii* (1).

In *Oxyruncus cristatus*, the caudal process of the synsacrum is laterally fused with the *scapus ischii* (Figure 54B).

Character 147. Synsacrum, caudal process, shape: not dilated (0); dilated (1).

In *Muscigralla brevicauda* the caudal process of the synsacrum is dilated laterally and medially, thus differentiating itself from the synsacrum of all other taxa.

Character 148. Synsacrum, caudal process, position: lateral (0); medial (1).

The representative species of the recently ranked families Oxyruncidae (*Oxyruncus cristatus*), Onychorhynchidae (*Onychorhynchus coronatus* and *Myiobius barbatus*), and Tityridae (*Tityra cayana* and *Pachyramphus polychopterus*) present an apomorphy in which the caudal process of the synsacrum is medially positioned, so the gap between it and the caudal margin of the ilium is reduced (Figure 54B) compared to the rest of the studied families.

Character 149. Ischium, *foramen obturatum*, configuration: separated from the ischiopubic space (0); united with the ischiopubic space (1).

All the ingroup except *Anairetes*, *Uromyias*, *Culicivora*, *Serpophaga*, *Polystictus*, *Pseudocolopteryx* and *Mecocerculus leucophrys*, and the outgroup genera *Pseudotriccus*, *Lipaugus*, *Corythopis*, *Hirundinea*, *Hemitriccus*, *Todirostrum*, *Myiotriccus*, *Piprites*, *Onychorhynchus*, *Myiobius*, *Tityra*, *Pachyramphus*, *Knipolegus*, *Phylloscartes*, *Sublegatus*, *Pitangus*, *Myiozetetes*, *Tachuris*, and *Oxyruncus* presents the *foramen obturatum* not closed and separated from the "ischiopublic space" (*spatium ischiopubicum*) (Figure 55B). In the remaining groups the referred foramen is separated, in variable degrees of fusion (Figure 55A).

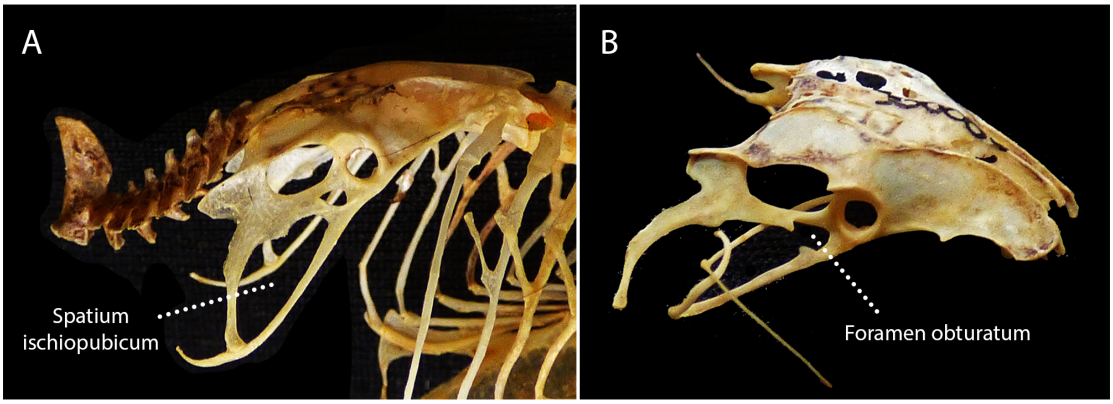

Figure 55. Lateral view of the synsacrum/pelvis of *Myiobius barbatus* (A; USNM 632573), and *Pseudotriccus pelzelni* (B; USNM 560009) illustrating character 149 and its postulated states, respectively: separated *foramen obturatum* (A, state 0) *vs.* united *foramen obturatum* and *spatium ischiopubicum* (B; state 1). Not scaled.

Character 150. Pubis, *scapus pubis*, length: long (0); short (1).

In *Tityra*, the *scapus pubis* is shorter than in the remaining taxa, what can be seen comparing its length with the ischium caudal/terminal process (the *scapus pubis* not trespass it).

Character 151. Sternum, rostrum, external spine process, length: short (0); long (1).

In *Oxyruncus* and *Onychorhynchus* the processes of the external spine of the sternum/manubrium are enlarged (Figure 56B) compared to the structure in the remaining taxa (Figure 56A).

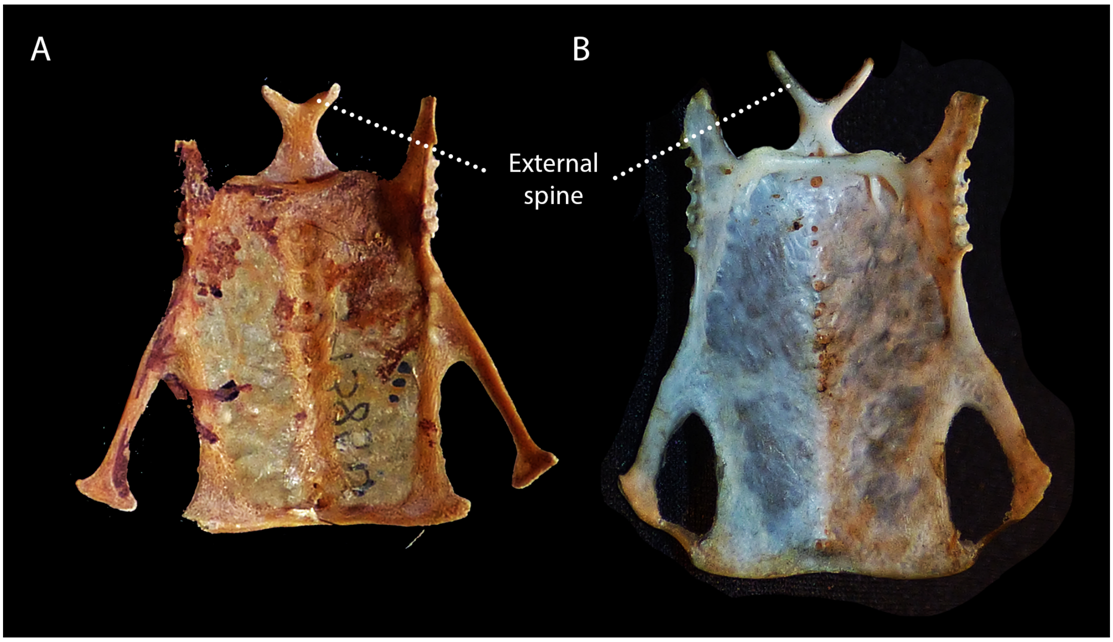

Figure 56. Dorsal view of the sternum of *Zimmerius parvus* (A; USNM 343856) and *Oxyruncus cristatus* (B; AMNH 410) illustrating character 151 and its postulated states, respectively: short external spine (A, state 0) *vs*. long external spine (B; state 1). Not scaled.

Phylogenetic analyses

Phylogenetic analysis with the matrix of 151 characters and 112 terminal species (Appendix 2) resulted in 24 maximally parsimonious trees with 564 of length ("steps"; the character transformations can be consulted in the Appendix 3). The topology of the strict consensus tree (Consistency Index = 0.66, Retention Index = 0.85) differs slight from the more parsimonious ones, remaining intact with regard to the composition of taxa at the generic level and their relationships at more inclusive levels, and losing resolution in intrageneric relationships. The Elaeniinae subfamily was recovered as monophyletic (Figure 57) with a Bremer support of 4.

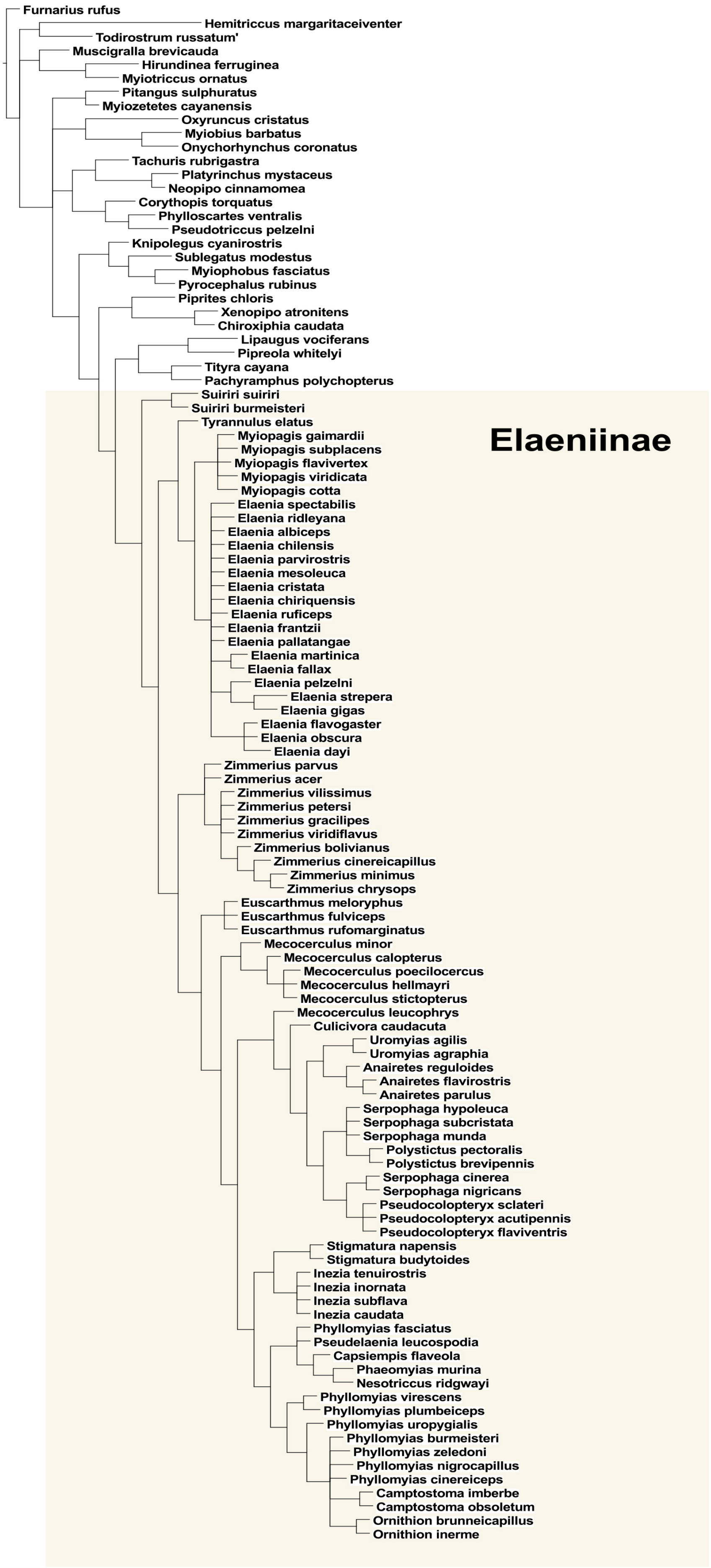
Furnarius rufus
Hemitriccus margaritaceiventer
Todirostrum russatum'
Muscigralla brevicauda
Hirundinea ferruginea
Myiotriccus ornatus
Pitangus sulphuratus
Myiozetetes cayanensis
Oxyruncus cristatus
Myiobius barbatus
Onychorhynchus coronatus
Tachuris rubrigastra
Platyrinchus mystaceus
Neopipo cinnamomea
Corythopis torquatus
Phylloscartes ventralis
Pseudotriccus pelzelni
Knipolegus cyanirostris
Sublegatus modestus
Myiophobus fasciatus
Pyrocephalus rubinus
Piprites chloris
Xenopipo atronitens
Chiroxiphia caudata
Lipaugus vociferans
Pipreola whitelyi
Tityra cayana
Pachyramphus polychopterus
Suiriri suiriri
Suiriri burmeisteri
Tyrannulus elatus
Elaeniinae
Myiopagis gaimardii
Myiopagis subplacens
Myiopagis flavivertex
Myiopagis viridicata
Myiopagis cotta
Elaenia spectabilis
Elaenia ridleyana
Elaenia albiceps
Elaenia chilensis
Elaenia parvirostris
Elaenia mesoleuca
Elaenia cristata
Elaenia chiriquensis
Elaenia ruficeps
Elaenia frantzii
Elaenia pallatangae
Elaenia martinica
Elaenia fallax
Elaenia pelzelni
Elaenia strepera
Elaenia gigas
Elaenia flavogaster
Elaenia obscura
Elaenia dayi
Zimmerius parvus
Zimmerius acer
Zimmerius vilissimus
Zimmerius petersi
Zimmerius gracilipes
Zimmerius viridiflavus
Zimmerius bolivianus
Zimmerius cinereicapillus
Zimmerius minimus
Zimmerius chrysops
Euscarthmus meloryphus
Euscarthmus fulviceps
Euscarthmus rufomarginatus
Mecocerculus minor
Mecocerculus calopterus
Mecocerculus poecilocercus
Mecocerculus hellmayri
Mecocerculus stictopterus
Mecocerculus leucophrys
Culicivora caudacuta
Uromyias agilis
Uromyias agraphia
Anairetes reguloides
Anairetes flavirostris
Anairetes parulus
Serpophaga hypoleuca
Serpophaga subcristata
Serpophaga munda
Polystictus pectoralis
Polystictus brevipennis
Serpophaga cinerea
Serpophaga nigricans
Pseudocolopteryx sclateri
Pseudocolopteryx acutipennis
Pseudocolopteryx flaviventris
Stigmatura napensis
Stigmatura budytoides
Inezia tenuirostris
Inezia inornata
Inezia subflava
Inezia caudata
Phyllomyias fasciatus
Pseudelaenia leucospodia
Capsiempis flaveola
Phaeomyias murina
Nesotriccus ridgwayi
Phyllomyias virescens
Phyllomyias plumbeiceps
Phyllomyias uropygialis
Phyllomyias burmeisteri
Phyllomyias zeledoni
Phyllomyias nigrocapillus
Phyllomyias cinereiceps
Camptostoma imberbe
Camptostoma obsoletum
Ornithion brunneicapillus
Ornithion inerme

Figure 57. Strict consensus of 564 equally most parsimonious trees derived from the cladistic analysis of the character state matrix in Appendix 2. The ingroup (Elaeniinae subfamily) was indicated. All characters are non-additive and unweighted.

