

FACULDADE DE BIOCÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA

NÚBIA GALVEZ

**ANATOMIA COMPARADA E ANÁLISE FILOGENÉTICA DE UM ANFÍBIO TEMNOSPÔNDILO
DO PERMIANO DO RIO GRANDE DO SUL**

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DISSERTAÇÃO DE MESTRADO

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Orientador: Dr. Marco Brandalise de Andrade

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RESUMO

Temnospôndilos são anfíbios primitivos, com uma grande diversidade morfológica e ecológica, que habitaram o planeta entre o Carbonífero e Cretáceo. Representam um grupo de espécies fósseis de grande importância na evolução das biotas continentais e muito possivelmente tem uma relação estreita com os grupos de anfíbios atuais. No Brasil, o grupo faz parte da importante paleofauna tetrápoda e está bem representado em sedimentos Permo-Triássicos, contando com nove espécies descritas até o momento. No Rio Grande do Sul, quatro espécies são registradas em sedimentos permianos da Formação Rio do Rasto, onde o material apresentado aqui (MCP-4275PV) foi coletado. O espécime é representado por uma hemimandíbula preservada em duas porções e possui aproximadamente 50 cm de comprimento, o que indica pertencer a um animal de grande porte. A preparação do material, com remoção de sedimentos, evidenciou características importantes para o diagnóstico do espécime em nível taxonômico mais exclusivo. A análise morfológica mostrou que o espécime apresenta características típicas de Capitosauria e a análise filogenética (TNT, PAUP; 76 terminais, 271 caracteres) revelou que MCP-4275PV consistentemente surge dentro de Capitosauria, um grupo com distribuição até então exclusivamente triássica. MCP-4275PV representa atualmente o capitosaurio mais antigo, posicionando a origem do grupo no Permiano (Guadalupiano) da América do Sul. Tais resultados trazem evidências que estão de acordo com outros estudos sobre possíveis rotas de dispersão através do supercontinente Panga, a partir do Gondwana para a Laurásia e sobre a radiação e especiação do grupo em relação ao limite Permo-Triássico.

Palavras-chave: Capitosauria, Gondwana, Formação Rio do Rasto, Bacia do Paraná.

ABSTRACT

Temnospondyls are early amphibians, with a broad morphological and ecological diversity that inhabited the planet between the Carboniferous and Cretaceous. They represent a grade of fossil species, which are very important for evolution of the continental fauna and, possibly, have a strict relationship with current amphibians (Lissamphibia). In Brazil, the group is well represented in Permo–Triassic sediments, with nine species described so far. In Rio Grande do Sul, two species were recorded in Permian sediments from Rio do Rasto Formation, where the material MCP-4275PV was collected. This specimen is represented by a hemimandible preserved in two portions, roughly 50 cm long, indicating that it was a large animal. Preparation of the specimen, with sediment removal, evidenced important characteristics for the diagnose of the specimen in a less inclusive taxonomic level. The morphological analyses suggests that the specimen belong to Capitosauria group and the phylogenetic analysis (TNT, PAUP; 76 terminals, 271 characters) showed that MCP-4275PV is consistently placed within Capitosauria, a group so far exclusively Triassic in distribution. Therefore, the new specimen is the oldest capitosaur and its record points out to a South American origin to the group. Such results bring evidences that according with other studies about possible dispersion routs through Pangaea, from Gondwana to Laurasia and about the radiation and speciation of the group relative to the Permo–Triassic boundary.

Key words: Capitosauria, Gondwana, Rio do Rasto Formation, Paraná Basin.

APRESENTAÇÃO

Temnospondyli é um grupo de tetrápodes não-amniotos extintos, frequentemente referidos como ‘anfíbios primitivos’ por suas características morfológicas e ontogenéticas. Assim como os anfíbios atuais, os temnospôndilos eram adaptados ao ambiente aquático em fase larval e ambiente terrestre em fase adulta. (Romer 1966). Os ovos não possuíam nem um tipo de proteção mecânica eficiente, eram postos nos ambientes aquáticos e os embriões não tinham fonte imediata de nutrientes como, por exemplo, os répteis (Romer 1966). As larvas possuíam brânquias como sistema respiratório inicial e posteriormente desenvolviam um sistema respiratório interno, exceto em algumas espécies neotênicas, as quais mantinham as características larvais (e. g. Branchiosaurids: Schoch & Frobisch 2006; Schoch 2014).

Este é considerado o maior grupo de tetrápodes do Paleozoico e Mesozóico (Schoch 2013, 2014). As mudanças geológicas e climáticas durante os 225 m.a. em que os temnospôndilos habitaram o planeta contribuíram para o surgimento das diferentes características morfológicas entre espécies, que refletem muito o comportamento e modo de vida do grupo (Schoch 2014; Benton 2015). Em algumas espécies o crânio não passa de 4 cm na fase adulta (alguns Branchiosauridae), enquanto que em outras espécies o crânio pode chegar a medir 150 cm (e.g. *Mastodonsaurus giganteus*; Schoch 2014). Algumas espécies são pedomórficas (e.g. *Branchiosaurus*), outras são grandes e possuem rostro bastante alongado, assemelhando-se aos atuais crocodilos (e.g. *Australerpeton cosgriffi*), alguns grupos são terrestres quando adultos (e.g. *Eryops megacephalus*), outros são predadores aquáticos (e.g. *Archegosaurus*; ver Schoch 2014; Benton 2015). No final do Carbonífero e início do Permiano, a formação do supercontinente Pangeia determinou o estabelecimento de um clima continental e progressivo processo de desertificação (registro eólico), o que acarretou no desaparecimento de algumas espécies de tetrápodes basais. No entanto, outras sobreviveram, dentre elas, espécies representantes de Temnospondyli, grupo que teve sua maior radiação no Permiano (Schoch 2014, Benton 2015; Fig.1). O grande evento de extinção permo-triássico dizimou a maioria das famílias de temnospôndilos, sobrando apenas as famílias inseridas nas linhagens: Dvinosauria, Capitosauria e Trematosauria (Benton 2015).

Aproximadamente 300 espécies foram descritas mundialmente até o momento (Schoch 2013), sendo o registro mais antigo o da espécie *Balanerpeton wood*, coletada em sedimentos do Carbonífero Superior (340 m.a.) da Escócia (Milner & Sequeira 1993), enquanto que o registro mais novo é o da espécie australiana *Koolasuchus cleelandi*, coletada em sedimentos do Cretáceo Inferior (115 m.a.; ver Warren *et al.* 1997).

No Brasil, o primeiro registro de temnospôndilo foi feito por Price em 1948, *Prionosuchus plumeri*, referente a um rostro coletado na Formação Pedra do Fogo, no Estado do Maranhão. Os próximos registros - *Australerpeton cosgriffi* e *Bageherpeton longignathus*, foram feitos apenas em meados do ano 2000 (Barberena 1998; Dias e Barberena 2001). Apesar de ainda serem escassos os registros de temnospônulos brasileiros, nota-se um crescimento considerável no número de descrições para o grupo nos últimos anos. De 2006 até 2017 sete táxons foram formalmente descritos para o Brasil: *Sangaia lavinae*, *Compsocerops* sp., *Timonya annea* e *Procuhy nazariensis*, *Parapytanga catarinenses*, *Konzhukovia sangabrielensis* e *Tomeia witecki* (ver Dias-da-Silva *et al.* 2006; 2015; Cisneros *et al.* 2015; Strapasson *et al.* 2015; Eltink *et al.* 2016; Pacheco *et al.* 2016). Destes táxons, cinco são provenientes de sedimentos Permianos da Formação Rio do Rasto: *Bageherpeton longignathus*, *Australerpeton cosgriffi*, *Compsocerops* sp., *Parapytanga catarinenses*, *Konzhukovia sangabrielensis*.

O presente trabalho teve como objetivo descrever uma hemimandíbula fóssil pertencente ao grupo Temnospondyli e que está depositada no Museu de Ciências e Tecnologia da PUCRS (Pontifícia Universidade Católica do Rio Grande do Sul) sob o número de tombo MCP4275-PV. Após descrição do material, foi feita uma análise filogenética utilizando o conjunto de dados apresentados por Schoch (2013), com algumas modificações, resultando em uma matriz de 76 táxons e 271 caracteres. Outras análises foram feitas, retirando os táxons problemáticos adicionados na análise pelo autor. No entanto todos os resultados foram mantidos neste documento e estão inseridos no artigo.

A presente dissertação está organizada em formato de artigo, respeitando as normas de formatação da Revista Zootaxa, à qual será submetido o manuscrito apresentado neste documento.

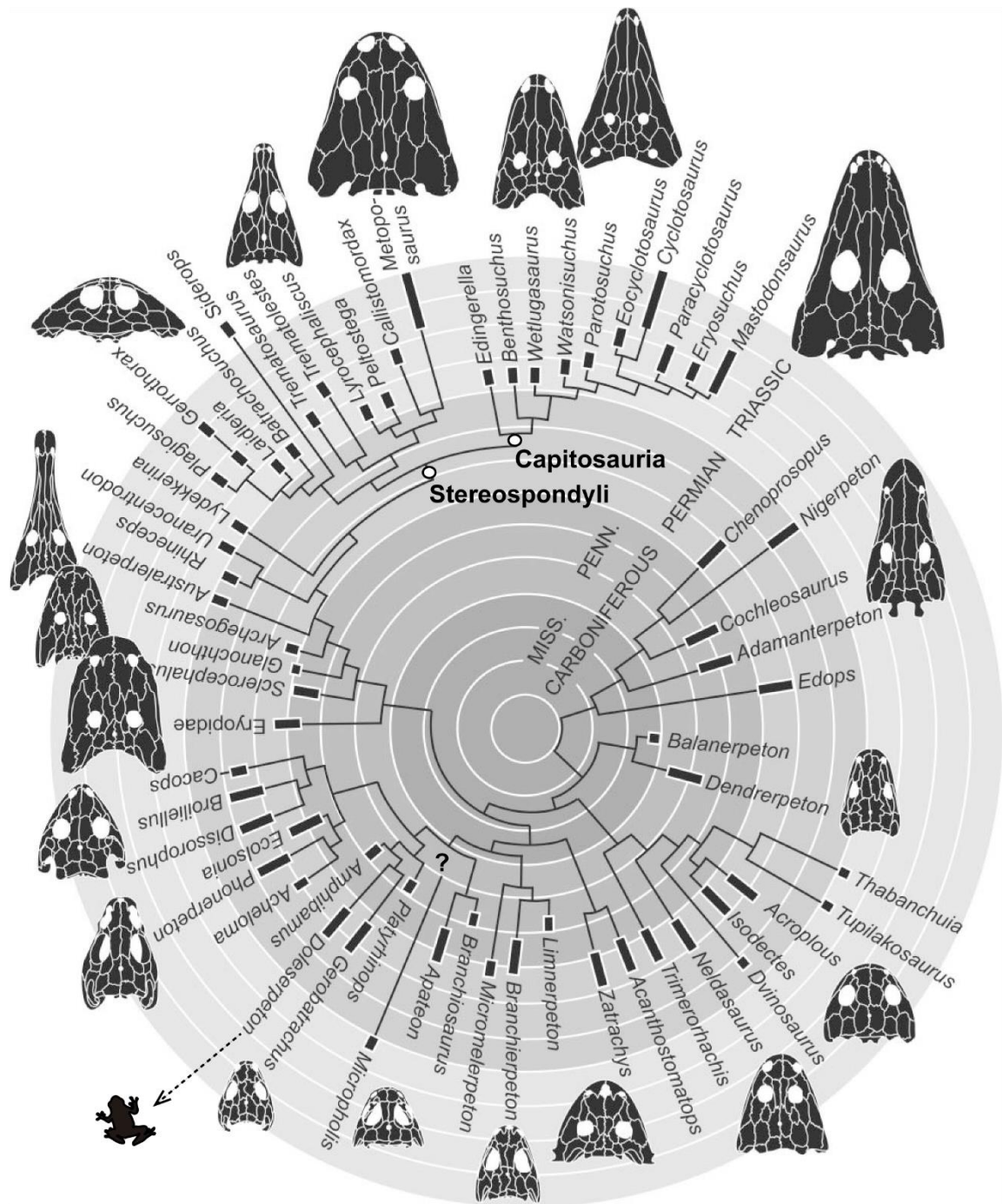


Fig 1. Filogenia calibrada das principais linhagens de Temnospondyli, onde é possível identificar registros preponderantemente permianos e triássicos. Observa-se que o registro dos Stereospondyli e Capitosauria está restrito ao Triássico, havendo um ‘gap’ considerável de registro entre esses representantes triássicos e formas basais do Permiano Inferior, como *Archeosaurus*. Calibragem referente ao registro, não aplicando-se aos eventos cladogenéticos. Retirado de Schoch (2013).