In the outgroup, the taxa selected as representatives of the families and subfamilies listed resulted in the recovery of most of the groups accepted today, including monophyly of the newly ranked families Onychorhynchidae, Tachurisidae, Pipritidae, Oxyruncidae, Tityridae, and Platyrinchidae. Although it was not the main aim of the present study to examine the monophyletic nature of external groups to Elaeniinae, the cladistic analysis demonstrated that there is evidence of morphological support for the definition of subfamilies within Tyrannoidea and related groups, and from families that have been questioned in the past as Rhynchocyclidae (the genus *Phylloscartes*, for example, was part of the "*Elaenia* assemblage" of Lanyon 1988a). Thus, the monophyly of the other subfamilies of Tyrannidae was recovered, namely: Hirundineinae, Fluvicolinae, Tyranninae and Muscigrallinae, as well as Todirostrinae and Pipromorphinae (Rhynchocyclidae) and the families Pipridae and Cotingidae (Figure 58).

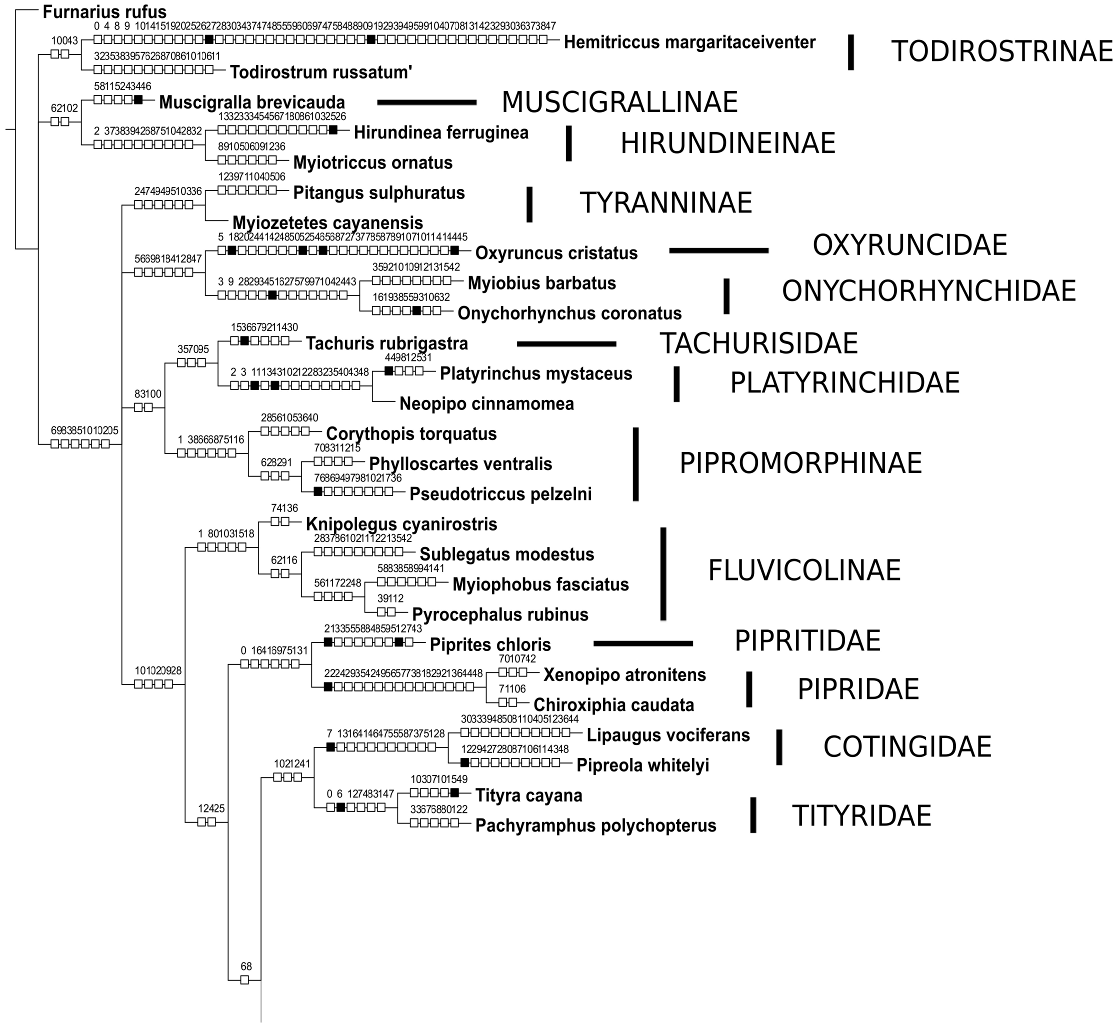

Figure 58. Partition of the strict consensus of 564 equally most parsimonious trees derived from the cladistic analysis of the character state matrix in Appendix 2 (Figure 57), representing the outgroup relationships. Black squares indicate exclusive synapomorphies and white squares the homoplastic traits (numbers above squares are [character number -1]). All characters are non-additive and unweighted.

Unexpectedly, *Suiriri* emerged as a more basal group in Elaeniinae, possibly for sharing some osteological features with representatives of outgroups (*e.g. Sublegatus*, *Pseudotriccus*). The genera *Elaenia* and *Myiopagis* were recovered as monophyletic (Figure 59), corroborating the previous knowledge.

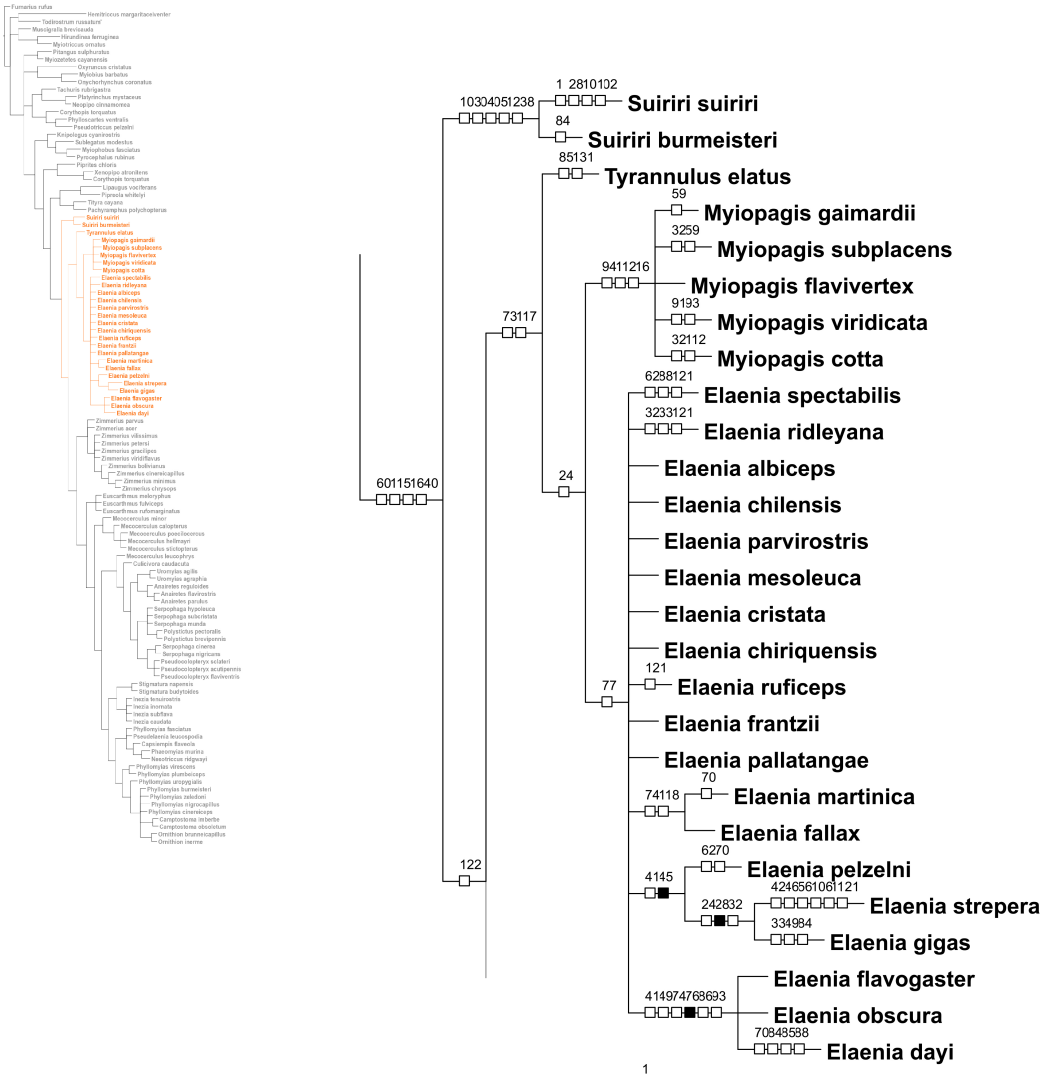

Figure 59. Partition of the strict consensus of 564 equally most parsimonious trees derived from the cladistic analysis of the character state matrix in Appendix 2 (Figure 57), representing part of the ingroup relationships including *Suiriri*, *Myiopagis* and *Elaenia*. The tree on detail shows the position of the partition considered. Black squares indicate exclusive synapomorphies and white squares the homoplastic traits (numbers above squares are [character number -1]). All characters are non-additive and unweighted.

The genus *Zimmerius* was recovered as monophyletic supported by three synapomorphies. Also monophyletic were the genera *Euscarthmus*, *Culicivora*, *Uromyias*, *Anairetes*, *Polystictus* and *Pseudocolopteryx*. *Serpophaga* is for the first time suggested as polyphyletic, with two of its representatives (*S. nigricans* and *S. cinerea)* grouping with *Pseudocolopteryx* (Figure 60). Also, *Mecocerculus* was indicated as polyphyletic, with at least two groups (*Mecocerculus leucophrys* separated from the others), as previously indicated by Lanyon (1988a).