CARACTERÍSTICAS ANATÔMICAS DE TEMNOSPONDYLI

As características que unem a grande diversidade de espécies dentro de Temnospondyli são, principalmente, caracteres morfo-anatômicos cranianos (Fig. 2). A porção ventral do crânio apresenta duas aberturas palatais (vacuidades interpterigóides), separadas por um processo cultriforme do parasfenóide e pterigoides trirradiados (Fig. 2A). Algumas hipóteses sobre a função dessas aberturas em temnospôndilos foram levantadas: auxílio na respiração através da ativação da musculatura periocular (*retractor bulbi* e *elevator bulbi*); captura de presas por sucção bucal; e ancoragem da musculatura adutora anterior da mandíbula; e ampliação da intensidade da mordida (Olson 1961; Clack 1992; Laurin 2000; Schoch 2014; Lautenschlager *et al.* 2016). Vacuidades interpterigóides são encontradas também nos anfíbios atuais (Lissamphibia), e representam evidência de que os lissanfíbios compartilham um ancestral comum com os temnospôndilos (Lautenschlager *et al.* 2016). Diferente dos anfíbios mais derivados, o crânio dos temnospôndilos possuem um padrão de ossificação mais complexo. Mesmo dentro do grupo podemos notar algumas diferenças na quantidade de ossos do crânio, em *Dendrerpeton*, um temnospôndilo mais primitivo, pode-se observar a presença de um osso intertemporal localizado na parte anterior do supratemporal e a ausência da sutura entre a base do crânio e o pterigoide, o que permitia a motilidade desta porção do crânio (Carroll 1988). No gênero *Cacops*, o intertemporal já não está presente (Carroll 1988), assim como nos anfíbios atuais houve a perda do lacrimal, supratemporal, tabular, pré e pós-orbital, pré e pós-frontal e fusão do frontal e parietal em um elemento único, o frontoparietal (Guayasamin 2004). Em vista occipital, as características mais marcantes do grupo são a presença de côndilos occipitais duplos, suturas entre exoccipital, pós-parietal e tabular e estribo em formato de bastão, o qual é responsável pela transmissão de som para o ouvido médio através da vibração do ar (Fig. 2C) (Schoch 2014). Já o entalhe ótico, melhor observado em vista dorsal (Fig. 2B), indica formação de uma estrutura que viria suportar o tímpano nos vertebrados mais derivados (Carroll 1988).

As características mandibulares (Fig. 3) do grupo também são diagnósticas, muitas vezes sendo cruciais para a determinação de táxons dentro de grupos menos abrangentes (Jupp & Warren 1986). São dez ossos compondo a estrutura mandibular, nove originários a partir de elementos do dermatocrânio e apenas o articular originário de elementos do esplancocrânio (Jupp & Warren 1986; Kardong 2011). Assim como os ossos do crânio, a estrutura morfo-anatômica mandibular dos temnospôndilos sofreu bastante modificação durante o processo evolutivo. Por ser um grupo originário durante o Carbonífero, com uma distribuição temporal e geográfica abrangente, foi bastante influenciado por mudanças no ambiente, tanto climáticas quanto geológicas, influenciando nas diferentes especializações anatômicas do grupo (Schoch

2014). Um exemplo pode ser visto na variação do tamanho da sínfise mandibular dentro do grupo (que reflete o tamanho e formato do rostro, evidenciando possíveis nichos ecológicos desempenhados pelos táxons), como pode ser visto em *Australerpeton cosgriffi*, cuja sínfise e rostro longos lembram superficialmente o crânio dos gaviais e alguns crocodilos que, por convergência evolutiva, provavelmente ocupavam um nicho que atualmente é explorado por estes crocodiliformes (Eltink & Langer 2014).

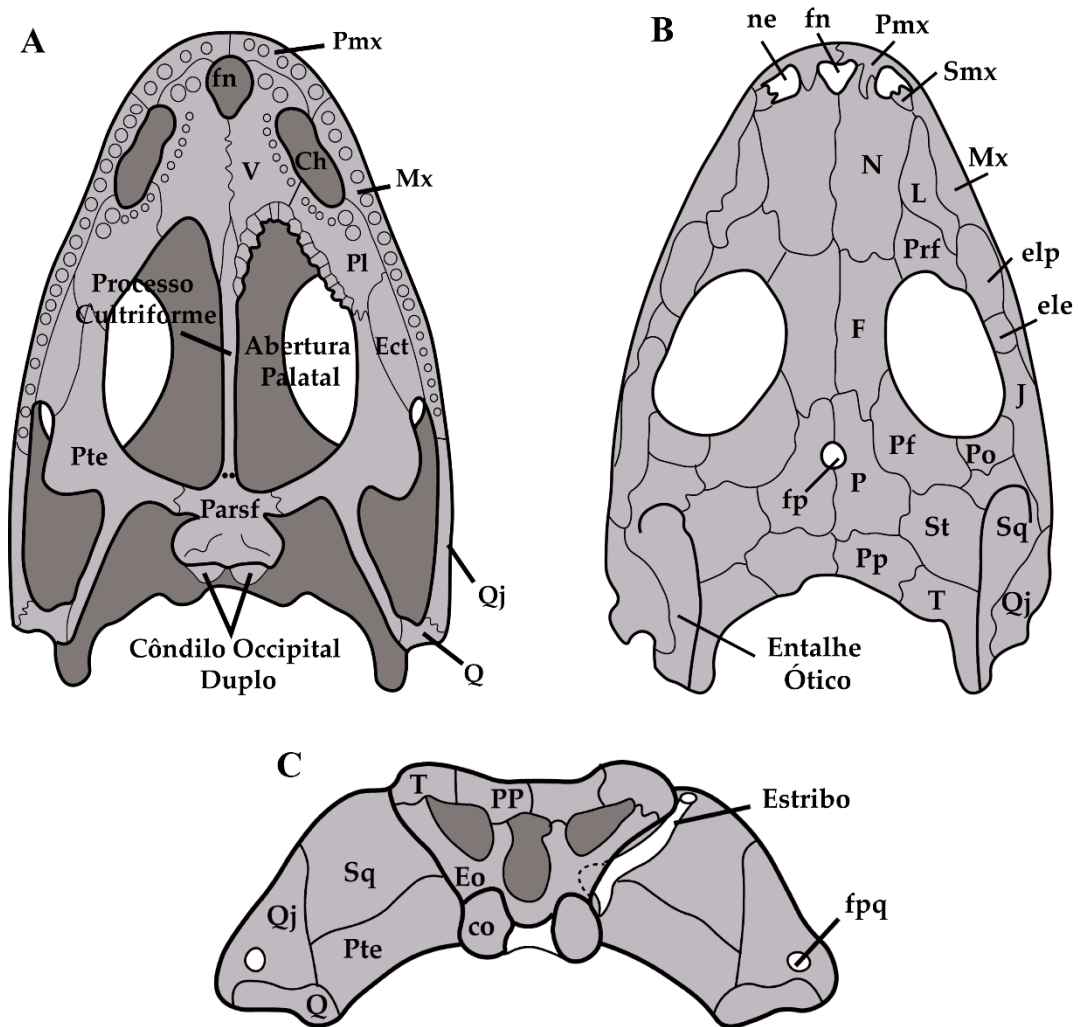


Fig 2. Vista ventral e dorsal do crânio de *Cacops* (Dissorophoidea) (A e B) e vista occipital do crânio de *Sclerocephalus* (Stereospondylomorpha), ilustrando as principais características morfo-anatômicas cranianas que unem o grupo Temnospondyli, em especial a dupla articulação occipital, compartilhada com anfíbios atuais. **Ch.** coana; **co.** cômulo occipital; **Ect.** ectopterigóide; **ele.** exposição lateral do ectopterigóide; **elp.** exposição lateral do palatino; **Eo.** exoccipital; **F.** frontal; **fn.** fontanela; **fp.** foramen pineal; **fpq.** foramen paraquadrado; **J.** jugal; **L.** lacrimal; **Mx.** maxila; **N.** nasal; **ne.** narina externa; **P.** parietal; **Pf.** pós-frontal; **Pl.** palatino; **Pmx.** prémaxila; **Po.** pós-orbital; **Prf.** pré-frontal; **Pp.** pós-parietal; **Pte.** pterigóide; **Q.**

quadrado; **Qj.** *quadradojugal*; **Smx.** *septomaxila*; **Sq.** *esquamosal*; **St.** *supratemporal*; **T.** *tabular*. Adaptado de Schoch & Witzmann (2009) e Schoch (2014).

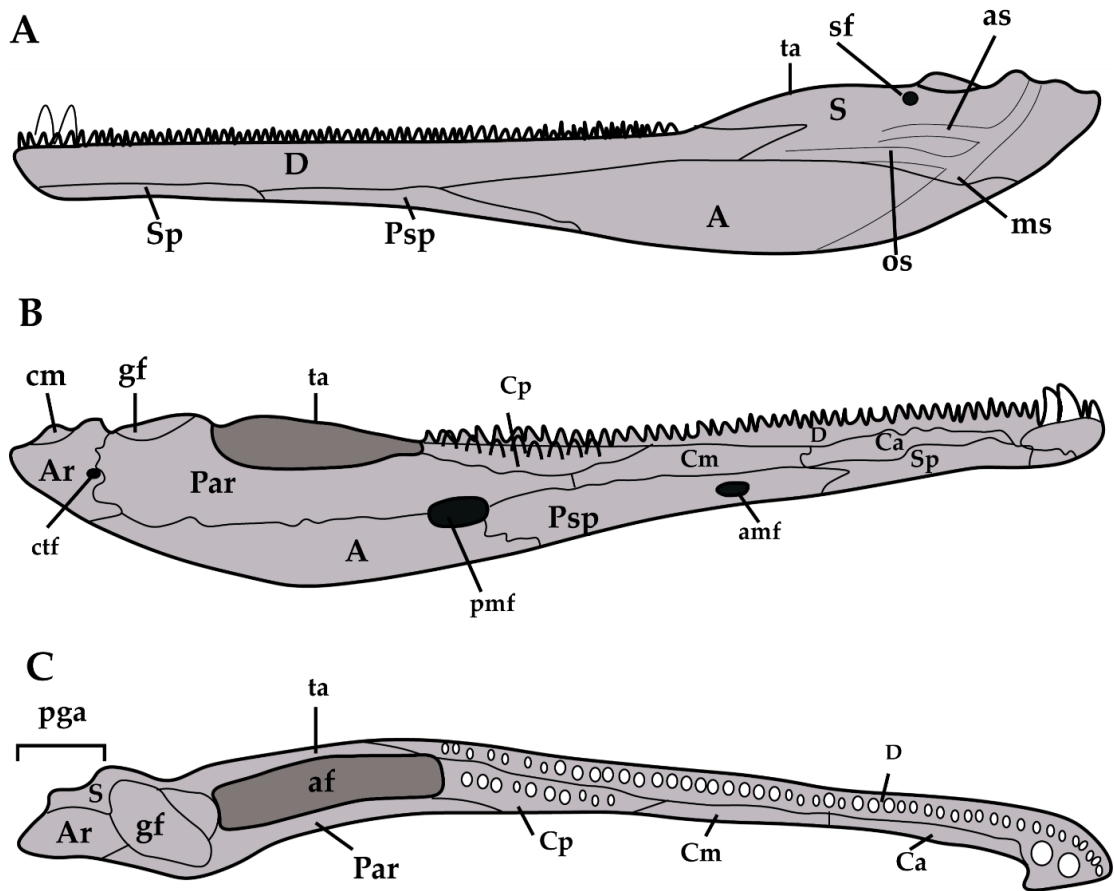


Fig 3. Vistas labial (A), lingual (B) e dorsal (C) da mandíbula de *Benthosuchus sushkini*. **A.** *angular*; **af.** *fossa adutora*; **amf.** *forâmen meckeliano anterior*; **Ar.** *articular*; **as.** *sulco acessório*; **Ca.** *coronóide anterior*; **Cm.** *crista muscularis*; **Cp.** *coronóide posterior*; **ctf.** *forâmen corda timpânico*; **D.** *dentário*; **gf.** *fossa glenóide*; **mc.** *coronóide médio*; **ms.** *sulco mandibular*; **os.** *sulco oral*; **Par.** *pré-articular*; **pga.** *área pós glenóide*; **pmf.** *forâmen meckeliano posterior*; **Psp.** *pós-esplénial*; **S.** *surangular*; **Sp.** *esplénial*; **st.** *Forâmen surangular*; **ta.** *torus arcuatus*. Adaptado de Damiani (2001).