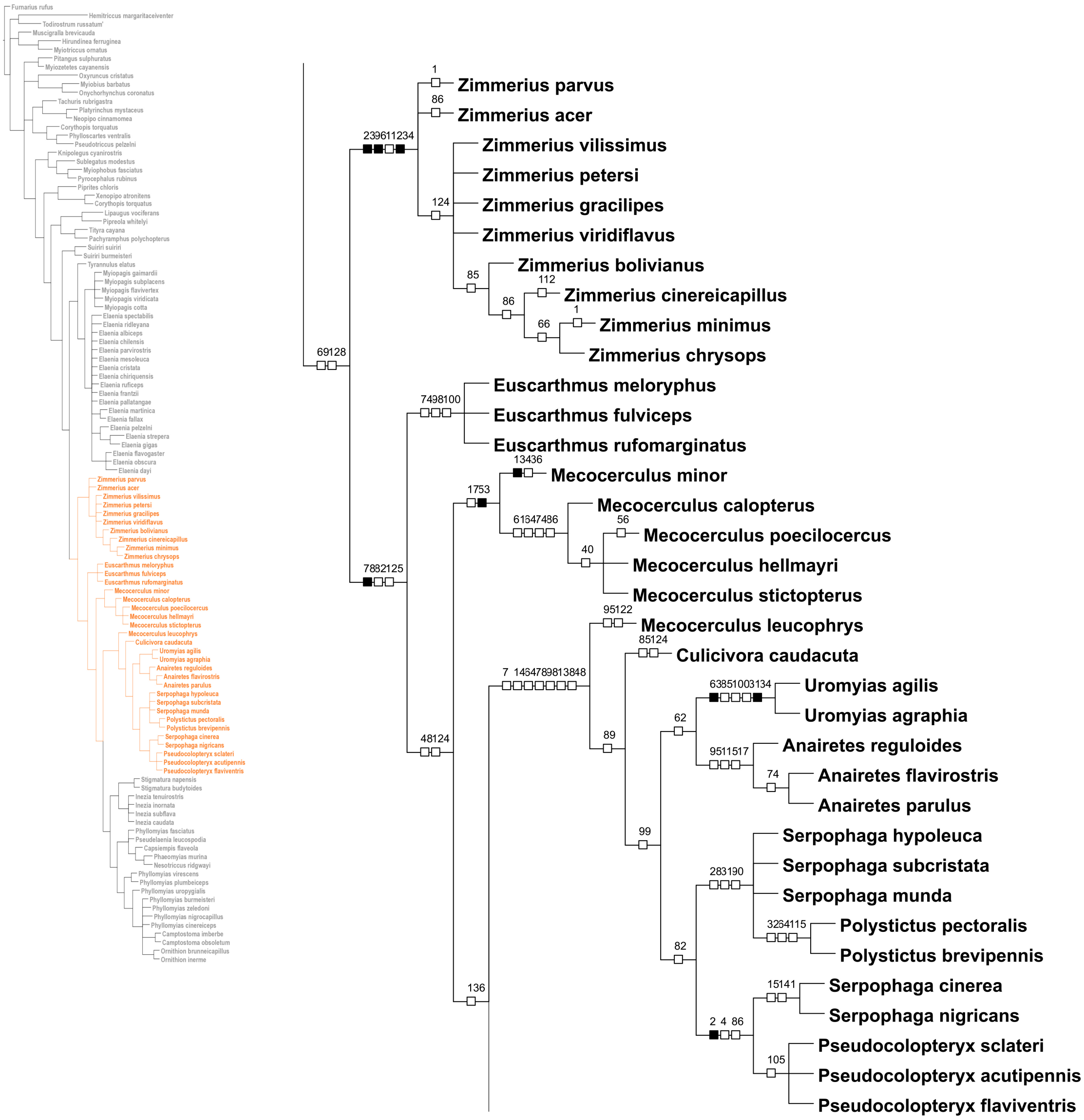

Figure 60. Partition of the strict consensus of 564 equally most parsimonious trees derived from the cladistic analysis of the character state matrix in Appendix 2 (Figure 57), representing part of the ingroup relationships including *Zimmerius*, *Euscarthmus*, *Mecocerculus*, *Uromyias*, *Anairetes*, *Serpophaga*, *Culicivora*, *Polystictus* and *Pseudocolopteryx*. The tree on detail shows the position of the partition considered. Black squares indicate exclusive synapomorphies and white squares the homoplastic traits (numbers above squares are [character number -1]). All characters are non-additive and unweighted.

Finally, the genera *Stigmatura* and *Inezia* were recovered as monophyletic, as well as *Pseudelaenia*, *Capsiempis*, *Phaeomyias* and *Nesotriccus*. *Phyllomyias*, as expected, was proved polyphyletic (Figure 61). Although it was the lowest-represented genus in the present study because of its uncommonness in collections, it apparently composes three or more groups that are not clearly circumscribed but whose need for taxonomic adjustments, as suggested (species have already been allocated in genera such as *Xanthomyias*, *Tyranniscus* and *Acrochordopus*).

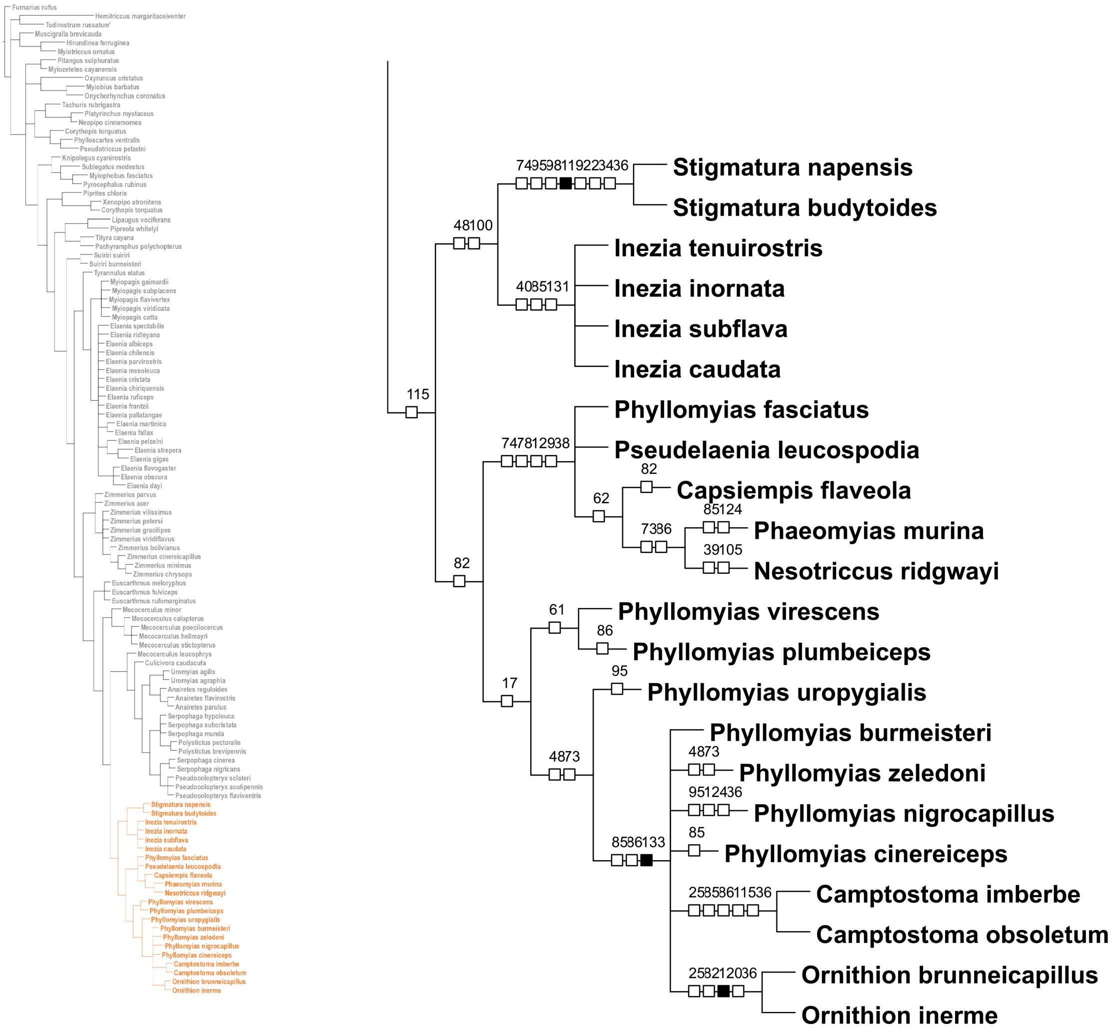

Figure 61. Partition of the strict consensus of 564 equally most parsimonious trees derived from the cladistic analysis of the character state matrix in Appendix 2 (Figure 57), representing part of the ingroup relationships including *Stigmatura*, *Inezia*, *Phyllomyias*, *Pseudelaenia*, *Capsiempis*, *Phaeomyias*, *Nesotriccus*, *Camptostoma* and *Ornithion*. The tree on detail shows the position of the partition considered. Black squares indicate exclusive synapomorphies and white squares the homoplastic traits (numbers above squares are [character number -1]). All characters are non-additive and unweighted.

DISCUSSION

Elaeniinae monophyly and interfamilial relationships

From the dataset gathered here based on the comparative osteology and cladistic analysis of all Elaeniinae genera, the subfamily was recovered as monophyletic (Figure 57). Despite this, no exclusive synapomorphy was identified, and the clade was grouped by four non-exclusive synapomorphies. Presence of a transverse trabecular plate in the nasal septum, referred to by Lanyon (1988) as being synapomorphic of the group, was also identified in *Sublegatus*, *Myiophobus*, *Pyrocephalus* (Tyrannidae: Fluvicolinae), *Pseudotriccus*, *Corythopis*, *Phylloscartes* (Rhynchocyclidae: Pipromorphinae), and is absent in the ingroup genus *Myiopagis* (character 117, Figure 45). But it is important to note that the grouping for which Lanyon (1988) considered this a "synapomorphic" condition, its "*Elaenia* assemblage", also brought together *Phylloscartes*, *Pseudotriccus*, *Mionectes*, *Myiophobus*, *Leptopogon*, *Sublegatus*, *Myiotriccus* and *Corythopis*. Therefore, not even in the study of that author this neomorphic character is indicated as a synapomorphy of Elaeniinae with the composition considered nowadays. Neither for Lanyon's "*Elaenia* group", of more similar composition with that of the subfamily Elaeniinae *sensu* Ohlson *et al.* (2013), the structure would be synapomorphic in that and in the present study.

One of the reasons the subfamily does not present exclusive synapomorphies in the present study is in the osteology of *Suiriri*, which shares some conditions with representatives of the outgroup. For example, features of the orbit and interorbital septum (characters 102, 103, 104), premaxilla (105), and a completely obliterated nasal capsule (character 113 here; character 7 in Lanyon 1988). The distribution of these five characters in the trees caused *Suiriri* to appear as basal in Elaeniinae (or outside and sister to the subfamily depending on the interpretation) and weakened the support of that grouping at the subfamily level. These characters, therefore, deserve detailed analysis in order to know its evolutionary history and significance. In the hypothesis of Rheindt *et al.* (2007) based on ND2 and Fib5 genes, *Suiriri* appears as sister of *Capsiempis* + *Phaeomyias* + *Phyllomyias fasciatus*, relationships also recovered by Ohlson *et al.* (2008). In Lopes *et al.* (2017), *Suiriri* appears as sister of a clade formed by *Myiopagis*, *Capsiempis*, *Phyllomyias* and *Phaeomyias*. In the present study, with a more complete terminal coverage, a similar grouping was recovered, still with *Nesotriccus* and *Pseudelaenia*, but distant from *Suiriri* (Figure 61). In Ohlson *et al.* (2013), *Suiriri* appears as basal in relation to these taxa, but also to *Mecocerculus*, *Polystictus*, *Culicivora* and *Serpophaga*. Lanyon (1988a) suggested proximity between *Suiriri* and *Ornithion*, but stated that *Suiriri* has a particular anatomy. Tello *et al.* (2009), using RAG-1 and RAG-2, recovered *Suiriri* as sister of *Myiopagis*, here recovered as the basal group, along with *Elaenia*, in the Elaeniinae excluding *Suiriri* (Figure 59). Thus, it is clear that a detailed assessment of all *Suiriri* representatives, with different sets of evidence, is highly recommended. Not only to investigate the phylogenetic position of the genus, but also in order to allow a clearer and more reliable delineation of the Elaeniinae subfamily itself and to answer why *Suiriri* shares so many similarities with Pipromorphinae and Fluvicolinae. In the present study, no specimen of *Guyramemua affinis* (formerly *Suiriri affinis* or *Suiriri islerorum*), identified as a member of Fluvicolinae sister to *Sublegatus* (Lopes *et al.*, 2017), was included in the matrix. It would be important to evaluate whether the tissues used in the molecular studies are only from *Suiriri* or if they could have included specimens of *Guyramemua* and thus interfered in the recovered phylogenetic position.

In the present study, Elaeniinae appears as the sister of Tityridae + Cotingidae, rather than relating to the other subfamilies of Tyrannidae, especially Hirundineinae, as expected. This can be interpreted as an artifact of sampling in each outgroup taxa (between one and four species in each family or subfamily). Even so, Bremer support of only 1 for Elaeniinae + (Tityridae + Cotingidae) shows that this recovered relationship appears to be artificial. Lopes *et al.* (2017) recovered Elaeniinae in a polytomy that includes both Hirundineinae and Tyranninae + Muscigrallinae + Fluvicolinae, the same relationship hypothesis recovered in the study by Ohlson *et al.* (2013). Similarly, in Rheindt *et al.* (2007), Elaeniinae appears as sister of the other subfamily-level groups within the core Tyrannidae.

Internal relationships

As seen, *Suiriri* appears as basal in the tree from osteological evidences. In the next clade, the relationship of (*Tyrannulus* (*Myiopagis* + *Elaenia*)) is recovered. *Tyrannulus* is absent from the studies of Ohlson *et al.* (2008, 2013), Lopes *et al.* (2017) and Ericson *et al.* (2006), making it impossible to compare the hypotheses. In the Lanyon's (1988) phenogram the three genera appear also grouped, but with *Tyrannulus* more related to *Myiopagis*, as in Rheindt *et al.* (2007), the only molecular phylogeny to include *Tyrannulus*. Tello *et al.* (2009) recover a somewhat different relationship with (*Elaenia* (*Myiopagis* + *Suiriri*)), but also without *Tyrannulus* samples. The topology resulting from the present study, therefore, brings together *Myiopagis* + *Elaenia* for the first time. Within *Elaenia*, we recovered at least two clades: *E. flavogaster* + *E. obscura* + *E. dayi*, in addition to *E. strepera* + *E. gigas*. These species present the most particular anatomy among the representatives of the genus, even with some character states shared with the external group. *Elaenia strepera*, the only *Elaenia* species with entire gray plumage and with some characteristics distinct from the others regarding form (like the slightly curved maxilla) presents the most particular osteology.

The two recognized tribes, Elaeniini and Euscarthmini, were not recovered as monophyletic. Elaeniini polyphyly was determined by the position of two clades, one with (*Phyllomyias fasciatus* + *Pseudelaenia leucospodia* + (*Capsiempis* + *Phaeomyias* + *Nesotriccus*)) and another with (*Mecocerculus leucophrys* (*Culicivora* ((*Uromyias* + *Anairetes*) + ((part of *Serpophaga* + *Polystictus*) + (part of *Serpophaga* + *Pseudocolopteryx*)))). Or it would be the same as to consider that these two groupings are responsible for the paraphyly of Euscarthmini. Inclusion of the missing ingroup species and a clarification of the *Suiriri* distinct anatomy may help in this understanding and result in a slightly different topology.

Zimmerius was recovered as monophyletic and represents one of the genera with higher support and more synapomorphies. The genus appears basal to a clade containing all the other Euscarthmini and the two clades of Elaeniini that cause the polyphyly of the tribe. Ohlson *et al*. (2013) also recovered *Zimmerius* as a basal clade in Euscarthmini, as well as Lopes *et al*. (2017). Lanyon (1988a) reunites *Zimmerius* between his "*Phylloscartes* group", among Rhynchocyclidae, therefore out of Elaeniinae.

Lanyon (1988) drew attention to the non-monophyletic *Mecocerculus*, previously treated as a "wastebasket" genus, because of features in the nasal septum and internal cartilages of the syrinx. According to the author, there would be three groups: (1) *M. leucophrys*; (2) *M. calopterus* and *M. minor*; (3) *M. hellmayri*, *M. stictopterus*, *M. poecilocercus*. In the present study, the genus was polyphyletic (two groups: 1 and 2/3). *M. leucophrys* is basal in a well supported group (Bremer of 6) of small birds of dry grasslands and wetlands. The present phylogeny indicates the need for taxonomic adjustments in the genus *Mecocerculus*, with the description of at least one new genus for all *Mecocerculus* except *M. leucophrys*, the type-species of the genus. Even so, it is important to evaluate the position of *M. minor*, here basal in relation to the others, for presenting osteology somewhat different. The polyphyly of *Mecocerculus* will also be demonstrated in a massive phylogeny of all Tyranni passerines using Ultraconserved Elements that is in the process of conclusion (Brumfield *et al. in prep.*), so that the taxonomic problems can be solved with the combination of distinct phylogenetic evidences (genomics and “phenomics”).

We highlight the recovery of *Uromyias* and *Anairetes* as reciprocally monophyletic, reinforcing the results of Dubay and Witt (2012) through a molecular phylogeny of the group. Previously, *Uromyias* had been integrated as part of *Anairetes* in a study with poor molecular markers (Roy *et al.* 1999).

In the present study, *Serpophaga* appears as polyphyletic for the first time, despite the rather questionable results due to the methodology presented by Chebez and Agnolin (2012). The “small *Serpophaga*” (*S. munda*, *S. subcristata*, *S. hypoleuca*) are grouped with *Polystictus*, while the "gray *Serpophaga*" appear as the sister clade of *Pseudocolopteryx* (Figure 60). Although the name "*Holmbergphaga*" has been proposed (Chebez and Agnolin 2012), the name *Ridgwayornis* Bertoni, 1925 is available and has priority so should be adopted for the two species of gray *Serpophaga*.

Stigmatura and *Inezia* are recovered as sister monophyletic groups, corroborating the molecular phylogeny of Ohlson *et al*. (2013), but in that study these genera still appear with *Euscarthmus*, here monophyletic though separate and "basal" in Euscarthmini. In the comparative study of Lanyon (1988), the two genera are outside of their "*Elaenia* group": *Stigmatura* with *Pseudelaenia*, and *Inezia* sister of *Sublegatus* among others Fluvicolinae and Rhynchocyclidae. Thus, the present study presents more congruence compared to molecular phylogenies.

Although it was the genus with less representation in this study due to the unavailability of osteological material, the represented species of *Phyllomyias* were recovered as polyphyletic. All species grouped with *Ornithion* and *Camptostoma*. Ohlson *et al*. (2013) included only two species of *Phyllomyias* (eight in the present study), one grouping with *Camptostoma* (*P. uropygialis*) and the other (*P. griseiceps*) with *Phaeomyias* and *Capsiempis*. In the present study, one species (*P. fasciatus*, type-species of the genus) grouped with *Phaeomyias*, *Nesotriccus*, *Capsiempis* and *Pseudelaenia*. Lopes *et al*. (2017) included four species of *Phyllomyias* (*P. fasciatus*, *P. griseiceps*, *P. virescens* and *P. uropygialis*) and identified three distinct locations for them. Thus, based on the present study and molecular phylogenies, at least two or three groups can be recognized. But an adequate taxonomic proposal requires the inclusion of all species of the genus that we consider the true “wastebasket”.

Perhaps more important than the taxonomic implications and necessary adjustments themselves is the demonstration of the existing phylogenetic signal and the usefulness of anatomical characters to construct the kinship relationships of passerines, even at the intrageneric level, in opposition to the pessimism of the past whose theoretical background lacked appropriate testing (Livezey and Zusi 2006). With reliable and well supported trees by different sets of evidences and matrices of phenotypic characteristics more extensive and well documented, it will be possible to trace the morphological evolution of this important radiation of birds. Finally, we emphasize the need to find for characters and to produce morphological matrices of other groups of Tyranni never investigated for this purpose as Rhynchocyclidae, other subfamilies inside Tyrannidae like Tyranninae and Fluvicolinae, smaller families like Onychorhynchidae, Platyrinchidae, Tityridae, and taxa outside Tyrannoidea, Cotingoidea and Pipridae. With knowledge of their well-supported kinship relationships through integrated analyzes, it will be important to have a good foundation on bird morphology to understand the evolutionary process in space and time.

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Appendix 1. Material examined for the construction of the character matrix and phylogenetic analysis of Elaeniinae based in osteological evidences. Acronyms are: MCP - Museu de Ciências da PUCRS; AMNH - American Museum of Natural History; FMNH - Field Museum of Natural History; USNM - National Museum of Natural History; YPM - Yale Peabody Museum; BMNH - British Museum of Natural History; MPEG - Museu Paraense Emílio Goeldi; LSU - Louisiana State University Museum of Natural History. c&s = cleared and stained.

INGROUP

Anairetes flavirostris: AMNH 7318 [?], Arequipa, Peru (complete skeleton); AMNH 26904 [m], Neuquen, Argentina (complete skeleton); USNM 637888 [f], Ica, Peru (complete skeleton); USNM 227516 [m], General Roca, Argentina (complete skeleton).

Anairetes parulus: FMNH 376886 [m], Pichincha, Ecuador (complete skeleton); USNM 321562 [?], Talcahuano, Chile (complete skeleton); USNM 318424 [?], Santiago, Chile (complete skeleton); BMNH 1891.7.20.255 [?], Chile (complete skeleton).

Anairetes reguloides: LSU 86575 [f], Ancash, Peru (complete skeleton); LSU 113685 [f], Huanuco, Peru (complete skeleton).

Camptostoma imberbe: AMNH 11393 [m], Tapanatepec, Mexico (complete skeleton); USNM 621008 [m], Quintana Roo, Mexico (partial skeleton); USNM 621009 [m], Quintana Roo, Mexico (partial skeleton).

Camptostoma obsoletum: MCP uncatalogued (field number IF1301) [m], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1423) [f], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1440) [m], Rio Grande do Sul, Brazil (complete c&s).

Capsiempis flaveola: USNM 555591 [m], Guayas, Ecuador (complete skeleton); YPM 104203 [m], Misiones, Argentina (complete skeleton).

Culicivora caudacuta: LSU 151790 [f], Santa Cruz, Bolivia (complete skeleton); MCP uncatalogued (field number IF1503) [m], Rondônia, Brazil.

Elaenia chilensis: USNM 343086 [f], Llico, Chile (complete skeleton).

Elaenia chiriquensis: USNM 622241 [m], Wiwitau, Guyana (complete skeleton).

Elaenia cristata: MCP uncatalogued (field number IF1402) [m], Roraima, Brazil (complete c&s); MCP uncatalogued (field number IF1403) [m], Roraima, Brazil (complete c&s).

Elaenia dayi: AMNH 22226 [m], Bolivar, Venezuela (complete skeleton); AMNH 22266 [m], Bolivar, Venezuela (complete skeleton); AMNH 22269 [m], Bolivar, Venezuela (complete skeleton).

Elaenia fallax: YPM 105963 [f], Haiti (complete skeleton); USNM 291004 [m], Constanza, Dominican Republic (complete skeleton); YPM 105179 [m], Constanza, Dominican Republic (complete skeleton); USNM 555840 [f], Dominican Republic (complete skeleton); USNM 555841 [f], Dominican Republic (complete skeleton).

Elaenia flavogaster: USNM 492275 [m], Pará, Brazil (complete skeleton).

Elaenia frantzii: USNM 540599 uncatalogued (complete skeleton); USNM 560224 [f], Matagalpa, Nicaragua (complete skeleton); 488501 [m], Chiriqui, Panama (complete skeleton).

Elaenia gigas: FMNH 291858 [f], Cuzco, Peru (complete skeleton).

Elaenia martinica: USNM 487918 [m], Saint Joseph, Dominica (complete skeleton); USNM 558134 [m], Barbuda (complete skeleton); USNM 555036 [m], Antigua (complete skeleton).

Elaenia mesoleuca: AMNH 13749 [?], Rio Grande do Sul, Brazil (complete skeleton); YPM 101122 [m], Cerro Largo, Uruguai (complete skeleton); MCP uncatalogued (field number IF1401) [m], Rio Grande do Sul, Brazil (complete c&s).

Elaenia obscura: MCP uncatalogued (field number IF1426) [m], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1427) [f], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1428) [m], Rio Grande do Sul, Brazil (complete c&s).

Elaenia pallatangae: USNM 622813 [m], Roraima, Guyana (complete skeleton); USNM 428746 [f], Cauca, Colombia (complete skeleton).

Elaenia parvirostris: MCP uncatalogued (field number D148380) [m], Rio Grande do Sul, Brazil (complete c&s).

Elaenia pelzelni: LSU 121380 [f], Loreto, Peru (complete skeleton).

Elaenia ridleyana: USNM 491935 [m], Fernando de Noronha, Brazil (complete skeleton).

Elaenia ruficeps: USNM 639175 [f], Cuyuni-Mazaruni, Peru (complete skeleton).

Elaenia spectabilis: AMNH 25676 [m], Santa Cruz, Bolivia (complete skeleton).

Elaenia strepera: USNM 645291 [m], Tucuman, Argentina (complete skeleton).

Euscarthmus fulviceps: AMNH 7183 [f], Cayamanca, Peru (complete skeleton).

Euscarthmus meloryphus: MCP uncatalogued (field number IF1424) [m], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1425) [m], Rio Grande do Sul, Brazil (complete c&s).

Euscarthmus rufomarginatus: USNM 622325 [f], Karaudanawa, Guyana (complete skeleton); YPM 137614 [m], Sipaliwini, Suriname (complete skeleton); YPM 137622 [f], Sipaliwini, Suriname (complete skeleton); YPM 137638 [f], Sipaliwini, Suriname (complete skeleton).

Inezia caudata: MCP uncatalogued (field number IF1412) [m], Roraima, Brazil (complete c&s).

Inezia inornata: FMNH 334478 [m], Santa Cruz, Bolivia (complete skeleton).

Inezia subflava: MCP uncatalogued (field number IF1406) [m], Roraima, Brazil (complete c&s).

Inezia tenuirostris: FMNH 313436 [?], Falcon, Venezuela (complete skeleton).

Mecocerculus calopterus: USNM 643793 uncatalogued (complete skeleton); USNM 643958 uncatalogued (complete skeleton).

Mecocerculus helmayri: AMNH 26988 [f], Caballeros, Bolivia (complete skeleton).

Mecocerculus leucophrys: AMNH 22877 [m], Amazonas, Venezuela (complete skeleton); USNM 428279 [f], Paramo de Frontera, Colombia (complete skeleton);

USNM 428280 [m], Paramo de Frontera, Colombia (complete skeleton); USNM 428859 [m], Cauca, Colombia (complete skeleton); USNM 620744 [f], Tucuman, Argentina (complete skeleton); USNM 429599 [m], Chiriqui, Panama (complete skeleton).

Mecocerculus minor: USNM 560008 [f], Morona-Santiago, Ecuador (complete skeleton).

Mecocerculus poecilocercus: LSU 840039 [f], Amazonas, Peru (complete skeleton).

Mecocerculus stictopterus: AMNH 7308 [f], Junin, Peru (complete skeleton); LSU 170468 [f], Cajamarca, Peru (complete skeleton); 1891.7.20.344 [?], Ecuador (complete skeleton).

Myiopagis cotta: USNM 502802 uncatalogued (complete skeleton); USNM 558912 [m], Jamaica (complete skeleton).

Myiopagis cotta: USNM 507692 [m], Jamaica (complete skeleton); USNM 558913 [f], Jamaica (complete skeleton).

Myiopagis flavivertex: USNM 623195 [f], Washikura, Guyana (complete skeleton); USNM 637159 [m], Takutu-Essequibo, Guyana (complete skeleton).

Myiopagis gaimardii: MCP uncatalogued (field number IF1405) [m], Roraima, Brazil (complete c&s); YPM 137000 [m], Commewijne, Suriname (complete skeleton).

Myiopagis subplacens: USNM 643796 [?], uncatalogued (complete skeleton); USNM 643882 [?] uncatalogued (partial skeleton).

Myiopagis viridicata: USNM 555998 [f], Itapua, Paraguay (complete skeleton).

Nesotriccus ridgway: USNM 560207 [m], Cocos Island, Costa Rica (complete skeleton).