Outra característica mandibular importante e geralmente encontrada na maioria dos temnospôndilos mais derivados, é a presença de um conjunto de sulcos (mandibular, oral e acessório) localizado na porção labial do surangular (Jupp & Warren 1986). A área pós glenóide (pga) é considerada diagnóstica entre os grupos de temnospôndilos mais derivados. Os táxons mais primitivos carecem desta estrutura e segundo Jupp & Warren (1986) esta estrutura pode ser dividida em pga Tipo I (Fig. 4) e pga Tipo II (Fig. 5). As principais diferenças entre estes

dois tipos de pga são a quantidade de ossos que compõem a estrutura e a relação de comprimento e largura (Jupp & Warren 1986), sendo o Tipo II estruturalmente mais complexo.

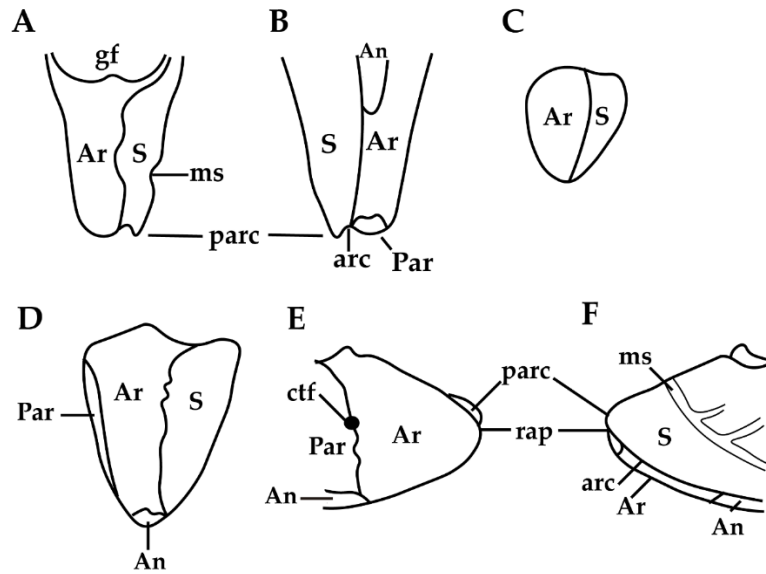


Fig 4. Ilustração das características gerais da área pós glenóide (pga) **Tipo I**. Vista dorsal (A), vista ventral (B), corte transversal (C), vista posterior (D), vista lingual (E) e vista labial (F). **An.** angular; **Ar.** articular; **arc.** cavidade arcadiana; **ctf.** forâmên corda timpânico; **gf.** fossa glenóide; **ms.** sulco mandibular; **Par.** pré-articular; **parc.** processo arcadiano; **rap.** processo retroarticular; **S.** surangular. Adaptado de Jupp & Warren (1986).

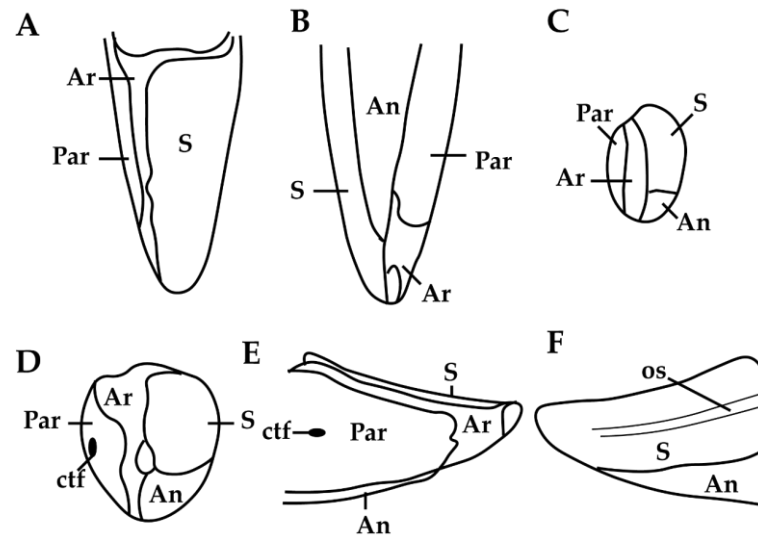


Fig 5. Ilustração das características gerais da área pós glenóide (pga) **Tipo II**. Vista dorsal (A), vista ventral (B), corte transversal (C), vista posterior (D), vista lingual (E) e vista labial (F).

An. angular; **Ar.** articular; **ctf.** forâmen corda timpânico; **os.** sulco oral; **Par.** pré-articular; **S.** surangular. Adaptado de Jupp & Warren (1986).

A estrutura do pós-crânio segue o mesmo padrão da maioria dos tetrápodes, os quais apresentam uma cintura escapular (Fig. 6A) e uma cintura pélvica (Fig. 6B). A cintura escapular é separada do crânio devido à perda dos ossos operculares (característica encontrada nos peixes ósseos) e cujos elementos têm origem tanto dérmica (cleitrum, clavícula e interclavícula) quanto endocondral (escápula e coracóide) (Schoch 2014). Estes dois últimos elementos podem ser ossificados juntos (escapulocoracóide) e realizam a articulação com o úmero. A cintura pélvica é trirradiada e formada por elementos ósseos de origem endocondral: o ílio, localizado dorsalmente e conectado com a coluna vertebral, ísquio e púbis (Schoch 2014). Os membros superiores e inferiores possuem uma estrutura básica semelhante. Os ossos longos úmero e fêmur articulam com a cintura escapular e pélvica, respectivamente, seguidos por um par de ossos longos (ulna e rádio nos membros anteriores e fíbula e tíbia nos membros posteriores). Diferente dos outros tetrápodes primitivos, os temnospôndilos possuem quatro dígitos nas mãos e cinco dígitos nos pés (Schoch 2014).

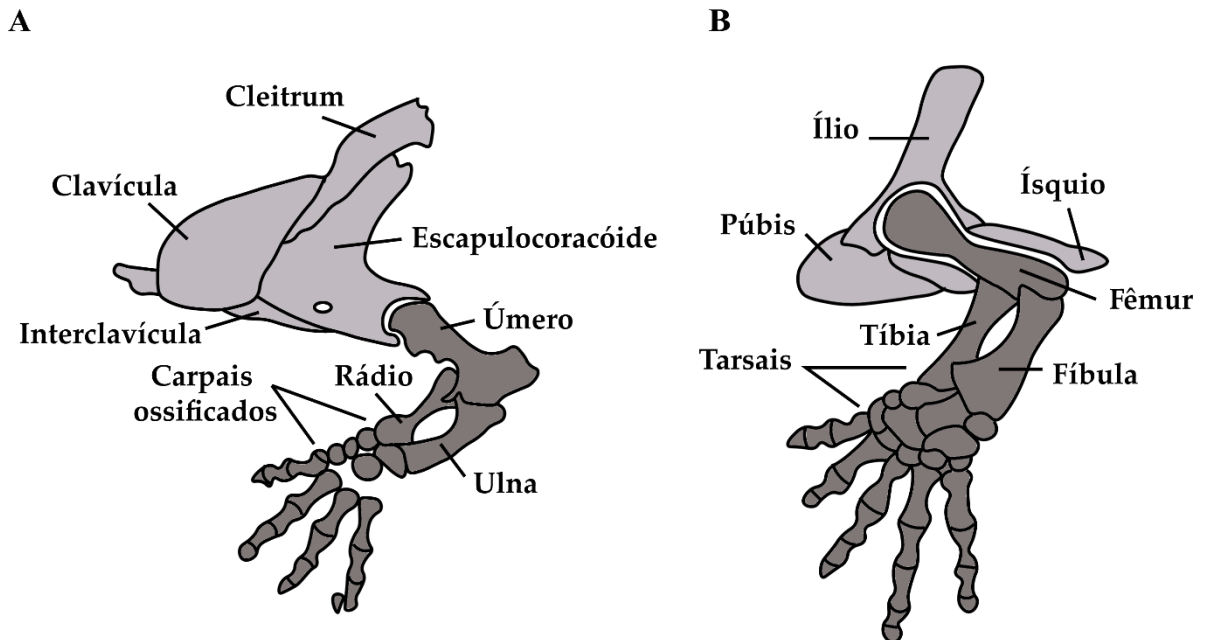


Fig 6. Representação da cintura escapular (A) e cintura pélvica (B) do temnospôndilo *Sclerocephalus*. Adaptado de Schoch (2014).

Existe uma nítida variação no padrão vertebral entre os tetrápodes basais, onde as espécies mais primitivas possuem vértebras cujo elemento dominante é o intercentro (padrão

raquírome; =intercentro-dominante; e.g Romer 1966). Por outro lado, no grupo Reptiliomorpha, o pleurocentro é o elemento dominante, tendendo ao desaparecimento em Amniota e dando origem ao centro vertebral de padrão esquizomero (=pleurocentro-dominante; e.g. Benton 2015).

O padrão vertebral dos temnospôndilos é predominantemente raquírome, uma vez que o intercentro sempre tem o papel estrutural mais importante. No entanto, no processo evolutivo do grupo surgiram variações deste padrão. Nas espécies mais basais (e.g. Eriopidae Fig. 7A) o intercentro está situado ventralmente, em formato de cunha em vista lateral com a presença de dois pleurocentros entre o arco neural e o intercentro. Neste último caso, existe efetivamente uma situação de co-dominância entre pleuro- e intercentro, mas o intercentro permanece como o elemento estrutural central. Já nos temnospôndilos do Permiano Superior e Triássico, os pleurocentros são reduzidos ou ausentes e o intercentro localiza-se abaixo do arco neural, formando um anel ao redor da notocorda (Fig. 7B; Romer 1966), sendo que estes efetivamente retomam o padrão raquírome primitivo, encontrado em tetrápodes basais e peixes. Os anfíbios atuais (Lissamphibia) apresentam apenas um centro, sem qualquer indicação de homologia com pleuro- ou intercentro (apenas pelas filogenias, supõe-se tratar de um intercentro).

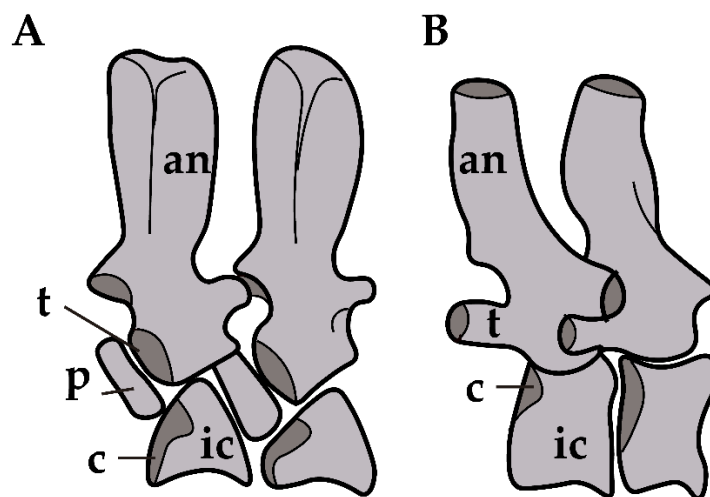


Fig 7. Tipos de vértebras em temnospôndilos, em vista lateral direita. (A) Vértebra raquírome, encontrada em espécies primitivas (e.g. *Eryops*) e (B) vértebra com intercentro plenamente dominante, comum em espécies derivadas (e.g. *Mastodonsaurus*). Notar que, em ambos os casos, existe dominância do intercênro e o pleurocentro representa uma estrutura acessória. **an.**

arco neural; c. centro; ic. intercentro; p. pleurocentro; t. área de articulação para o tubérculo da costela. Adaptado de Romer (1966).

RELAÇÕES FILOGENÉTICAS DOS TEMNOSPONDYLI

O primeiro trabalho envolvendo a classificação e as relações evolutivas dos temnospôndilos foi realizado por Zittel (1888), o qual cunhou o nome do grupo (derivado do grego *temnein* = cortar e *spondylos* = vértebra; *apud* Schoch 2013). Trabalhos posteriores ao de Zittel (1888) foram realizados, no entanto contemplando poucos grupos, visto que não utilizavam análises computacionais, como no caso dos trabalhos de Romer (1947), Boy (1990, 1993), Warren & Black (1985) e Milner (1990) (Yates & Warren 2000). A primeira análise filogenética computacional mais inclusiva foi realizada por Yates e Warren (2000), a qual resultou no suporte da monofilia de Stereospondyli, corroborando a visão tradicional de Romer (1947), e onde outros novos táxons foram estabelecidos (e.g. Dvinosauria, Stereospondylomorpha, Capitosauria e Trematosauria). Um dos mais recentes trabalhos sobre filogenia de temnospôndilos, também bastante inclusivo, é o de Schoch (2013; Fig. 8). Neste trabalho, Schoch define o ramo Capitosauria incluindo Capitosauroida (como definido em Schoch 2008 ou Mastodonsauroida *sensu* Damiani (2001b)), no entanto incluindo também os táxons *Edingerella*, *Benthosuchus*, *Wetlugasaurus*, e *Watsonisuchus*, que até então eram suportados dentro Trematosauria (e.g. Schoch & Milner 2000). Além do suporte à alguns agrupamentos propostos em estudos prévios como a monofilia de Stereospondyli por exemplo, Schoch (2013) reuniu evidências para dois novos táxons: Eryopiformes, que agrupa Eryopidae e Stereospondylomorpha e Eustemnospondyli que reúne, em uma monofilia, todos os táxons exceto Edopoidea.

A filogenia de Temnospondyli ainda é bastante discutida. Alguns trabalhos trazem evidências de que os lissanfíbios compartilham um ancestral comum com os temnospôndilos (e.g. Gardner, 2001; Ruta *et al.* 2003ab; Schoch & Milner 2004; Ruta & Coates 2007, Coates *et al.* 2008; Sigurdsen & Green 2011; Madin & Anderson 2012; Schoch 2013), corroboradas neste estudo. Outros autores, no entanto, defendem a hipótese de que os lissanfíbios tiveram origem a partir dos leospôndilos (eg. Marjanović & Laurin 2013). Aqui seguiremos a hipótese dos temnospôndilos como grupo de origem dos lissanfíbios, como ilustrado por Benton (2014), o qual usa o termo Batrachomorpha para indicar um clado monofilético que inclui os temnospôndilos e os anfíbios atuais.

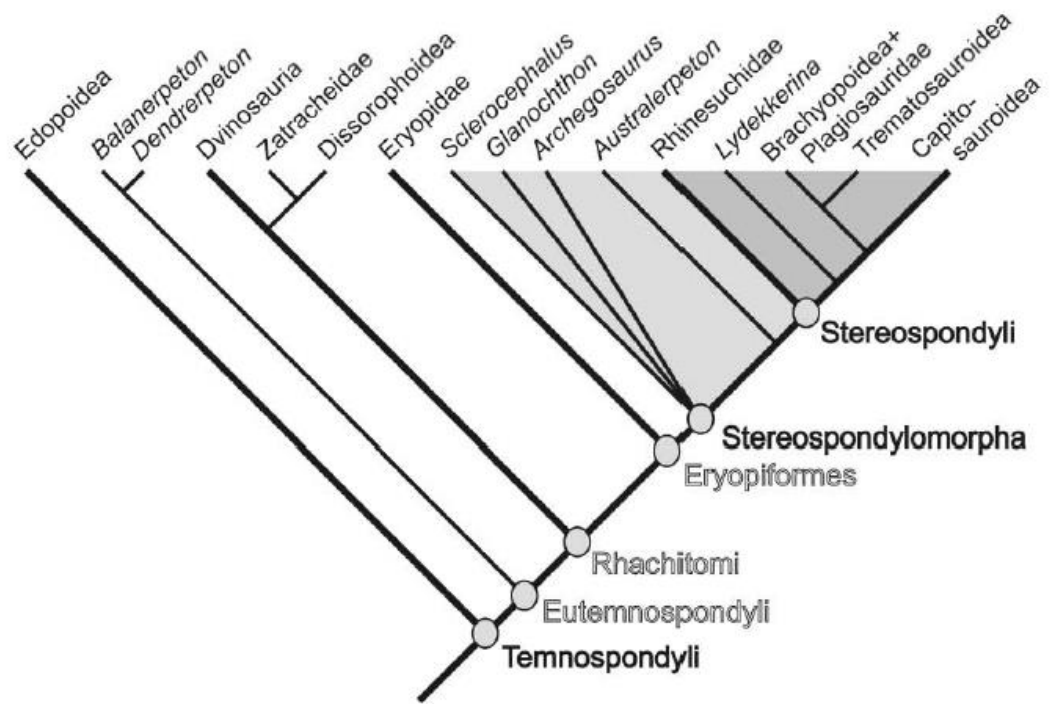


Fig 8. Relações evolutivas de Temnospondyli, como propostas por Schoch (2013).

GEOLOGIA DA ÁREA DE ESTUDO

O exemplar MCP 4275 PV corresponde a um material razoavelmente bem preservado, extremamente friável e fragmentado em porções mediana-anterior e posterior de uma mandíbula de temnospôndilo, proveniente de sedimentos permianos (Formação Rio do Rasto) da Bacia do Paraná. A Bacia do Paraná (Fig. 9) está localizada na América do Sul, com uma superfície de aproximadamente 1.700.000 Km². É uma bacia originada dentro de áreas continentais estáveis (intracratônica), ocupando parte do Brasil, Uruguai, Paraguai e Argentina (Milani *et al.* 2007; Holz *et al.* 2010). O acúmulo de sedimentos e a evolução da Bacia do Paraná teve início entre os períodos Ordoviciano–Siluriano e se estendeu até o Cretáceo, contabilizando aproximadamente 400 milhões de anos de sedimentação (Milani & Ramos, 1998; Milani *et al.* 2007; Guerra-Sommer *et al.* 2008; Holz *et al.* 2010). Milani (1997) reconheceu seis supersequências (Fig. 10) resultantes de eventos eustáticos e tectônicos no registro estratigráfico da Bacia do Paraná, que representam a evolução do Oeste do subcontinente Gondwana: Rio Ivaí (Ordoviciano–Siluriano), Paraná (Devoniano), Gondwana I (Carbonífero–Eotriássico), Gondwana II (Meso–Neotriássico), Gondwana III (Neojurássico–Eocretáceo) e Bauru (Neocretáceo). O estrato Permiano, de especial interesse neste estudo, está incluso na Supersequência Gondwana I e abrange os grupos Itararé, Guatá e Passa Dois (Milani *et al.* 2007, Dias-da-Silva 2012).



Fig 9. Representação da área da Bacia sedimentar do Paraná em território brasileiro.

Adaptado de Strapasson *et al.* (2015)

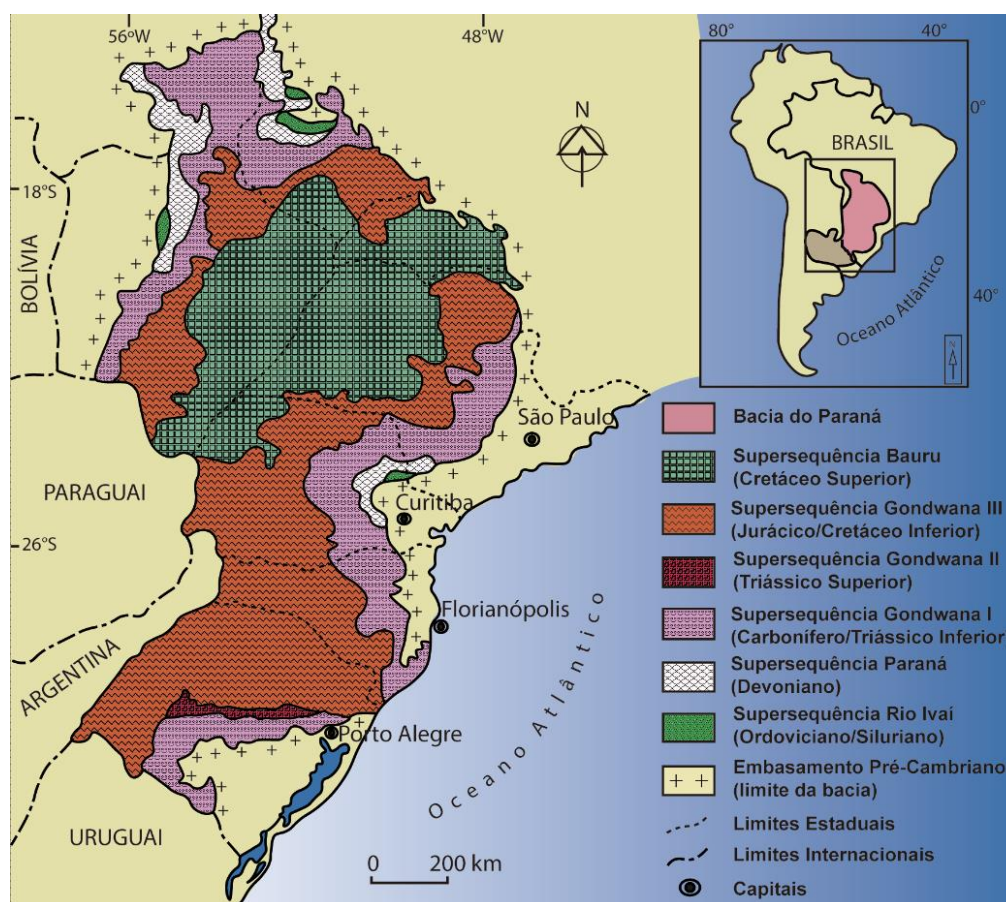


Fig 10. Mapa geológico da Bacia do Paraná ilustrando as seis seqüências sedimentares (Ordoviciano–Cretáceo) reconhecidas por Milani (1997). Adaptado de Guerra-Sommer *et al.* (2008).

A Formação Rio do Rasto (Fig.11) se estende pelos Estados de São Paulo, Paraná, Santa Catarina e Rio Grande do Sul (Holz *et al.* 2010) e está inserida no topo do Grupo Passa Dois fazendo contato transicional com a Formação Teresina na base e Formação Pirambóia acima (Milani *et al.* 2007; Dias-da-Silva 2012). Com idade Guadalupana/Lonpingiana (Wordiano–Wuchiapingiano; Holz *et al.* 2010), a Formação Rio do Rasto está incluída em um contexto geológico de continentalização da região que reflete o fim de um sistema deposicional gradual que ocorreu durante este período (Lavina, 1991). Esta Formação pode ser subdividida nos Membros Serrinha e Morro Pelado, cujas características estratigráficas mostram um processo gradual tendendo à aridez total do ambiente no final do Permiano (Milani *et al.* 2007). O Membro Serrinha está localizado na base da Formação e representa um período mais antigo de sedimentação, composto por lamitos e siltitos intercalados por camadas de arenitos finos com coloração esverdeados a acinzentados, evidenciando um ambiente de mar epicontinental raso

sem conexão persistente com o oceano. No entanto, observa-se o registro da ocorrência de grandes ondas, provavelmente provocadas por tempestades e furacões, evidenciada pelo característico remodelamento e acomodamento dos sedimentos observado de modo intermitente nessa unidade geológica. Já o Membro Morro Pelado, de onde provém o material de estudo do presente trabalho, está localizado no topo da Formação, intercalando camadas de pelitos com arenitos tabulares e lenticulares de estratos amarelo, roxo e vermelho, representando um sistema de deposição característico de um ambiente recoberto por conjuntos de lagos rasos, alimentados por deltas e tendendo à aridez total no final do Período (Milani *et al.* 2007; Warren *et al.* 2008; Dias-da-Silva 2012).

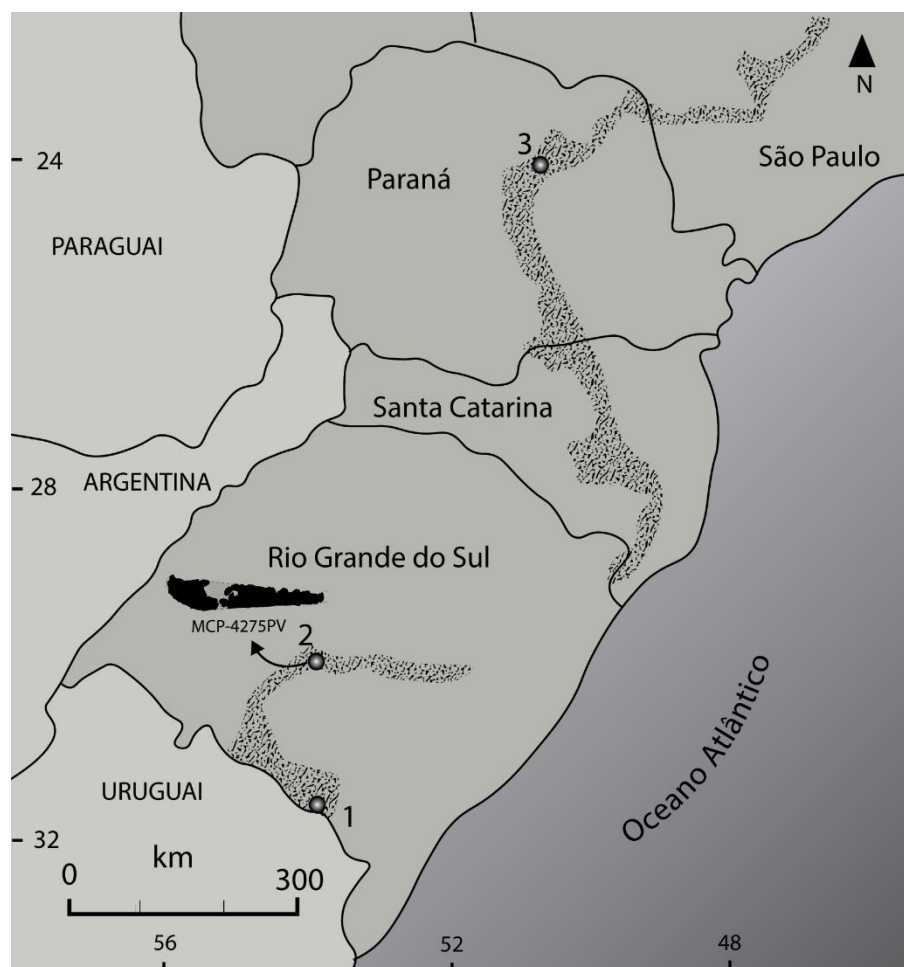


Fig 11. Mapa mostrando a localização da Formação Rio do Rasto e as localidades das faunas locais: 1, Aceguá; 2, Localidade Fazenda Fagundes (Boos 2015); 3, Serra do Cadeado. Modificado de Dias-da-Silva (2012).