Ornithion bruneicapillum: AMNH 14470 [m], “Canal Zone” (complete skeleton); USNM 430962 [m], Darien, Panama (partial skeleton).

Ornithion inerme: USNM 491501 [?], Cuzco, Peru (complete skeleton); USNM 623083 [f], Linden, Guyana (complete skeleton).

Phaeomyias murina: USNM 344210 [f], Yacua Paria, Venezuela (complete skeleton); LSU 90092 [f], Lambayeque, Peru (complete skeleton); USNM 432172 [m], Coclé, Panama (complete skeleton); USNM 500565 [m], Playas, Ecuador (complete skeleton); USNM 622252 [f], Karaudanawa, Guyana (complete skeleton); MPEG 1155 [f], Pará, Brazil.

Phyllomyias burmeisteri: FMNH 389212 [f], São Paulo, Brazil (complete skeleton); MCP uncatalogued (field number IF1442) [m], Rio Grande do Sul, Brazil (complete c&s).

Phyllomyias cinereiceps: LSU 97508 [?], Cajamarca, Peru (complete skeleton).

Phyllomyias fasciatus: MCP uncatalogued (field number IF1438) [m], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1441) [m], Rio Grande do Sul, Brazil (complete c&s).

Phyllomyias nigrocapillus: LSU 107330 [m], Pasco, Peru (complete skeleton).

Phyllomyias plumbeiceps: LSU 129957 [f], Pasco, Peru (complete skeleton).

Phyllomyias uropygialis: AMNH 14154 [f], Puno, Peru (complete skeleton); AMNH 25989 [m], La Paz, Bolivia (complete skeleton); LSU 101528 [?], La Paz, Bolivia (complete skeleton).

Phyllomyias virescens: MCP uncatalogued (field number IF1438) [m], Rio Grande do Sul, Brazil (complete c&s)

Phyllomyias zeledoni: USNM 429780 [m], Chiriqui, Panama (complete skeleton).

Polystictus brevipennis: MCP uncatalogued (field number IF1409) [m], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1410) [m], Rio Grande do Sul, Brazil (complete c&s); YPM 137549 [f], Sipaliwini, Suriname (complete skeleton); YPM 137623 [m], Sipaliwini, Suriname (complete skeleton).

Polystictus pectoralis: MCP uncatalogued (field number IF1415) [m], Rio Grande do Sul, Brazil (complete c&s).

Pseudelaenia leucospodia: USNM 643784 uncatalogued (complete skeleton); USNM 643841 [m], Tumbes, Peru (complete skeleton).

Pseudocolopteryx acutipennis: LSU 125911 [f], Beni, Peru (complete skeleton).

Pseudocolopteryx flaviventris: MCP uncatalogued (field number IF1413) [m], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1414) [m], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1421)

[m], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1422) [m], Rio Grande do Sul, Brazil (complete c&s).

Pseudocolopteryx sclateri: USNM 227412 [m], Las Palmas, Argentina (complete skeleton); MCP uncatalogued (field number IF1436) [m], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1437) [m], Rio Grande do Sul, Brazil (complete c&s).

Serpophaga cinerea: USNM 428895 [m], Huila, Colombia (complete skeleton).

Serpophaga hypoleuca: LSU 111585 [f], Loreto, Peru (complete skeleton).

Serpophaga munda: LSU 125910 [m], Santa Cruz, Bolivia (complete skeleton).

Serpophaga nigricans: MCP uncatalogued (field number IF1416) [m], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1504) [m], Rio Grande do Sul, Brazil (complete c&s).

Serpophaga subcristata: FMNH 335182 [m], Potosi, Bolivia (complete skeleton); MCP4600 [m], Rio Grande do Sul, Brazil (complete c&s); MCP4603 [f], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1201) [m], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1202) [m], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1203) [m], Rio Grande do Sul, Brazil (complete c&s).

Stigmatura budytoides: AMNH 23985 [?], Buenos Aires, Argentina (complete skeleton); AMNH 26902 [m], Neuquen, Argentina (complete skeleton); USNM 227781 [f], Tucuman, Argentina (complete skeleton).

Stigmatura napensis: USNM 491716 [m], Bahia, Brazil (complete skeleton); MCP uncatalogued (field number IF1407) [m], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1408) [m], Rio Grande do Sul, Brazil (complete c&s).

Suiriri burmeisteri: YPM 137277 [f], Sipaliwini, Suriname (complete skeleton); YPM 137324 [f], Sipaliwini, Suriname (complete skeleton); YPM 137594 [m], Sipaliwini, Suriname (complete skeleton).

Suiriri suiriri: USNM 631022 [m], Soriano, Uruguay (complete skeleton); USNM 631046 [m], Paysandu, Uruguay (complete skeleton); YPM 101054 [f], Artigas, Uruguay (complete skeleton); YPM 137015 [m], Sipaliwini, Suriname (complete skeleton); YPM 137138 [m], Sipaliwini, Suriname (complete skeleton).

Tyrannulus elatus: USNM 559392 [m], Kartabo, Guyana (complete skeleton); MPEG 3730 [?], Pará, Brazil (complete skeleton).

Uromyias agilis USNM 614866 [f], Sucumbios, Ecuador (complete skeleton); USNM 615945 uncatalogued (complete skeleton).

Uromyias agraphia: LSU 90080 [m], Amazonas, Peru (complete skeleton); USNM 511974 [?], Cuzco, Peru (complete skeleton).

Xenopipo atronitens: USNM 621075 [f], Berbice, Guyana (complete skeleton).

Zimmerius acer: USNM 621450 [m], Baramita, Guyana (complete skeleton); USNM 621784 [m], Acari, Guyana (complete skeleton).

Zimmerius bolivianus: LSU 99434 [m], Puno, Peru (complete skeleton); USNM 512039 [?], Ayacucho, Peru (complete skeleton).

Zimmerius chrysops: USNM 428800 [m], Caqueta, Colombia (complete skeleton); USNM 428801 [m], Caqueta, Colombia (complete skeleton).

Zimmerius cinereicapillus: FMNH 315849 [m], Madre de Dios, Peru (complete skeleton).

Zimmerius gracilipes: LSU 118515 [m], Loreto, Peru (complete skeleton).

Zimmerius minimus: USNM 344215 [f], Yacua Paria, Venezuela (complete skeleton); USNM 344216 [f], Yacua Paria, Venezuela (complete skeleton).

Zimmerius parvus: USNM 343856 [?], Panama (complete skeleton).

Zimmerius petersi: AMNH 24095 [f], Aragua, Venezuela (complete skeleton).

Zimmerius vilissimus: AMNH 14553 [m], Limón, Costa Rica (complete skeleton); USNM 431175 [f], Chiriqui, Panama (complete skeleton).

Zimmerius viridiflavus: AMNH 7190 [f], Peru (complete skeleton).

OUTGROUP

Chiroxiphia caudata: MCP uncatalogued (field number IF1433) [m], Rio Grande do Sul, Brazil (complete c&s).

Corythopis torquatus: YPM 106312 [f], Pará, Brazil (complete skeleton); MPEG 3667 [m] Pará, Brazil (complete skeleton); MPEG 2630 [m] Acre, Brazil (complete skeleton); MPEG 3481 [m] Pará, Brazil (complete skeleton).

Furnarius rufus: MCP uncatalogued [m], Rio Grande do Sul, Brazil (complete skeleton).

Hemitriccus margaritaceiventer: USNM 639313 [f], Cuyuni-Mazaruni, Guyana (complete skeleton).

Hemitriccus obsoletus: MCP uncatalogued (field number IF1435) [m], Rio Grande do Sul, Brazil (complete c&s).

Hirundinea ferruginea: USNM 622772 [m], Roraima, Guyana (complete skeleton).

Knipolegus cyanirostris: YPM 101146 [f], Cerro Largo, Uruguay (complete skeleton); MCP uncatalogued (field number IF1429) [m], Rio Grande do Sul, Brazil (complete c&s).

Lipaugus vociferans: USNM 562337 [f], Pará, Brazil (complete skeleton).

Muscigralla brevicauda: USNM 643765 [m], Tumbes, Peru (complete skeleton); USNM 643825 uncatalogued (complete skeleton).

Myiobius barbatus: USNM 632573 [m], Kopinang, Guyana (complete skeleton).

Myiophobus fasciatus: USNM 639312 [m], Cuyuni-Mazaruni, Guyana (complete skeleton).

Myiotriccus ornatus: USNM 560012 [?], Morona-Santiago, Ecuador (complete skeleton).

Myiozetetes cayanensis: MCP uncatalogued (field number IF1404) [m], Roraima, Brazil (complete c&s).

Neopipo cinnamomea: MPEG 3675 [?], Pará, Brazil (complete skeleton).

Onychorhynchus coronatus: USNM 562365 [m], Pará, Brazil (complete skeleton).

Oxyruncus cristatus: AMNH 410 [?], Brazil (complete skeleton).

Pachyramphus polychopterus: MCP uncatalogued (field number IF1207) [m], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1206) [f], Rio Grande do Sul, Brazil (complete c&s).

Phylloscartes ventralis: YPM 101145 [m], Cerro Largo, Uruguay (complete skeleton); YPM 103430 [m], Misiones, Argentina (complete skeleton); MCP uncatalogued (field number IF1431) [m], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1432) [m], Rio Grande do Sul, Brazil (complete c&s); MCP uncatalogued (field number IF1439) [m], Rio Grande do Sul, Brazil (complete c&s).

Pipreola whitelyi: USNM 622783 [f], Roraima, Guyana (complete skeleton).

Piprites chloris: USNM 622076 [m], Linden, Guyana (complete skeleton).

Pitangus sulphuratus: USNM 346013 [m], Mato Grosso, Brazil (complete skeleton); USNM 346014 [f], Mato Grosso, Brazil (complete skeleton).

Platyrinchus mystaceus: USNM 556422 [m] Itapua, Paraguay (complete skeleton); MCP uncatalogued (field number IF1434) [m], Rio Grande do Sul, Brazil (complete c&s).

Pseudotriccus pelzelni: USNM 560009 [f], Morona-Santiago, Ecuador (complete skeleton); USNM 615947 [?], Sucumbios, Ecuador (complete skeleton); USNM 491511 [m], Cuzco, Peru (complete skeleton); USNM 491512 [?], Peru (complete skeleton).

Pyrocephalus rubinus: MCP4491 [m], Rio Grande do Sul, Brazil (complete c&s); YPM 104142 [?], Entre Rios, Argentina (complete skeleton).

Sublegatus modestus: USNM 620773 [m], Corrientes, Argentina (complete skeleton).

Tachuris rubrigastra: MCP uncatalogued (field number IF1319) [m], Rio Grande do Sul, Brazil (complete c&s).

Tityra cayana: MCP uncatalogued (field number IF1209) [m], Rio Grande do Sul, Brazil (complete c&s).

Todirostrum russatum: USNM 622765 [m], Roraima, Guyana (complete skeleton).

Xenopipo atronitens: USNM 621075 [f], Berbice, Guyana (complete skeleton).

Appendix 2. Character matrix (112 terminals *versus* 151 characters) of the phylogenetic analysis of Elaeniinae based in osteological evidences.

Notation: ? = missing data; - = inapplicable; #&# = polymorphism.

Species/Character	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**
Phyllomyias fasciatus	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllomyias burmeisteri	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Phyllomyias zeledoni	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllomyias virescens	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllomyias plumbeiceps	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyllomyias nigrocapillus	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Phyllomyias cinereiceps	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Phyllomyias uropygialis	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Tyrannulus elatus	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Myiopagis gaimardii	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Myiopagis subplacens	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Myiopagis flavivertex	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Myiopagis viridicata	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Myiopagis cotta	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Elaenia flavogaster	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1
Elaenia martinica	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Elaenia spectabilis	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Elaenia ridleyana	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Elaenia albiceps	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Elaenia chilensis	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Elaenia parvirostris	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Elaenia mesoleuca	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Elaenia strepera	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	2	0	1	0	2	0	0	1	0	1	1	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0
Elaenia gigas	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	2	0	1	0	2	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1
Elaenia pelzelni	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0
Elaenia cristata	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0