O material do Presente trabalho é proveniente da Formação Rio do Rasto, Membro Morro Pelado, de um afloramento designado como Fazenda Fagundes por Boos (2015), originalmente

conhecido como Posto Queimado (sensu Malabarba *et al.* 2003; = Fazenda Fagundes Boos 2015), situado nos arredores do município de São Gabriel, em uma propriedade particular na região de Timbaúva, Estado do Rio Grande do Sul, Brasil. Os sedimentos estão expostos através de um sistema de ravinas e são compostos por lamitos e siltitos vermelhos, evidenciando a oxigenação do ambiente e a baixa energia de movimentação dos lagos, com conglomerados intercalados, indicando que estes lagos eram abastecidos por deltas de alta energia (Langer 2000). Além disso, esta localidade pode ter uma paleofauna que sugere uma potencial correlação com a Associação faunística Ocher e Isheevoo da Plataforma Russa e com a Zona de Assembleia *Eodicynodon* e *Tapinocephalus* na Bacia do Karoo na África, indicando uma idade Mesopermiana (Langer 2000; Malabarba *et al.* 2003). No entanto, segundo Boos (2015), são necessários mais dados para poder estabelecer uma correlação mais confiante entre estas unidades. A idade dos sedimentos de Posto Queimado é considerada como sendo Wordiano–Capitaniano (Guadalupiano), de acordo com Langer (2000), Malabarba *et al.* (2003) e Pacheco *et al.* (2016).

CAPÍTULO 1: A new Permian temnospondyl from South America, Brazil, shedding light on the origin of Capitosauria (Temnospondyli: Stereospondyli)

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1 **A new Permian temnospondyl from South America, Brazil, shedding light on the origin of**
2 **Capitosauria (Temnospondyli: Stereospondyli)**

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13

14 **Abstract**

15 A new Permian temnospondyl is described from Brazil (South America). The material MCP-
16 4275PV sheds light on the origin and radiation of the Capitosauria, an important evolutionary
17 branch of Stereospondyli. It consists of two parts of a right mandible without their ends.
18 Roughly ~50 cm long, the hemimandible likely pertain to a large-sized animal, larger than most
19 of the Brazilian temnospondyls. Morphological and anatomical features were crucial to the
20 identification of the specimen as a capitosaur, such as: hamate process; teeth morphology;
21 distribution of ornamentation, foramina and sulci at the lateral surface of the distal end of the
22 mandible. A phylogenetic analysis (TNT, PAUP; 76 terminals, 271 characters) corroborates
23 that MCP-4275PV is a derived Capitosauria, positioned close to *Parotosuchus*. This new
24 temnospondyl is one of the earliest representative among capitosaurs, whose oldest record is
25 otherwise limited to the Triassic. MCP-4275PV is currently the earliest record of a
26 Capitosauria, placing this group firmly within the Mid–Late Permian strata.

27 Key words: Capitosauria; Gondwana, Rio do Rasto Formation, Paraná Basin.

28

29 **Introduction**

30 Temnospondyli is a group of basal tetrapods, also referred to as primitive amphibians.
31 Main features shared by the group include: wide palatal openings (interpterygoid vacuities);
32 skull flat and braincase wide; double-headed occiput, wide vomers, short ribs and rod-like
33 stapes, as well as the typical labyrinthodont dentition (Schoch 2014). This group has a temporal
34 distribution of roughly 220 millions of years (Early Carboniferous–Early Cretaceous) and
35 comprises about 300 species (Schoch 2013). The oldest representative – *Balanerpeton woodi*
36 – was collected from Early Carboniferous (Visean) sediments at Scotland (Milner & Sequeira
37 1993 *apud* Schoch 2013), while the most recent record is an Australian species – *Koolasuchus*
38 *cleelandi* (Warren *et al.* 1997), of Early Cretaceous age (Aptian). It has been proposed that the
39 temnospondyl is a paraphyletic group that shares a common ancestor with extant amphibians
40 (Lissamphibia) (e.g., see Milner 1990; Gardner 2001; Schoch & Milner 2004; Ruta & Coates
41 2007; Maddin & Anderson 2012). Accordingly, the temnospondyl distribution would
42 encompass lissamphibians, therefore extending the total distribution of this group to about 355
43 millions of years (Schoch 2013). Regardless of putative relationship of extant forms, the “core”
44 Temnospondyli diversity ranges from the Late Carboniferous to the Triassic. The dominant
45 Triassic temnospondyls were the Stereospondyli, and among these, are the diverse
46 Capitosauria.

47 So far, nine species of Temnospondyli were described from Brazil (Fig. 1): *Bageherpeton*
48 *longignathus*, *Australerpeton cosgriffi*, *Parapytanga catarinenses* and *Konzhukovia*
49 *sangabrielensis*, from Rio do Rasto Formation (respectively, Dias & Barbarena 2001;
50 Barbarena 1998; Strapasson *et al.* 2015; Pacheco *et al.* 2016). Temnospondyl from Pedra do
51 Fogo Formation include *Prionosuchus plummeri* (the first Brazilian representative of the
52 group), *Timonya anneae* and the Trimerorhachidae *Procuhy nazariensis*, from Pedra do Fogo
53 Formation (see Price 1948; Cisneros *et al.* 2015). Two taxa come from Sanga do Cabral

54 Formation: *Sangaia lavinai* and *Tomeia witecki* (see Dias-da-Silva *et al.* 2006; Eltink *et al.*
55 2016).

56 Capitosauria *sensu* Schoch (2013) is widely distributed in the Mesozoic Era (Fig. 2), with
57 representative taxa over the Triassic (Schoch & Milner 2000; Damiani *et al.* 2001). These
58 massive tetrapods had a body length of 2–9 m, *Mastodonsaurus giganteus* being the largest
59 representative of the group (Schoch 2008). Capitosauroida are the most abundant tetrapods
60 within the Triassic deposits of Pangaea and, consequently, provide potential data for
61 biostratigraphic correlations (Damiani 1999a; Piñeiro *et al.* 2007). Moreover, the group has a
62 worldwide distribution, with representatives in South African deposits (e.g. Damiani *et al.*
63 2001), Antarctica (Sidor *et al.* 2008), Australia (Warren 1991 *apud* Piñeiro *et al.* 2007), India
64 (Mukherjee & Sengupta 1998), Algeria (Dahoumane *et al.* 2016), Japan (Nakajima & Schoch
65 2011), as well as Germany and the European Russian Platform. Therefore, the capitosauroid
66 geological record is known both from Laurasian and Gondwanan territories (Damiani 1999a). In
67 South America, Piñeiro *et al.* (2007) showed three specimens (mandibular fragments) related
68 with Capitosauroida in Buena Vista Formation (Permo–Triassic deposits), which was the first
69 and oldest capitosaur so far recorded to South America. More recently, Eltink *et al.* (2016),
70 report a new capitosauroid from South Brazil Lower Triassic deposits (Sanga do Cabral
71 Formation), preserving parts of the skull, right mandible and some small fragments.

72 Key characters of the Capitosauroida, which can be considered as synapomorphies of
73 the group, were listed by Schoch & Milner (2000): (i) transverse row of teeth posterior to
74 aperture praemaxillaris, (ii) quadrate trochlea extended laterally and strictly transverse ; (iii)
75 preorbital region very flat, without lateral slope; (iv) aperture premaxillaris embedded in
76 depression whose posterior margin is straightly transverse (this also applies for genera with
77 medially divided aperture; (v) palatine ramus of pterygoid stout in large specimens.

78 The evolution and radiation of Temnospondyli is a much-debated subject. Zittel (1888)
79 implemented the first work related with temnospondyl evolution. The principal subsequent
80 works were made by Romer (1947), Boy (1993), Warren & Black (1985) e Milner (1990). Yates
81 & Warren (2000) made the first computational analysis, which comprised a great number of
82 taxa and data, resulting in the establishment of the Dvinosauria, Stereospondylomorpha,
83 Capitosauria, Trematosauria, Euskelia and Limnarchia (these last two being further discussed
84 in later analyzes e.g. Schoch (2013)) and providing support for the idea of the Stereospondyli
85 monophyly. The evolutive history of Capitosauria was discussed in a range of works, Schoch
86 (2000, 2008) and Damiani (2001a) made the most inclusive analysis attempt to investigate the
87 Capitosauria affinities. Other not as inclusive works discussed a wide range of problems and
88 data (Steyer 2003; Liu & Wang 2005; Stayton & Ruta 2006; Schoch *et al.* 2007; Ruta *et al.*
89 2007; Maganuco *et al.* 2009; Fortuny *et al.* 2011). Schoch (2013) is one of the most inclusive
90 analysis, combining the best-know taxa from Carboniferous–Cretaceous. In this work,
91 Capitosauria group was defined including Capitosauroida (sensu Shoch 2008; =
92 Mastodonsauroida sensu Damiani 2001a) and also *Edingerella*, *Benthosuchus*,
93 *Wetlugasaurus*, e *Watsonisuchus*, which until then were seen as part of the Trematosauria group
94 (e.g. Schoch & Milner 2000). In addition, his results supports some groups established by
95 previous works, like the Stereospondyli, for instance. Schoch (2013) brought evidence for two
96 new taxa: Eryopiformes (Eryopidae plus Stereopondylomorpha) and Eutemnospondyli
97 (assembles all temnospondyl except Edopoidea).

98 Here we redescribe a temnospondyl material for the Rio do Rasto Formation, represented
99 by a hemimandible (MCP-4275PV), preliminarily presented by Malabarba *et al.* (2003). This
100 material was collected at the Fazenda Fagundes outcrop (*sensu* Boos 2015; = Posto Queimado
101 *sensu* Malabarba et al. 2003), located in Rio Grande do Sul State, Southern Brazil. Malabarba
102 *et al.* (2003) presented a preliminary description of the anterior part of the specimen.

103 Notwithstanding this preview description, the specimen was not taxonomically classified and
104 the posterior and most informative part remained undescribed. Here we describe the whole
105 specimen in detail, build morpho-anatomical comparisons with other Temnospondyli and use
106 a phylogenetic analysis to recognize MCP-4275PV as a derived Capitosauria. MCP-4275PV
107 as a derived Capitosauria.

108

109 **Materials and Methods**

110 **Geological settings**

111 The Paraná Basin (Fig. 3) is located in South America, and encompasses parts of Brazil,
112 Uruguay, Paraguay and Argentina (Milani *et al.* 2007; Holz *et al.* 2010). This intracratonic
113 basin has a surface of roughly 1,700,000 km² and exhibit a set of six sedimentary
114 supersequences of second order (eustatic and tectonic events) that emphasizes the West
115 Gondwanan evolution (Ordovician–Late Cretaceous) (Milani & Ramos, 1998; Milani *et al.*
116 2007; Guerra-Sommer *et al.* 2008; Holz *et al.* 2010). The Permian strata is located at Gondwana
117 I Supersequence (Carboniferous–Triassic) and comprises of groups Itararé, Guatá and Passa
118 Dois (Milani *et al.* 2007, Dias-da-Silva 2012).

119 The Rio do Rasto Formation (Fig. 4) is placed at the top of the Passa Dois Group and
120 contacts the Teresina and Pirambóia formation respectively at the base and the top (Milani *et*
121 *al.* 2007; Dias-da-Silva 2012). Its outcrop system extends through São Paulo, Paraná, Santa
122 Catarina and Rio Grande do Sul states (Holz *et al.* 2010). The Rio do Rasto Formation has a
123 Wordian–Wuchiapingian (Guadalupian/Lopingian) age (Holz *et al.* 2010), reflecting the end of
124 a gradual depositional system and the continentalization of the region in this period (Lavina
125 1991). Such geochronological and stratigraphic information is attested by a plentiful of
126 conchostracean fossils found at Rio do Rasto Formation (Ferreira-Oliveira & Hohn 2009). The
127 Formation is divided in two units: (i) Serrinha Member, located at the base, with earliest

128 sediments composed of green and grey sandstones; and (ii) Morro Pelado Member, placed in
129 the uppermost of the sedimentary sequence, featured by interspersing layers of pelites with
130 tabular and lenticular sandstones of yellow, purple and red strata (Milani *et al.* 2007; Warren *et*
131 *al.* 2008; Dias-da-Silva 2012).

132 Specimen MCP-4275PV comes from Fazenda Fagundes outcrop (=Posto Queimado in
133 Malabarba *et al.* 2003) is part of the Morro Pelado Member and is located in the municipality
134 of São Gabriel, Rio Grande do Sul State, Southern Brazil (30° 01' S, 54° 09' W). The sediments
135 are exposed through a system of ravines, and are composed of red laminated mudstones,
136 emphasizing an oxidizing ambient of low-energy lakes interleaved with conglomerate,
137 translating into occasional high-energy sedimentary flows to this shallow lacustrine system
138 (Langer 2000). Moreover, this site has a paleofauna that suggest a potential correlation with the
139 Ocher and Ishevo Faunistic Association at Russian Platform and with the *Eodicynodon* and
140 *Tapinocephalus* Assemblage Zone in the Karoo Basin (South Africa). Accordingly, the site has
141 a Wordian–Capitanian (Guadalupian) age (Langer 2000; Malabarba *et al.* 2003; Pacheco *et al.*
142 2016). MCP-4275PV is therefore regarded as Wordian–Capitanian.

143 **Institution Abbreviation:** AMNH, American Museum of Natural History, New York, NY;
144 MCP-PUCRS, Museu de Ciências e Tecnologia, PUCRS, Porto Alegre, Brazil; PUCRS,
145 Pontifícia Universidade do Rio Grande do Sul, Porto Alegre, Brazil; UFRGS, Universidade
146 Federal do Rio Grande do Sul, Porto Alegre, Brazil; UFSM, Universidade Federal de Santa
147 Maria, Rio Grande do Sul, Brazil.

148

149 **Systematic Palaeontology**

150 **TETRAPODA Goodrich, 1930**

151 **TEMNOSPONDYLI Zittel, 1887–1890**

152 **STEREOSPONDYLOMORPHA Yates and Warren, 2000**

153 **STEREOSPONDYLI Fraas, 1889**

154 **CAPITOSAURIA Schoch, 2013**

155 The specimen MCP-4275PV is housed at the Museu de Ciências e Tecnologia da
156 PUCRS, Porto Alegre, Rio Grande do Sul State. The material was previously prepared, however
157 it needed to remove the sediment embedded in the specimen. For anatomic comparisons, some
158 specimens were first-hand examined. Data on other taxa is taken both from the original matrix
159 (Schoch 2013) and bibliography. The anatomical photographs were made with the Nikon DRLS
160 D-40 and Fujifilm FinePix HS25EXR Digital Camera.

161

162 **Description and comparisons**

163 **General characteristics and preservation:** The material MCP-4275PV (Figs. 5–8) represents
164 the right ramus of a hemimandible of about 500 mm long, which is divided in two parts due a
165 median fracture (taphonomic), 330 mm (anterior portion) and 102 mm (posterior). The distal
166 end of the hemimandible was folded over during the preservation process so the posterior part
167 was laterally displaced and broken. Part of the ventral edge of the mandible remained in the
168 flexed position, so it is possible to connect both parts in this displaced arrangement.
169 Preservation is overall good, as fine details of the structure are fairly visible, but conservation
170 is difficult as the specimen itself is quite friable. The anteriormost tip of the mandible was also
171 damaged, but the nature of the break is such that a long symphysis (such as in *Prionosuchus*) is
172 unlikely. The glenoid cavity lay beyond the dorsal limit of the dentary bone, suggesting a
173 decreasing anteroposterior height pattern. It features a side compression in the fullest extent.
174 There is a damage in the posterior end, where it is positioned the post-glenoid area (PGA), and
175 in the anterior end, where lay the symphysis. The middle-posterior portion displays a break,
176 making it impossible to view the posterior coronoid and anterior limit of adductor cavity. There
177 is a break in the prearticular bone portion, impairing the posterior boundary with the articular

178 recognition. However, damage do not prevent the identification of some important
179 characteristics such the three sensorial sulci and surangular foramina. The majority of the bone
180 sutures could not be observed though, due to a superficial cracked aspect and sediment
181 aggregation. Since it is a fragile material and to avoid damage to the specimen, the full removal
182 of whole sediment was not possible (e.g. labial face of teeth crowns).

183 **Labial view:** In this view (Fig. 5), the hemimandible shows the dentary, splenial, post-splenial,
184 angular and surangular bones. The dentary displays typical temnospondyls amphibian
185 ornamentation, with elongated pits assembling horizontal grids extending across the bone.
186 Despite of the hard sutures identification, a ventral suture to the dentary is visible, limiting the
187 splenial, post-splenial and angular. The angular lies in hemimandible ventral edge. It sutures
188 posteriorly and dorsally with the surangular, but such sutures are not fully recognizable due to
189 preservation. The ornamentation on the angular is “fan-like” with elongated pits, yet shorter
190 than in the other bones, displaying an ossification center in their ventral edge. The surangular
191 is present from the posterior portion (Fig. 6), showing a suture antero-ventral with the angular,
192 antero-dorsal with the dentary and posterodorsal with the articular. There is a break in the
193 hemimandible posterior portion, which would be formed by surangular labially and articular
194 lingually. Although it is a seemingly small break, it can be inferred that there was some
195 extension of the PGA. The retroarticular process is composed by the surangular labially and is
196 “hook-like” arched, which the tip is anteriorly directed. It is notable the presence of a set of
197 sensorial sulci – accessory sulci, oral sulci and mandibular sulci – that begins in the posterior
198 portion of the surangular and is totally opened. The mandibular sulci is the most evident and
199 crosses the hemimandible from posterodorsal to antero-ventral part. The oral and mandibular
200 sulci extend beyond surangular while the accessory sulci is shorter. The surangular foramen
201 (typical for capitosaur: Damiani 1999b; Damiani *et al.* 2001a) is posteriorly located behind the
202 retroarticular process showing a well-developed and oblong shape. In the specimen MCP-

203 4275PV, a set of four foramina can be noted, however, they are located anteriorly to the wall
204 of retroarticular process – two of them are located in the accessory sulci and two in the oral
205 sulci. The dorsal part of the surangular composes the pre-glenoid area, named *torus arcuatus*,
206 which composes the dorsal edge of adductor cavity. Such edge is thick and straight, like some
207 capitosaur taxa (Damiani 1999b, 2001b). The surangular shows ornamentation in dorsal
208 portion, beyond the accessory sulci and in the posterior portion, however, the pits are
209 horizontally elongated and robust. The hemimandible shows an evident upward curvature
210 which inclination begins before the angular ossification center.

211 **Lingual view:** (Fig. 7) Anteriorly, the MCP-4275PV shows an apparently short symphysis.
212 However, it is not possible to claim the exact size of the symphysis since the anterior end is
213 broken. The dentary, splenial, post-splenial, angular, prearticular, anterior and middle coronoid
214 are present in this view. It is noted an anterior Meckelian foramen where lays the post-splenial.
215 Despite the damages, it is noted that this foramen has an anterior bone declivity, which the
216 anatomy features a foramen and not a simple opening by break. MCP-4275PV shows a well-
217 developed posterior Meckelian foramen, with length greater than its height, representing about
218 $\frac{1}{4}$ of the hemimandible size, but with shorter length than the adductor cavity. This foramen is
219 located close to the ventral base of the hemimandible, with the center laying anteriorly to the
220 adductor cavity edge. The anterior and middle coronoid do not have any type of dentition and
221 the posterior coronoid cannot be identified since there is an injury in this region. The
222 prearticular can be seen in lingual view. It is impossible to identify the ventral suture of the
223 prearticular and angular, however, the dorsal portion of the prearticular surrounds the lingual
224 edge of the adductor cavity and lingual edge of the glenoid cavity. Its height is not reaching the
225 dorsal portion of the hemimandible, just reaching about $\frac{1}{3}$ of the height. This bone shows a
226 break in the postero-ventral portion and is damaged in the posterodorsal region, and it is
227 impossible to identify its posterior edge with the articular. The articular composes the postero-

228 dorsal portion in lingual view. Despite the damages, it is noted the presence of an incomplete
229 hamate process, which the structure represents a prearticular process that is located in the
230 lingual lateral of the glenoid cavity.

231 **Dorsal view:** (Fig. 8) MCP-4275PV shows the anterior portion slightly arched lingually,
232 however this can be due to fossilization process. The dentary surrounds the major part of the
233 hemimandible in this view, where are inserts the labyrinthodont teeth. It is impossible to
234 identify the posterior coronoid and the surangular anterior edge that composes the adductor
235 cavity dorsal edge (*torus arcuatus*), which is dorsolaterally expanded. The glenoid cavity, in
236 “L” shape (due to the hamate process placed laterolingually), is composed by the articular. Such
237 anatomy is typical for capitosaur (Damiani 1999b). The hamate process acts as an extension
238 of the articular and its contact with the distal quadrate ramus of the pterygoid provides a strict
239 articulation with the skull, which optimizes the open-close mouth motion (Damini 2001 *apud*
240 Howie 1970). The glenoid cavity is well developed, measuring 14 mm by 14 mm. The hamate
241 process is not preserved, however it is possible to identify its break point. The dorsal suture
242 between articular and surangular cannot be seen. There is a break in the posterior PGA
243 extremity, what indicates that this structure was more extensive. The post-condilar process is
244 hook-like shaped and exceed the *torus arcuatus* and prearticular hamate process in height. This
245 hook-like structure is seen as like a triangle tip in dorsal view.

246 **Dentition:** The hemimandible has about 48 marginal labyrinthodont teeth, but the material is
247 broken in the portion before the adductor cavity, so, it is impossible to claim if there was some
248 tooth in this portion. The teeth tips are rounded and conic, they are anteroposteriorly flattened
249 (Fig. 9), typical of more derived temnospondyl (Damiani 1999b; Warren & Davey 1992). We
250 can find this characteristic in the Brazilian species *Konzhukovia sangabrielensis* (Permian) and
251 *Tomeia witecki* (Triassic) while the other Brazilian species *Australerpeton cosgriffii* and
252 *Bageherpeton longignathus* (both Permian) shows a rounded teeth pattern (e.g. Barberena 1998,

253 Dias & Barberena 2001). All the teeth show similar morphology, nonetheless, vary in size,
254 where are inserts the labyrinthodont teeth. According to Damiani (2001a), in capitosaur,
255 generally, there is a reduction in teeth size in both symphyseal and posterior mandible portion.
256 In MCP-4275PV it is notable the posterior size teeth reduction, while the symphyseal teeth are
257 not visible. The teeth are seen in lingual view mainly, where the teeth bases lay behind of the
258 dorsal extremity of dentary labial portion.

259

260 **Phylogenetic methods**

261 **Terminal taxa**

262 All terminals are represented and coded as specific taxa. The analyzed taxa, including the
263 references used here to codify the specimens in the additional characters, are given in appendix
264 1. This work was based in the dataset by Schoch (2013; originaly with 63 taxa). We choose to
265 maintain the *Greererpeton burkemorani* and *Sangaia lavinai* (a Brazilian species). Taxa added
266 were *Triadobatrachus massinoti* (the earliest known Lissamphibian; e.g. Ascarrunz *et al.* 2016),
267 *Eleutherodactylus orecesi* (a well know extant anuran; e.g. Guayasamin 2004), *Parotosuchus*
268 *haughtoni* (a well know Capitosauria), and the Brazilian taxa *Konzhukovia sangabrielensis*,
269 *Parapytanga catarinensis*, *Prionosuchus plummeri*, *Procuhy nazariensis*, *Timonya anneae* and
270 *Tomeia witecki*. *Acanthostega gunnari* was added as a new, less related, outgroup. As
271 relationships between non-reptilomorph basal tetrapods remain somehow disputed, the new
272 outgroup provides an undisputed external reference to the analysis. This creates the base for
273 new forthcoming analysis of basal tetrapods, to be presented elsewhere.