Species/Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Elaenia chiriquensis	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Elaenia ruficeps	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Elaenia frantzii	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Elaenia obscura	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1
Elaenia dayi	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1
Elaenia pallatangae	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Elaenia fallax	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Ornithion brunneicapillus	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	?	1	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Ornithion inerme	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Camptostoma imberbe	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Camptostoma obsoletum	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Suiriri suiriri	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Suiriri burmeisteri	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Mecocerculus leucophrys	0	1	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mecocerculus poecilocercus	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Mecocerculus hellmayri	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Mecocerculus calopterus	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mecocerculus minor	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mecocerculus stictopterus	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Anairetes reguloides	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anairetes flavirostris	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anairetes parulus	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Uromyias agilis	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Uromyias agraphia	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Serpophaga cinerea	0	1	1	0	1	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Serpophaga hypoleuca	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Serpophaga nigricans	0	1	1	0	1	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Serpophaga subcristata	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Serpophaga munda	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Species/Character	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**
Phaeomyias murina	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capsiempis flaveola	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polystictus pectoralis	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polystictus brevipennis	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nesotriccus ridgwayi	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Pseudocolopteryx sclateri	0	1	1	0	1	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudocolopteryx acutipennis	0	1	1	0	1	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudocolopteryx flaviventris	0	1	1	0	1	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euscarthmus meloryphus	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Euscarthmus fulviceps	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Euscarthmus rufomarginatus	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pseudelaenia leucospodia	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stigmatura napensis	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Stigmatura budytoides	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Zimmerius minimus	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Zimmerius parvus	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Zimmerius vilissimus	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Zimmerius petersi	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Zimmerius bolivianus	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Zimmerius cinereicapillus	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Zimmerius gracilipes	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Zimmerius acer	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Zimmerius chrysops	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Zimmerius viridiflavus	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Inezia tenuirostris	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Inezia inornata	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Inezia subflava	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Inezia caudata	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Culicivora caudacuta	0	1	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Species/Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Hirundinea ferruginea	0	-	2	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1	0
Myiotriccus ornatus	0	-	2	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	1	1	1	0	0	1	0	0	0	0	0	1	0
Muscigralla brevicauda	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pitangus sulphuratus	0	1	0	0	0	0	0	0	1	0	1	0	2	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Myiozetetes cayanensis	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Myiophobus fasciatus	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Sublegatus modestus	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Pyrocephalus rubinus	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Knipolegus cyanirostris	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Phylloscartes ventralis	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Pseudotriccus pelzelni	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Corythopis torquatus	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Hemitriccus margaritaceiventer	0	1	0	0	0	1	-	-	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Todirostrum russatum	0	-	0	0	0	1	-	-	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0
Platyrinchus mystaceus	0	-	2	1	-	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0
Neopipo cinnamomea	0	-	2	1	0	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Piprites chloris	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	-	0	0	1	1	0	0	0	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Tityra cayana	1	1	0	0	0	0	1	0	1	0	1	0	2	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pachyramphus polychopterus	1	1	0	0	0	0	1	0	1	0	1	0	2	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Myiobius barbatus	0	1	0	1	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Onychorhynchus coronatus	0	1	0	1	0	0	0	0	1	1	1	0	0	0	0	1	1	-	0	1	-	-	0	0	0	0	1	0	0	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Oxyruncus cristatus	0	1	0	0	0	1	-	-	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	2	0
Tachuris rubrigastra	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Lipaugus vociferans	0	1	0	0	0	0	0	2	1	0	1	0	0	1	0	1	1	-	0	0	1	0	0	0	2	0	1	0	1	0	1	1	1	0	1	0	0	0	0	1	0	1	0	0	0	0	1	1	2	0
Pipreola whitelyi	0	1	0	0	0	0	0	2	1	0	1	0	1	1	0	1	1	-	0	0	1	0	0	0	2	0	1	0	1	1	0	1	1	1	1	0	0	0	0	0	0	1	1	0	0	0	1	1	1	0
Xenopipo atronitens	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	-	0	0	1	0	1	0	2	0	1	0	1	1	0	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1
Chiroxiphia caudata	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	-	0	0	1	0	1	0	2	0	1	0	1	1	0	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1
Furnarius rufus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Species/Character	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Phyllomyias fasciatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	2	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Phyllomyias burmeisteri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0	2	0	1	2	0	0	0	0
Phyllomyias zeledoni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0	2	0	1	2	0	0	0	0
Phyllomyias virescens	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Phyllomyias plumbeiceps	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	1	0	0	0	1	0	0	1	1	0	0	1	1	0	2	0	1	2	0	0	0	0
Phyllomyias nigrocapillus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	1	0	2	0	1	0	0	0	0	0
Phyllomyias cinereiceps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	1	0	0	1	1	0	2	0	1	2	0	0	0	0
Phyllomyias uropygialis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	1	0	2	0	1	0	0	0	0	0
Tyrannulus elatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	2	0	1	2	0	0	0	0
Myiopagis gaimardii	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	2	0	2	2	0	0	0	0
Myiopagis subplacens	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	2	0	2	2	0	0	0	0
Myiopagis flavivertex	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1	0	0	1	1	0	2	0	2	2	0	0	0	0
Myiopagis viridicata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1	0	0	1	1	1	2	1	2	2	0	0	0	0
Myiopagis cotta	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1	0	0	1	1	0	2	0	2	2	0	0	0	0
Elaenia flavogaster	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	2	1	0	0	0	0	1	1	0	1	1	0	0	1	1	0	2	1	1	2	0	0	0	0
Elaenia martinica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	2	1	0	1	0	0	0	0	1	1	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Elaenia spectabilis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	1	1	1	0	2	0	1	2	0	0	0	0
Elaenia ridleyana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Elaenia albiceps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Elaenia chilensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Elaenia parvirostris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Elaenia mesoleuca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Elaenia strepera	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Elaenia gigas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Elaenia pelzelni	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Elaenia cristata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Elaenia chiriquensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Elaenia ruficeps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0

Species/Character	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**
Elaenia frantzii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Elaenia obscura	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	2	1	0	0	0	0	1	1	0	1	1	0	0	1	1	0	2	1	1	2	0	0	0	0
Elaenia dayi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	2	1	0	0	0	0	1	1	1	0	1	0	1	1	1	0	2	1	1	2	0	0	0	0
Elaenia pallatangae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Elaenia fallax	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2	1	0	1	0	0	0	0	1	1	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Ornithion brunneicapillus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	2	0	0	0	1	0	0	1	1	0	2	0	1	2	0	0	0	0
Ornithion inerme	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	2	0	0	0	1	0	0	1	1	0	2	0	1	2	0	0	0	0
Camptostoma imberbe	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Camptostoma obsoletum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Suiriri suiriri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	2	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Suiriri burmeisteri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	2	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Mecocerculus leucophrys	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	2	0	1	0	0	0	1	0
Mecocerculus poecilocercus	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	2	2	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	2	0	1	2	0	0	0	0
Mecocerculus hellmayri	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	2	2	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	2	0	1	2	0	0	0	0
Mecocerculus calopterus	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	2	2	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	2	0	1	2	0	0	0	0
Mecocerculus minor	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Mecocerculus stictopterus	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	2	2	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	2	0	1	2	0	0	0	0
Anairetes reguloides	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	2	0	1	0	0	0	1	1
Anairetes flavirostris	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	2	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	2	0	1	0	0	0	1	1
Anairetes parulus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	2	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	2	0	1	0	0	0	1	1
Uromyias agilis	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	2	0	1	2	0	0	1	1
Uromyias agraphia	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	2	0	1	2	0	0	1	1
Serpophaga cinerea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	2	0	1	2	0	0	1	1
Serpophaga hypoleuca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2	0	1	2	0	0	1	1
Serpophaga nigricans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	2	0	1	2	0	0	1	1
Serpophaga subcristata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2	0	1	2	0	0	1	1
Serpophaga munda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2	0	1	2	0	0	1	1
Phaeomyias murina	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	2	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	2	0	1	2	0	0	0	0
Capsiempis flaveola	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	2	2	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0

Species/Character	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Polystictus pectoralis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2	0	1	2	0	0	1	1
Polystictus brevipennis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2	0	1	2	0	0	1	1
Nesotriccus ridgwayi	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	2	1	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	2	0	1	2	0	0	0	0
Pseudocolopteryx sclateri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	2	0	1	2	0	0	1	1
Pseudocolopteryx acutipennis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	2	0	1	2	0	0	1	1
Pseudocolopteryx flaviventris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	2	0	1	2	0	0	1	1
Euscarthmus meloryphus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	2	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	2	0	1	2	0	0	1	0
Euscarthmus fulviceps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	2	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	2	0	1	2	0	0	1	0
Euscarthmus rufomarginatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	2	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	2	0	1	2	0	0	1	0
Pseudelaenia leucospodia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	2	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Stigmatura napensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	2	0	1	0	0	0	1	0
Stigmatura budytoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0	2	0	1	0	0	0	1	0
Zimmerius minimus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	2	0	1	2	1	0	0	0
Zimmerius parvus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	2	0	1	2	1	0	0	0
Zimmerius vilissimus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	2	0	1	2	1	0	0	0
Zimmerius petersi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	2	0	1	2	1	0	0	0
Zimmerius bolivianus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	2	0	1	2	1	0	0	0
Zimmerius cinereicapillus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	2	0	1	2	1	0	0	0
Zimmerius gracilipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	2	0	1	2	1	0	0	0
Zimmerius acer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	0	2	0	1	2	1	0	0	0
Zimmerius chrysops	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0	2	0	1	2	1	0	0	0
Zimmerius viridiflavus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	2	0	1	2	1	0	0	0
Inezia tenuirostris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	1	0	0	0	0	0	0	2	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Inezia inornata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	1	0	0	0	0	0	0	2	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Inezia subflava	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	1	0	0	0	0	0	0	2	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Inezia caudata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1	0	0	1	0	0	0	0	0	0	2	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Culicivora caudacuta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	2	0	1	2	0	0	1	0
Hirundinea ferruginea	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	2	0	2	0	0	0	0	1	0	1	0	0	2	1	0	0	1	1	0	2	0	1	2	0	0	0	0
Myiotriccus ornatus	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	2	0	2	0	0	0	0	0	0	1	0	0	2	0	0	0	0	1	0	2	0	1	2	0	0	0	0

Species/Character	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Muscigralla brevicauda	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0	0	2	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Pitangus sulphuratus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	2	2	1	0	0	0	0	0	0	2	1	0	1	0	0	0	1	1	0	2	0	0	1	0	0	0	0
Myiozetetes cayanensis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	2	2	1	0	0	0	0	0	0	2	1	0	1	0	0	0	1	1	0	2	0	0	1	0	0	0	0
Myiophobus fasciatus	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	2	0	1	0	0	0	0	1	0	1	0	0	2	0	0	0	0	1	0	2	0	0	2	0	0	0	0
Sublegatus modestus	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	2	0	1	0	0	0	0	1	0	1	1	0	1	1	0	0	1	1	0	2	0	1	2	0	0	0	0
Pyrocephalus rubinus	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	2	0	1	0	0	0	0	1	0	1	1	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Knipolegus cyanirostris	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	2	2	1	0	0	0	0	1	0	1	1	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Phylloscartes ventralis	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	1	1	0	0	2	0	2	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	1	2	0	1	2	0	0	0	0
Pseudotriccus pelzelni	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	1	0	0	0	2	0	2	1	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	2	0	0	2	0	1	1	0
Corythopis torquatus	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	2	0	2	0	0	0	0	0	0	1	0	0	1	0	1	0	1	1	0	2	0	1	2	0	0	0	0
Hemitriccus margaritaceiventer	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Todirostrum russatum	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	1	0	0	1	1	0	2	0	1	2	0	0	0	0
Platyrinchus mystaceus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	2	0	1	0	0	0	1	0	0	1	0	0	1	0	0	0	1	1	0	2	0	1	1	0	0	1	0
Neopipo cinnamomea	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	2	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	2	0	1	1	0	0	0	0
Piprites chloris	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	-	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	2	0	1	0	0	0	0	0
Tityra cayana	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	2	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Pachyramphus polychopterus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	2	1	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Myiobius barbatus	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	1	0	1	1	1	1	1	0	0	0	1	1	0	1	0	1	2	0	1	0	0
Onychorhynchus coronatus	0	1	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	2	0	2	0	0	0	1	0	1	2	1	1	1	0	0	0	1	1	0	2	2	1	2	0	1	0	0
Oxyruncus cristatus	1	0	1	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	1	1	0	1	0	1	0	0	0	1	2	1	1	0	0	1	0	0	1	0	2	0	1	2	0	0	0	0
Tachuris rubrigastra	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	2	0	1	0	0	0	1	0	0	1	0	0	1	0	0	0	1	1	0	1	0	1	1	0	0	0	0
Lipaugus vociferans	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	-	0	0	0	0	1	1	1	0	1	0	0	0	1	1	0	2	0	1	2	0	0	0	0
Pipreola whitelyi	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	-	0	0	0	1	0	1	1	0	1	0	1	0	1	1	0	2	0	1	2	0	0	0	0
Xenopipo atronitens	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	-	0	0	0	0	1	2	1	0	1	0	0	0	1	1	0	1	0	1	2	0	0	0	0
Chiroxiphia caudata	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	-	0	0	0	0	1	2	1	0	1	0	0	0	1	1	0	1	0	1	2	0	0	0	0
Furnarius rufus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0

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Phyllomyias fasciatus	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	1	0	0
Phyllomyias burmeisteri	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Phyllomyias zeledoni	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Phyllomyias virescens	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Phyllomyias plumbeiceps	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Phyllomyias nigrocapillus	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	1	0	0	2	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Phyllomyias cinereiceps	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Phyllomyias uropygialis	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Tyrannulus elatus	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Myiopagis gaimardii	0	0	1	0	0	2	0	0	1	1	0	0	1	0	1	1	0	-	0	0	0	-	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Myiopagis subplacens	0	0	1	0	0	2	0	0	1	1	0	0	1	0	1	1	0	-	0	0	0	-	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Myiopagis flavivertex	0	0	1	0	0	2	0	0	1	1	0	0	1	0	1	1	0	-	0	0	0	-	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Myiopagis viridicata	0	0	1	0	0	2	0	0	1	1	0	0	1	0	1	1	0	-	0	0	0	-	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Myiopagis cotta	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	0	-	0	0	0	-	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Elaenia flavogaster	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	1	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Elaenia martinica	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	1	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Elaenia spectabilis	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	1	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Elaenia ridleyana	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	1	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Elaenia albiceps	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Elaenia chilensis	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Elaenia parvirostris	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Elaenia mesoleuca	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Elaenia strepera	0	0	1	0	0	2	1	0	1	1	0	1	0	0	1	1	1	0	0	0	0	1	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Elaenia gigas	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Elaenia pelzelni	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Elaenia cristata	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Elaenia chiriquensis	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Elaenia ruficeps	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	1	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0

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Elaenia frantzii	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Elaenia obscura	0	0	1	0	0	2	0	0	1	1	0	0	1	0	1	1	1	0	0	0	0	1	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Elaenia dayi	0	0	1	0	0	2	0	0	1	1	0	0	1	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Elaenia pallatangae	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Elaenia fallax	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	1	0	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Ornithion brunneicapillus	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Ornithion inerme	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Camptostoma imberbe	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Camptostoma obsoletum	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Suiriri suiriri	0	1	2	1	1	1	0	0	1	1	0	0	2	0	1	1	1	1	0	0	0	0	0	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0
Suiriri burmeisteri	0	0	1	1	1	1	0	0	1	1	0	0	2	0	1	1	1	1	0	0	0	0	0	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0
Mecocerculus leucophrys	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0
Mecocerculus poecilocercus	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Mecocerculus hellmayri	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Mecocerculus calopterus	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Mecocerculus minor	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	0	2	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Mecocerculus stictopterus	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Anairetes reguloides	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0
Anairetes flavirostris	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0
Anairetes parulus	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0
Uromyias agilis	1	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	3	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0
Uromyias agraphia	1	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	3	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0
Serpophaga cinerea	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0
Serpophaga hypoleuca	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0
Serpophaga nigricans	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0
Serpophaga subcristata	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0
Serpophaga munda	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0
Phaeomyias murina	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	1	0	0
Capsiempis flaveola	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	1	0	0

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Polystictus pectoralis	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0
Polystictus brevipennis	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0
Nesotriccus ridgwayi	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	1	0	0
Pseudocolopteryx sclateri	0	0	1	0	0	1	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0
Pseudocolopteryx acutipennis	0	0	1	0	0	1	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0
Pseudocolopteryx flaviventris	0	0	1	0	0	1	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0
Euscarthmus meloryphus	1	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Euscarthmus fulviceps	1	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Euscarthmus rufomarginatus	1	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Pseudelaenia leucospodia	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	1	0	0
Stigmatura napensis	1	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	4	0	2	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Stigmatura budytoides	1	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	4	0	2	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Zimmerius minimus	0	0	1	0	0	2	0	0	1	1	0	0	1	0	1	1	1	1	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	2	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Zimmerius parvus	0	0	1	0	0	2	0	0	1	1	0	0	1	0	1	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	2	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Zimmerius vilissimus	0	0	1	0	0	2	0	0	1	1	0	0	1	0	1	1	1	1	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	2	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Zimmerius petersi	0	0	1	0	0	2	0	0	1	1	0	0	1	0	1	1	1	1	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	2	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Zimmerius bolivianus	0	0	1	0	0	2	0	0	1	1	0	0	1	0	1	1	1	1	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	2	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Zimmerius cinereicapillus	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	2	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Zimmerius gracilipes	0	0	1	0	0	2	0	0	1	1	0	0	1	0	1	1	1	1	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	2	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Zimmerius acer	0	0	1	0	0	2	0	0	1	1	0	0	1	0	1	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	2	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Zimmerius chrysops	0	0	1	0	0	2	0	0	1	1	0	0	1	0	1	1	1	1	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	2	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Zimmerius viridiflavus	0	0	1	0	0	2	0	0	1	1	0	0	1	0	1	1	1	1	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	2	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Inezia tenuirostris	1	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Inezia inornata	1	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Inezia subflava	1	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Inezia caudata	1	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	1	0	0
Culicivora caudacuta	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0
Hirundinea ferruginea	0	0	1	1	1	1	0	0	1	0	0	0	0	0	1	0	0	-	0	0	0	-	1	1	0	1	1	0	1	0	1	0	1	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0

Species/Character	**101**	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**	**111**	**112**	**113**	**114**	**115**	**116**	**117**	**118**	**119**	**120**	**121**	**122**	**123**	**124**	**125**	**126**	**127**	**128**	**129**	**130**	**131**	**132**	**133**	**134**	**135**	**136**	**137**	**138**	**139**	**140**	**141**	**142**	**143**	**144**	**145**	**146**	**147**	**148**	**149**	**150**	**151**
Myiotriccus ornatus	0	0	1	0	1	2	1	0	1	1	0	0	1	0	1	0	0	-	0	0	0	-	1	1	0	0	0	0	1	0	1	0	1	0	0	0	1	1	0	1	1	1	1	0	0	0	0	0	1	0	0
Muscigralla brevicauda	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	1	0	-	0	0	0	-	1	1	1	0	0	0	0	0	1	0	0	0	4	0	0	1	0	1	1	1	0	0	0	0	1	0	0	0	0
Pitangus sulphuratus	0	1	2	1	1	1	1	0	1	0	0	0	0	0	1	0	0	-	0	0	0	-	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0	0	0	1	0	0
Myiozetetes cayanensis	0	1	2	1	0	2	0	0	1	0	0	0	0	0	1	0	0	-	0	0	0	-	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0	0	0	1	0	0
Myiophobus fasciatus	0	0	1	1	1	2	1	0	1	1	0	0	0	0	1	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0
Sublegatus modestus	0	0	2	1	1	2	1	0	1	1	0	1	2	0	1	1	1	1	1	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0
Pyrocephalus rubinus	0	0	1	1	0	2	0	0	1	1	0	0	1	0	1	1	1	0	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0
Knipolegus cyanirostris	0	0	1	1	0	2	0	0	1	1	0	0	0	0	1	1	0	-	1	0	0	-	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0	0	0	1	0	0
Phylloscartes ventralis	1	1	2	0	0	2	0	0	1	1	0	0	1	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	1	0	0
Pseudotriccus pelzelni	1	1	0	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	2	1	0	1	1	0	1	0	0	0	0	0	1	0	0
Corythopis torquatus	1	1	2	0	0	1	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	0	0
Hemitriccus margaritaceiventer	1	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	-	0	0	0	-	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	0	0	1	0	0
Todirostrum russatum	1	1	0	0	0	1	1	0	1	0	0	1	0	0	1	0	0	-	0	0	0	-	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	1	1	1	0	0	0	0	1	0	0
Platyrinchus mystaceus	1	1	0	0	0	2	0	0	1	1	0	0	2	0	1	1	0	-	0	0	0	-	1	1	0	1	0	0	1	0	1	1	1	0	0	1	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0
Neopipo cinnamomea	1	1	0	0	0	2	0	0	1	1	0	0	2	0	1	1	0	-	0	0	0	-	1	1	0	0	0	0	1	0	1	0	1	0	0	1	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0
Piprites chloris	0	0	1	0	0	2	0	0	1	1	0	0	0	0	1	0	0	-	0	0	0	-	0	1	1	1	0	1	1	0	1	1	0	0	0	0	0	1	0	1	1	1	1	1	0	0	0	0	1	0	0
Tityra cayana	0	0	0&2	1	0	2	0	1	1	1	1	0	1	0	1	1	0	-	0	0	0	-	0	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1	1	0
Pachyramphus polychopterus	0	0	0&2	0	0	2	0	0	1	1	0	0	1	0	1	0	0	-	0	0	0	-	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	1	1	0	0
Myiobius barbatus	0	0	0&2	0	1	1	0	0	1	1	0	0	1	1	1	1	0	-	0	0	0	-	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	0	1	1	0	0
Onychorhynchus coronatus	0	1	2	0	1	0	1	0	1	0	0	0	0	0	1	0	0	-	0	0	0	-	0	1	1	0	0	0	1	0	1	0	1	0	0	0	0	1	0	1	1	1	1	1	0	0	0	1	1	0	1
Oxyruncus cristatus	0	1	2	0	0	2	0	1	1	0	1	1	0	0	1	0	0	-	0	0	0	-	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0	1	1	0	1	1	0	1
Tachuris rubrigastra	1	1	2	0	0	2	0	0	1	1	0	0	0	0	0	-	0	-	-	0	0	-	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	1	0	0
Lipaugus vociferans	0	0	0&2	0	1	1	0	0	1	1	0	0	2	0	1	0	0	-	0	0	0	-	0	1	1	1	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	1	0	1	0	0	0	1	0	0
Pipreola whitelyi	0	0	0&2	0	0	2	1	0	1	1	0	1	1	0	1	0	0	-	0	0	0	-	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	1	0	0	0	0	0	0	0
Xenopipo atronitens	0	0	1	0	0	2	0	1	1	1	0	0	0	0	1	0	0	-	0	0	0	-	0	1	1	1	0	0	1	0	1	1	0	0	0	0	1	1	0	1	1	1	0	0	1	0	0	0	0	0	0
Chiroxiphia caudata	0	0	1	0	0	2	1	0	1	1	0	0	0	0	1	0	0	-	0	0	0	-	0	1	1	1	0	0	1	0	1	1	0	0	0	0	1	1	0	1	1	1	1	0	1	0	0	0	0	0	0
Furnarius rufus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	-	-	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 3. List of character transformations within the clades recovered in the phylogenetic analysis of Elaeniinae based in osteological evidences.

Furnarius rufus:
No autapomorphies
Phyllomyias fasciatus:
No autapomorphies
Phyllomyias burmeisteri:
No autapomorphies
Phyllomyias zeledoni:
Char. 48: 1 --> 0
Char. 73: 0 --> 2
Phyllomyias virescens:
No autapomorphies
Phyllomyias plumbeiceps:
Char. 86: 0 --> 1
Phyllomyias nigrocapillus:
Char. 95: 2 --> 0
Char. 124: 0 --> 1
Char. 136: 1 --> 2
Phyllomyias cinereiceps:
Char. 85: 0 --> 1
Phyllomyias uropygialis:
Char. 95: 2 --> 0
Tyrannulus elatus:
Char. 24: 1 --> 0
Char. 77: 1 --> 0
Char. 83: 1 --> 0
Char. 85: 1 --> 0
Char. 86: 0 --> 1
Char. 131: 0 --> 1
Myiopagis gaimardii:
Char. 59: 0 --> 1
Char. 77: 1 --> 0
Char. 94: 1 --> 2
Char. 112: 0 --> 1
Char. 116: 1 --> 0
Myiopagis subplacens:
Char. 32: 1 --> 0
Char. 56: 0 --> 1
Char. 59: 0 --> 1
Char. 77: 1 --> 0
Char. 94: 1 --> 2
Char. 112: 0 --> 1
Char. 116: 1 --> 0
Myiopagis flavivertex:
Char. 56: 0 --> 1
Char. 77: 1 --> 0
Char. 86: 0 --> 1
Char. 94: 1 --> 2
Char. 112: 0 --> 1
Char. 116: 1 --> 0
Myiopagis viridicata:
Char. 77: 1 --> 0
Char. 86: 0 --> 1
Char. 91: 0 --> 1
Char. 93: 0 --> 1
Char. 94: 1 --> 2
Char. 112: 0 --> 1
Char. 116: 1 --> 0
Myiopagis cotta:
Char. 32: 1 --> 0
Char. 56: 0 --> 1
Char. 77: 1 --> 0
Char. 86: 0 --> 1

Char. 94: 1 --> 2
Char. 116: 1 --> 0
Elaenia flavogaster:
No autapomorphies
Elaenia martinica:
Char. 70: 0 --> 1
Elaenia spectabilis:
Char. 62: 0 --> 1
Char. 88: 0 --> 1
Char. 121: 0 --> 1
Elaenia ridleyana:
Char. 32: 1 --> 0
Char. 33: 1 --> 0
Char. 121: 0 --> 1
Elaenia albiceps:
No autapomorphies
Elaenia chilensis:
No autapomorphies
Elaenia parvirostris:
No autapomorphies
Elaenia mesoleuca:
No autapomorphies
Elaenia strepera:
Char. 42: 0 --> 1
Char. 46: 0 --> 1
Char. 56: 0 --> 1
Char. 106: 0 --> 1
Char. 111: 0 --> 1
Char. 121: 0 --> 1
Elaenia gigas:
Char. 33: 1 --> 0
Char. 49: 0 --> 1
Char. 84: 0 --> 1
Elaenia pelzelni:
Char. 41: 0 --> 1
Char. 45: 0 --> 1
Char. 62: 0 --> 1
Char. 70: 0 --> 1
Elaenia cristata:
No autapomorphies
Elaenia chiriquensis:
No autapomorphies
Elaenia ruficeps:
Char. 121: 0 --> 1
Elaenia frantzii:
No autapomorphies
Elaenia obscura:
No autapomorphies
Elaenia dayi:
Char. 70: 0 --> 1
Char. 84: 0 --> 1
Char. 85: 1 --> 0
Char. 88: 0 --> 1
Elaenia pallatangae:
No autapomorphies
Elaenia fallax:
No autapomorphies
Ornithion brunneicapillus:
No autapomorphies
Ornithion inerme:
No autapomorphies
Camptostoma imberbe:
No autapomorphies
Camptostoma obsoletum:
No autapomorphies
Suiriri suiriri:
Char. 1: 1 --> 0
Char. 28: 1 --> 0