274 The final matrix encompasses 76 taxa, of those eight being Brazilian temnospondyl (in
275 addition to MCP-4275PV).

276

277 **Characters**

278 The original dataset (Schoch 2013; 212 characters) was expanded both because resolution
279 was needed for the new capitosaur and Brazilian taxa, but also because of the use of a new,
280 distantly related outgroup as well as lissamphibian taxa. These included three new characters,
281 as well as 17 characters taken from previous works. Given their relevance, they are listed below:

282

283 **33.** Frontal and Parietal. Both present as paired ossifications (0), fused into a frontoparietal
284 (1) (adapted from Laurin & Reiz 1997);

285 **38.** Maxilla. Excluded from interpterygoid vacuity (0), reaches interpterygoid vacuity (1)
286 (Laurin & Reiz 1997);

287 **41.** Prefrontal. Present (0), absent (1) (Laurin & Reiz 1997);

288 **49.** Postfrontal. Reaches orbit (0), excluded from orbit (1), absent (2) (Laurin & Reiz 1997);

289 **51.** Postorbital. Reaches orbit (0), excluded from orbit (1), absent (2) (Laurin & Reiz 1997);

290 **58.** Supratemporal. Present (0), absent (1) (Laurin & Reiz 1997);

291 **63.** Jugal. Reaches orbit (0), excluded from orbit (1), absent (2) (Laurin & Reiz 1997);

292 **69.** Tabular. Present (0), absent (1) (Laurin & Reiz 1997);

293 **81.** Postparietal number. Two (0), one (1), absent (2) (Laurin & Reiz 1997);

294 **152.** Hamate process. Absent (0), present (1) (Damiani 2001b);

295 **155.** Torus arcuatus (Preglenoid process). Present thickening in the dorsal edge (0) dorsal
296 edge without thickening (1) (NEW);

297 **156.** Postglenoid process hook-Like. Absent (0), present, however poor developed, with
298 retroarticular process apex lower than or at the torus arcuatus level (1), present and
299 well developed, with retroarticular process apex above the torus arcuatus level (2)
300 (NEW);

- 301 **157.** Glenoid fossa and torus arcuatus. Glenoid fossa lie below the torus arcuatus level (0),
302 or above the torus arcuatus level (1) (Damiani 2001a);
- 303 **159.** PMF center. Placed anteriorly to the anterior edge of the adductor fossa (0),
304 approximately below to the anterior edge of the adductor fossa (1), placed posteriorly
305 to the anterior edge of the adductor fossa (2) (Jupp & Warren 1986);
- 306 **160.** PMF (Posterior Meckelian Foramen) position. Approximately equidistant between the
307 ventral and dorsal mandibular edge (0), close to, or on ventral mandibular edge (1)
308 (Jupp & Warren 1986);
- 309 **161.** PMF. Small round or oval opening (0), or elongate window shorter than the adductor
310 fossa (1), or as long or longer than adductor fossa (2) (NEW);
- 311 **166.** Mandibular sensory canal. Present (0), absent (1) (Clack 2002);
- 312 **167.** Mandibular canal exposure. Entirely enclosed (0), mostly enclosed (1), mostly or
313 entirely open (2) (Clack 2002);
- 314 **168.** Oral sulcus of mandibular canal. Absent (0), present (1) (Clack 2002);
- 315 **169.** Accessory sensory canal. Absent (0), present (1). (adapt. Jupp & Warren 1986).

316

317 The matrix was further updated with characters 235–271, from recent works on
318 temnospondyl relationships (Fortuny *et al.* 2011; Pacheco *et al.* 2016; Eltink *et al.* 2016), thus
319 totaling 271 characters. Finally, characters were all used as unordered series (Fitch 1971), to
320 avoid *a priori* assumptions on putative transformation series. For more information, see the
321 complete list of the characters in appendix 2.

322 **Analyses**

323 The phylogenetic analyses followed the overall procedures of the analysis by Schoch
324 (2013), with some modifications. It was implemented using TNT version 1.5 (Goloboff &
325 Catalano 2016) and PAUP version 4.0b10 (Swofford 2002). The search was conducted in the

326 heuristic mode, with 1000 replicates, tree bisection-reconnection (TBR) algorithm and ‘new
327 technologies’ search algorithms options (ratchet, drift, etc.; as in Goloboff *et al.* 2008a). Other
328 options were the use of random seed “0” and the collapse trees after search. All characters were
329 treated as unordered. This original protocol was followed by with the use of implied weighting
330 method in TNT (Goloboff 1993) to improve resolution. The implied weighting used a TNT
331 script (Setk.run) to calculate the appropriate value of K . The strict consensus and the bootstrap
332 values (Felsenstein, 1985) were calculate in both programs (TNT and PAUP) with 1000
333 replicates.

334

335 **Results**

336 **Phylogenetic results**

337 Our first analysis, utilizing all data set and without weighting differentiation (Fig. 10)
338 resulted in a strict consensus of 97 most parsimonious trees with 1050 steps, Consistence Index
339 (CI) = 0,28 and Retention Index (RI) = 0,73. The resulting topology is highly polytomic,
340 implying that a combination of missing data, homoplastic characters and the presence of rogue
341 taxa still affect the dataset.

342 The implied weighting method (Goloboff 1993) was used then to improve resolution. The
343 method assigns a different weight for the character based on their homoplasy. For this method
344 we use a script (setk.run) to calculate the appropriate value of K ($K= 13.110352$). This analysis
345 was performed with TBR search option and result in one tree, which best score was 40.76981,
346 Consistence Index (CI) = 0,28 and Retention Index (RI) = 0,73.

347 An overall low bootstrap support can be seen through the topology (Fig. 11), which may
348 be due to amount of missing data and homoplastic characters. However, low tree indexes and
349 bootstrap values are quite common in large matrixes with such comprehensive datasets.
350 Furthermore, the monophyly of the Capitosauria group recovered here agrees with well-

351 established results from the bibliography (e.g. Damiani 2000a; Schoch 2008; Schoch 2013).
352 Despite the use of implied weighting methodology be a controversial issue (Kluge 1997;
353 Goloboff *et al.* 2008b), we choose this tree for the preferred analysis, because, according to
354 Farris (1983; apud Golobof 1993), “*The most parcimonious tree is one that best explains the*
355 *data (...) giving the weights that the characters deserve*”.

356 In this analysis, the specimen MCP-4275PV is recovered as a derived Capitosauria,
357 nesting in a polytomy with *Parotosuchus nasutus* and *Parotosuchus haugtoni*. Genus
358 *Parotosuchus*, along with MCP-4275PV, is therefore recovered as a monophyletic group.
359 Higher-level groups such as Capitosauria, Captosauroida, Stereospondyli and
360 Stereospondylomorpha were also recovered as monophyletic, in accordance with the
361 bibliography, and the general structure of the topology reflects basic relationships seen in
362 Schoch (2013).

363 The position of the Brazilian taxa *Tomeia witechi*, *Procuhy nazariensis* and *Prionosuchus*
364 *plummeri* do not closely correspond to the results from the previous works (Price 1048; Cisneros
365 *et al.* 2015; Eltink *et al.* 2016). However, this may be due to the extent of this analysis. Given
366 the overall low support of Temnospondyl relationships the matter demands further
367 investigation, with the inclusion of further basal taxa. Naturally, this is out of the scope of the
368 present contribution.

369 *Triadobatrachus* and *Eleuterodactylus*, representing anuran lissamphibians, are shown to
370 be the sister group of *Doleserpeton*. Although this is congruent to the view of modern
371 amphibians as derived temnospondyls, lepospondyl taxa are not included herein and
372 Lissamphibia is only represented by anurans. Also, *Doleserpeton* shows a more exclusive
373 relationship with *Platyrhinops* than to *Gerobatrachus* (*contra* Schoch 2013), while *Micropholis*
374 appears as the immediate sister group to these taxa.

375

376 **Does morphology support phylogeny?**

377 The classification of the specimen MCP-4275PV to Capitosauria group through the
378 phylogenetical analysis finds strong morphological support. Morphological analysis was
379 possible due to the preservation, in parts, of the some diagnostic portions. Dentition patterns
380 with size differentiation (antero-posteriorly decreasing), and apparent mandibular and
381 accessory sulcus (e.g. Damiani *et al.* 2001; Piñeiro *et al.* 2007), are all clearly detected in MCP-
382 4275PV. The presence of a hook-like retroarticular process (post-condylar process *sensu*
383 Damiani 1999b) is however a curious feature that supposedly interfered in species ecology,
384 possibly related with jaw motion during the feed (Olson 1961). Damiani (1999b) considered
385 this feature diagnostic for Capitosauria, a hypothesis that is supported by the present
386 phylogenetic analysis. Overall, MCP-4275PV consistently bears characters typical of advanced
387 capitosaurids (sulci, hamate process, dentition pattern), congruent with the phylogenetic results.

388 **Discussion**

389 **MCP-4275PV as a derived Capitosauria**

390 Our results support the phylogenetic affinity of MCP-4275PV with Capitosauria group.
391 Furthermore, it provides evidence of a close relationship with *Parotosuchus nasutus* and *P.*
392 *haugthoni*, in an unresolved polytomy. Morphology and anatomic characteristics agree with the
393 phylogenetic results, particularly the presence of a set of sulci that is part of the superficial bony
394 ornamentation mandibular (the most evident), oral and accessory sulci (shorter). These
395 important characters are widely found in the Mesozoic taxa captosauroids, trematosaurids and
396 lydekkerinids (Jupp & Warren 1996; Damiani *et al.* 2001a,b), but can clearly be devised in this
397 Permian specimen. The surangular foramen is present and, according with Damiani (1999b)
398 and Damiani *et al.* (2001a), this anatomic feature is typical for capitosaurids, and previously is
399 known only from Triassic taxa. Unique features are also present, such as a well-developed
400 retroarticular process ("hook-like") and a set of four foramina on the surangular, providing

401 support for the idea that this new specimen does not correspond to any previously known
402 species. The shape of the reatroarticular process is indeed relevant also because the morphology
403 of this structure can be traced quite concisently through the major branches of the
404 temnospondyl evolutionary tree. In this case, the short, curved and posterodorsally oriented
405 retroarticular process is only found in Capitosauria. In comparison with the other Permian taxa,
406 MCP-4275PV is very different in size and mandibular structure. This is a large sized animal,
407 with parabolic snout (derived from the morphology of the symphysis) and antero-posteriorly
408 compressed dentition with differentiation on sizes (also typical of Mesozoic taxa).

409

410 **MCP-4275PV as a *Parotosuchus***

411 Although it seems clear enough that MCP-4275PV can be identified as a derived
412 capitosaurid, we prefer a somewhat more cautious approach regarding a generic assignment to
413 *Parotosuchus*. Most *Parotosuchus* are fragmentary and the use of only two species in this
414 analysis may not sufficient to corroborate assignment to this genus. Furthermore, it is
415 understood that the genus *Parotosuchus* is in need of a dedicated revision (see Damiani 1999).
416 The phylogenetic affinity between *Parotosuchus* and MCP-4275PV is however quite relevant,
417 as it would build support for the biostratigraphic correlation between Rio do Rasto fauna and
418 *Cynognathus* Assemblage Zone of South Africa (see Damiani 2001b). However, this affinity
419 may also bring forth problematic biostratigraphic implications, since that MCP-4275PV is
420 undoubtedly younger than the taxa found in the *Cynognathus* AZ. Currently, although the
421 phylogenetic results corroborate MCP-4275PV as a new taxon within *Parotosuchus*, it is
422 understood that further data is necessary to properly secure this assignment.

423

424 **A Permian capitosaur and its implications to the origin and dispersal of the group**

425 Damiani (2001a) presented a calibrated phylogenetic tree that included trematosaurids,
426 capitosauroids and lidekkerinids (Fig. 12). The author points to a single post PTE event
427 radiation that explains capitosaur diversity in the Triassic. His work gave us evidences about a
428 single linages in all the Late Permian for capitosaur and another for trematosaur, leading to
429 the hypothesis that in some moment of the Late Permian emerged the ancestor that gave rise to
430 these groups that, back in the end-Permian, constituted a single line (Capitosauroida). Damiani
431 (1999) also argued towards the Early Triassic origin of several capitosaur characteristics, based
432 on South African Olenekian specimen. The new capitosauroid presented in this work – MCP-
433 4275PV – brings further evidence on the origin and dispersion of Capitosauria. The earliest
434 Capitosauria specimen was recorded from Buena Vista Formation (Uruguay) and has a Permo-
435 Triassic age (~251 m.a.: Piñeiro *et al.* 2007). The new material is a second record of a
436 capitosauroid from Brazil, the first being *Tomeia witecki*, reported by Eltink *et al.* (2016) in
437 Sanga do Cabral Formation, of Triassic age. The Rio do Rasto Formation age is exclusively
438 Permian (~265 m.a., Guadalupian–Lopingian; Holz *et al.* 2010; Dias-da-Silva 2012), which
439 makes MCP-4275PV the earliest representative of the group. This expands the geographic
440 distribution of the Capitosauria in South America and confirms the gondwanan origin of the
441 group foreseen by Damiani (1999). Besides that, the new capitosaur represents the evidence of
442 an earlier radiation (Guadalupian, or anterior) of the Capitosauria and, conversely, of the
443 Stereospondyli. This implies into two major aspects: (i) at least five capitosauroid lineages
444 survived through the PTE event and; (ii) capitosauroid diversity is the result of two radiation
445 events, one *circa* the Capitanian and at least one other posterior to the PTE event. Finally, MCP-
446 4275PV supports the idea that derived characters typical of Capitosauria may have evolved
447 earlier than thought, however not just in the Eotriassic (as suspected by Damiani 1999), but much
448 earlier, in the Mesopermian.