Char. 101: 0 --> 1
Char. 102: 1 --> 2
Suiriri burmeisteri:
Char. 84: 0 --> 1
Mecocerculus leucophrys:
Char. 95: 2 --> 0
Char. 122: 1 --> 0
Mecocerculus poecilocercus:
Char. 56: 0 --> 1
Mecocerculus hellmayri:
No autapomorphies
Mecocerculus calopterus:
No autapomorphies
Mecocerculus minor:
Char. 134: 0 --> 1
Char. 136: 0 --> 2
Mecocerculus stictopterus:
No autapomorphies
Anairetes reguloides:
No autapomorphies
Anairetes flavirostris:
No autapomorphies
Anairetes parulus:
No autapomorphies
Uromyias agilis:
No autapomorphies
Uromyias agraphia:
No autapomorphies
Serpophaga cinerea:
No autapomorphies
Serpophaga hypoleuca:
No autapomorphies
Serpophaga nigricans:
No autapomorphies
Serpophaga subcristata:
No autapomorphies
Serpophaga munda:
No autapomorphies
Phaeomyias murina:
Char. 85: 1 --> 0
Char. 124: 0 --> 1
Capsiempis flaveola:
Char. 82: 1 --> 0
Polystictus pectoralis:
No autapomorphies
Polystictus brevipennis:
No autapomorphies
Nesotriccus ridgwayi:
Char. 39: 0 --> 1
Char. 105: 2 --> 0
Pseudocolopteryx sclateri:
No autapomorphies
Pseudocolopteryx acutipennis:
No autapomorphies
Pseudocolopteryx flaviventris:
No autapomorphies
Euscarthmus meloryphus:
No autapomorphies
Euscarthmus fulviceps:
No autapomorphies
Euscarthmus rufomarginatus:
No autapomorphies
Pseudelaenia leucospodia:
No autapomorphies
Stigmatura napensis:
No autapomorphies
Stigmatura budytoides:
No autapomorphies

Zimmerius minimus:
Char. 1: 1 --> 0
Zimmerius parvus:
Char. 1: 1 --> 0
Zimmerius vilissimus:
No autapomorphies
Zimmerius petersi:
No autapomorphies
Zimmerius bolivianus:
No autapomorphies
Zimmerius cinereicapillus:
Char. 112: 1 --> 0
Zimmerius gracilipes:
No autapomorphies
Zimmerius acer:
Char. 86: 0 --> 1
Zimmerius chrysops:
No autapomorphies
Zimmerius viridiflavus:
No autapomorphies
Inezia tenuirostris:
No autapomorphies
Inezia inornata:
No autapomorphies
Inezia subflava:
No autapomorphies
Inezia caudata:
No autapomorphies
Culicivora caudacuta:
Char. 85: 1 --> 2
Char. 124: 0 --> 1
Hirundinea ferruginea:
Char. 13: 0 --> 1
Char. 32: 1 --> 0
Char. 33: 1 --> 0
Char. 34: 1 --> 0
Char. 54: 0 --> 1
Char. 56: 0 --> 1
Char. 71: 0 --> 1
Char. 80: 0 --> 1
Char. 86: 0 --> 1
Char. 103: 0 --> 1
Char. 125: 0 --> 1
Char. 126: 0 --> 1
Myiotriccus ornatus:
Char. 89: 1 --> 0
Char. 105: 1 --> 2
Char. 106: 0 --> 1
Char. 109: 0 --> 1
Char. 112: 0 --> 1
Char. 136: 0 --> 1
Muscigralla brevicauda:
Char. 58: 0 --> 1
Char. 115: 0 --> 1
Char. 124: 0 --> 1
Char. 134: 0 --> 4
Char. 146: 0 --> 1
Char. 148: 1 --> 0
Pitangus sulphuratus:
Char. 12: 0 --> 2
Char. 39: 0 --> 1
Char. 71: 0 --> 1
Char. 104: 0 --> 1
Char. 105: 2 --> 1
Char. 106: 0 --> 1
Myiozetetes cayanensis:
No autapomorphies
Myiophobus fasciatus:

Char. 58: 0 --> 1

Char. 83: 1 --> 0

Char. 85: 1 --> 2

Char. 89: 1 --> 0

Char. 94: 1 --> 0

Char. 141: 1 --> 0

Sublegatus modestus:

Char. 28: 1 --> 0

Char. 37: 0 --> 1

Char. 86: 0 --> 1

Char. 102: 1 --> 2

Char. 111: 0 --> 1

Char. 112: 0 --> 2

Char. 121: 0 --> 1

Char. 135: 0 --> 1

Char. 142: 1 --> 0

Pyrocephalus rubinus:

Char. 39: 0 --> 1

Char. 112: 0 --> 1

Knipolegus cyanirostris:

Char. 74: 0 --> 2

Char. 136: 0 --> 1

Phylloscartes ventralis:

Char. 70: 0 --> 1

Char. 83: 0 --> 1

Char. 112: 0 --> 1

Char. 115: 0 --> 1

Pseudotriccus pelzelni:

Char. 76: 0 --> 1

Char. 86: 0 --> 1

Char. 94: 1 --> 0

Char. 97: 0 --> 1

Char. 98: 0 --> 1

Char. 102: 2 --> 0

Char. 117: 1 --> 0

Char. 122: 0 --> 1

Char. 136: 0 --> 2

Corythopis torquatus:

Char. 28: 1 --> 0

Char. 56: 0 --> 1

Char. 105: 2 --> 1

Char. 136: 0 --> 1

Char. 140: 1 --> 0

Hemitriccus margaritaceiventer:

Char. 56: 0 --> 1

Char. 144: 0 --> 1

Todirostrum russatum:

Char. 32: 1 --> 0

Char. 35: 0 --> 1

Char. 39: 0 --> 1

Char. 57: 0 --> 1

Char. 62: 0 --> 1

Char. 68: 0 --> 1

Char. 86: 0 --> 1

Char. 106: 0 --> 1

Char. 111: 0 --> 1

Char. 122: 0 --> 1

Platyrinchus mystaceus:

Char. 44: 0 --> 1

Char. 98: 0 --> 1

Char. 125: 0 --> 1

Char. 131: 0 --> 1

Neopipo cinnamomea:

No autapomorphies

Piprites chloris:

Char. 21: 0 --> 1

Char. 33: 1 --> 0

Char. 55: 0 --> 1

Char. 58: 0 --> 1

Char. 84: 0 --> 1

Char. 85: 1 --> 0

Char. 95: 2 --> 0

Char. 127: 0 --> 1

Char. 143: 0 --> 1

Tityra cayana:

Char. 103: 0 --> 1

Char. 107: 0 --> 1

Char. 110: 0 --> 1

Char. 115: 0 --> 1

Char. 149: 0 --> 1

Pachyramphus polychopterus:

Char. 33: 1 --> 0

Char. 67: 0 --> 1

Char. 68: 1 --> 0

Char. 80: 0 --> 1

Char. 122: 0 --> 1

Myiobius barbatus:

Char. 35: 0 --> 1

Char. 92: 2 --> 1

Char. 101: 1 --> 0

Char. 109: 0 --> 1

Char. 112: 0 --> 1

Char. 113: 0 --> 1

Char. 115: 0 --> 1

Char. 142: 1 --> 0

Onychorhynchus coronatus:

Char. 16: 0 --> 1

Char. 19: 0 --> 1

Char. 38: 0 --> 1

Char. 55: 0 --> 1

Char. 93: 0 --> 2

Char. 106: 0 --> 1

Char. 132: 0 --> 1

Oxyruncus cristatus:

Char. 5: 0 --> 1

Char. 18: 0 --> 1

Char. 20: 1 --> 0

Char. 24: 0 --> 1

Char. 41: 0 --> 1

Char. 42: 0 --> 1

Char. 48: 1 --> 2

Char. 50: 0 --> 1

Char. 52: 0 --> 1

Char. 54: 0 --> 1

Char. 65: 0 --> 1

Char. 68: 0 --> 1

Char. 72: 0 --> 1

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Char. 144: 0 --> 1

Char. 145: 0 --> 1

Tachuris rubrigastra:

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Char. 67: 0 --> 1

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Char. 130: 1 --> 0

Lipaugus vociferans:

Char. 30: 0 --> 1

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Char. 112: 1 --> 2

Char. 136: 0 --> 1

Char. 144: 0 --> 1

Pipreola whitelyi:

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Char. 143: 0 --> 1

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Xenopipo atronitens:

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Char. 107: 0 --> 1

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Chiroxiphia caudata:

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Node 113:

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Node 114:

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Node 120:

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Node 122:

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Node 124:

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Node 126:

No synapomorphies

Node 127:

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Char. 86: 0 --> 1

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Node 128:

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Node 130:

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Node 133:

Char. 74: 0 --> 2

Char. 118: 0 --> 1

Node 134:

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Char. 4: 0 --> 1

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Node 150:

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Node 151:

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Char. 86: 0 --> 1

Node 152:

Char. 62: 0 --> 1

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Node 154:

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Node 166:

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Char. 132: 0 --> 1
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Char. 148: 1 --> 0
Node 176:
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Char. 95: 2 --> 1
Char. 122: 0 --> 1
Node 177:
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Char. 41: 0 --> 1
Char. 69: 1 --> 0
Char. 75: 1 --> 0
Char. 131: 0 --> 1
Node 178:
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Char. 12: 0 --> 2
Char. 74: 0 --> 1
Char. 83: 1 --> 0
Char. 147: 0 --> 1
Node 179:
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Char. 112: 0 --> 1
Char. 141: 1 --> 0
Node 180:
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Char. 9: 0 --> 1
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Char. 34: 1 --> 0
Char. 51: 0 --> 1
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Char. 75: 1 --> 2
Char. 79: 0 --> 1
Char. 97: 0 --> 1
Char. 104: 0 --> 1
Char. 124: 0 --> 1
Char. 143: 0 --> 1
Node 181:
Char. 56: 0 --> 1
Char. 69: 1 --> 0
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Char. 84: 0 --> 1
Char. 128: 0 --> 1
Char. 147: 0 --> 1
Node 182:
Char. 7: 0 --> 2
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Node 183:

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Char. 57: 0 --> 1

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Char. 148: 1 --> 0

CONCLUSÕES GERAIS E PERSPECTIVAS

Por meio da osteologia comparada, produzimos uma nova matriz morfológica para a subfamília Elaeniinae, composta de 151 caracteres codificados para 112 espécies. A análise filogenética conduzida demonstrou que há um claro sinal filogenético nesse conjunto de informações, e resultou em árvores com boa resolução, mesmo analisando-se a partir do consenso estrito, somente. A topologia resultante trouxe algumas novidades em comparação com as relações conhecidas até então, bem como na complementação e congruência com as hipóteses de relacionamento produzidas a partir de caracteres moleculares. Novidades que incluem a necessidade de descrição de ao menos um gênero novo para o que antes foi chamado de *Mecocerculus* (Franz *et al. em prep.*); a ressurreição de *Ridgwayornis* para duas espécies de *Serpophaga*: *R. cinerea* e *R. nigricans*; a necessidade de ajustes na classificação de *Phyllomyias* com a revisão histórica dos nomes disponíveis e correta alocação em *Xanthomyias*, *Acrochordopus*, *Oreotriccus* ou *Tyranniscus* a partir da inclusão das espécies faltantes nesta matriz combinada com a matriz de Elementos Ultraconservados; a necessidade de uma avaliação voltada para a morfologia e as adaptações de *Suiriri* e sua relação com os demais Tyrannidae; entre outras.

Diversas perspectivas em termos de estudos taxonômicos e filogenéticos, não explorados diretamente aqui, emergiram a partir do presente estudo. O autor tem trabalhado, juntamente com parceiros de diversas instituições, na filogenia de todos os Tyranni (“Suboscines”) a partir de UCEs, cuja árvore com mais de 1.000 terminais acaba de ser produzida. A topologia resultante, na partição que inclui Elaeniinae, tem alta congruência com a filogenia aqui apresentada. A matriz originada nesta tese está sendo integrada com a referida filogenia genômica com vistas à atualizar toda a classificação de Elaeniinae. Do ponto de vista taxonômico, identificamos também a variação fenotípica em diversos gêneros e “complexos taxonômicos” da subfamília, com ajustes no sentido de separar ou agrupar espécies. Estão sendo produzidos manuscritos voltados para a taxonomia dentro de gêneros como *Euscarthmus*, *Polystictus*, *Serpophaga*, *Culicivora*, *Elaenia*, *Mecocerculus*, *Suiriri* e *Inezia*, incluindo a elevação ao status de espécie de um táxon extinto (*Polystictus pectoralis bogotensis*, que teve DNA extraído de uma amostra de escama seca com mais de 100 anos), e descrever ao menos dois táxons novos, algo infrequente na ornitologia atual. O panorama exposto, identificado durante a execução desta tese, demonstra a necessidade de envolver mais pesquisadores na ornitologia filogenética, pois há muito mais por se fazer do que a literatura das décadas passadas tem indicado.

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PREPARATION OF MANUSCRIPT

Manuscript format and structure/style

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- Burr FA, Evert RF. 1982. A cytochemical study of the wound-healing proteins in *Bryopsis hypnoides. Cytobios* 6: 199-215.
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