449 Biogeography and the origins of Capitosauria remains a problem. The best possible
450 evidence for the origin of the group is expected to come from basal capitosaur lineages, such
451 as the ones leading to *Edingerella* or *Watsonisuchus*. However, MCP-4275PV nests with
452 *Parotosuchus*, implying that the basal capitosaur radiation had already taken place in the
453 Permian, as discussed above. In the absence of representatives for these basal lineages, MCP-
454 4275PV remains as the best possible reference of the origin of the group, in this case supporting
455 a South American origin. Overall, the evidence so far known points towards the idea that the
456 group was endemic from South America and that dispersion through the Pangaea took place
457 during the Late Permian, with migration to Laurasia through the North Gondwana (Damiani
458 1999a) (Fig.13). Therefore, the radiation and speciation of the group may have occurred with
459 the emergence of the physic barriers and new ecologic opportunities in consequence of the
460 Permo–Triassic mass extinction (Sahney & Benton, 2008). Despite the Permo–Triassic
461 extinction has been the most destructive event on the planet (e.g., Sahney & Benton 2008),
462 Capitosauria and Trematosauria displayed a quick recovery, occupying the ecologic niche of
463 semi-aquatic predators. Since the geological records of Capitosauria are all from intracratonic
464 sediments (e.g. Damiani 1999, 2001ab; Piñeiro 2007; Nakajima & Schoch 2011; Eltink et al.
465 2016), dispersion may have taken place through continental route by means of a network of
466 hydrographic basins. Such evidences implies that the continental climate and the desertification
467 process that has been attributed to the end-Permian and Early Triassic may have been not as
468 abrupt as previously suggested.

469

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483

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693 **Figure captions**

694 **Fig. 1:** (A) Map showing the distribution of the Temnospondyli in Brazil (adapted from Eltink
695 *et al.* 2012). (B) Graphic displaying the geologic distribution and (C) the amount of described
696 Brazilian species per decade. **M-Per.** Meedle Permian. **M/U-Per.** Meedle-Upper Permian. **U-**
697 **Per.** Upper Permian. **E-Tri.** Early Triassic.

698 **Fig. 2:** Map showing the geographic distribution of Capitosauria (not including the new MCP
699 specimen). Note that the oldest previous record lays somewhat in the middle of the most
700 extreme occurrences of Capitosauria. Geographic distribution was based in the literature cited in
701 the text. (Map adapted from: <<http://suburbanodigital.blogspot.com>>).

702 **Fig. 3:** Geological map of the Paraná Basin, with the illustration of the six sedimentary
703 supersequences (Ordovician–Cretaceous). Modified from Guerra-Sommer *et al.* (2008).

704 **Fig. 4:** Map showing the location of Rio do Rasto Formation and its tetrapod-bearing locations:
705 1, Aceguá; 2, Posto Queimado; 3, Serra do Cadeado. Modified from Dias-da-Silva (2012).

706 **Fig. 5:** MCP-4275PV, anterior portion in lateral view. Photograph (A) and interpretive drawing
707 (B). **Ap.** *unidentified appendicular element*; **D.** *dentary*; **PSP.** *post-splenial*, **S.** *splenial*.

708 **Fig. 6:** MCP-4275PV, posterior portion in lateral view. Photograph (A) and interpretive
709 drawing (B). **A.** *angular*; **as.** *accessory sulcus*; **at.** *arcuatus torus*; **D.** *dentary*; **gf.** *glenoid fossa*;
710 **ms.** *mandibular sulcus*; **os.** *oral sulcus*; **rap.** *retroarticular process* (post-condylar process); **S.**
711 *surangular*; **sf.** *surangular foramen*.

712 **Fig. 7:** MCP-4275PV, anterior portion in medial view. Photograph (A) and interpretive drawing
713 (B). **A.** *angular*; **amf.** *anterior Meckelian foramen*; **D.** *dentary*; **PAR.** *prearticular*; **pmf.**
714 *posterior Meckelian foramen*; **PSP.** *post-splenial*; **S.** *splenial*.

715 **Fig. 8:** MCP-4275PV, anterior portion in dorsal view. Photograph (A) and interpretive drawing
716 (B). **af.** *adutor fossa*; **at.** *arcuatus torus*; **gf.** *glenoid fossa*; **hp.** *hamate process*; **PA.**

717 *prearticular*; **rap.** *retroarticular process*. *The hamate process was sectioned, leaving only its
718 base.

719 **Fig. 9:** MCP-4275PV, occlusal view of a mandibular tooth (mid-series) showing the
720 labyrinthodont pattern of folding and the anteroposterior flattening.

721 **Fig. 10:** Strict consensus from 97 more parsimonious trees with 1050 steps, using New
722 Technologies search option on TNT. Outgroup = **. Added taxa = *.

723 **Fig. 11:** Final topology with Implied Weighting, calibrated through the timescale. The bootstrap
724 is represented by numbers (≥ 50). Outgroup = **. Added taxa = *.

725 **Fig. 12:** Phylogenetic tree of capitosauroids and relative taxa, taken from the bibliography,
726 showing the current prevalent view on Capitosauria relationships and chronostratigraphic
727 distribution. Ghosts lineages indicated by a red dashed line; age of the Rio do Rasto Formation
728 indicated in blue, where the new capitosauroid (MCP4275PV) was collected (adapted from
729 Damiani 2001a). Note that the new specimen implies in a recalibration of all radiation events
730 prior to the *Parotosuchus* divergence, set in this image within the Early Triassic.

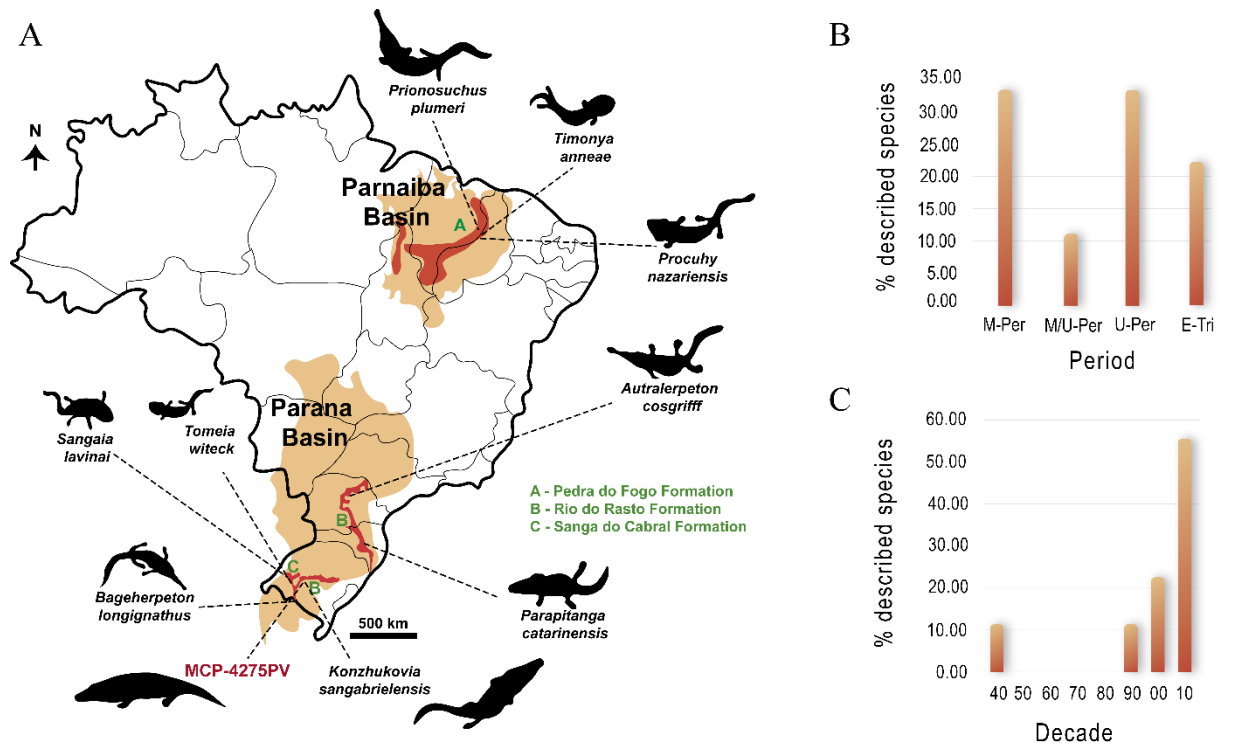
731 **Fig. 13:** Map showing the possible dispersion route of Capitosauria Group, proposed by the
732 authors and based in the evidences found in previous works (see references in the text). (Map
733 adapted from: <<http://suburbanodigital.blogspot.com>>.

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Figure 1:



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747 **Figure 2:**



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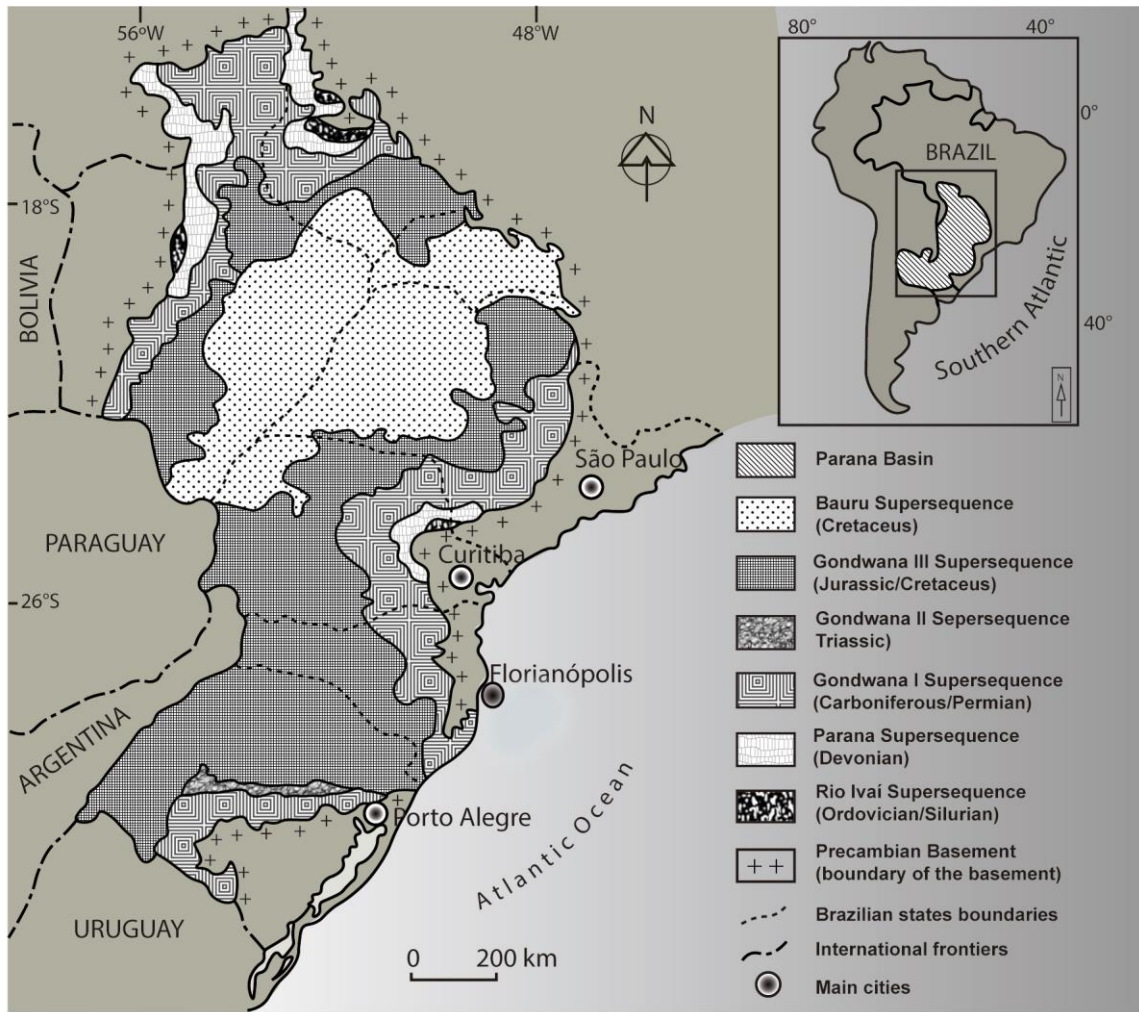
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759 **Figure 3:**



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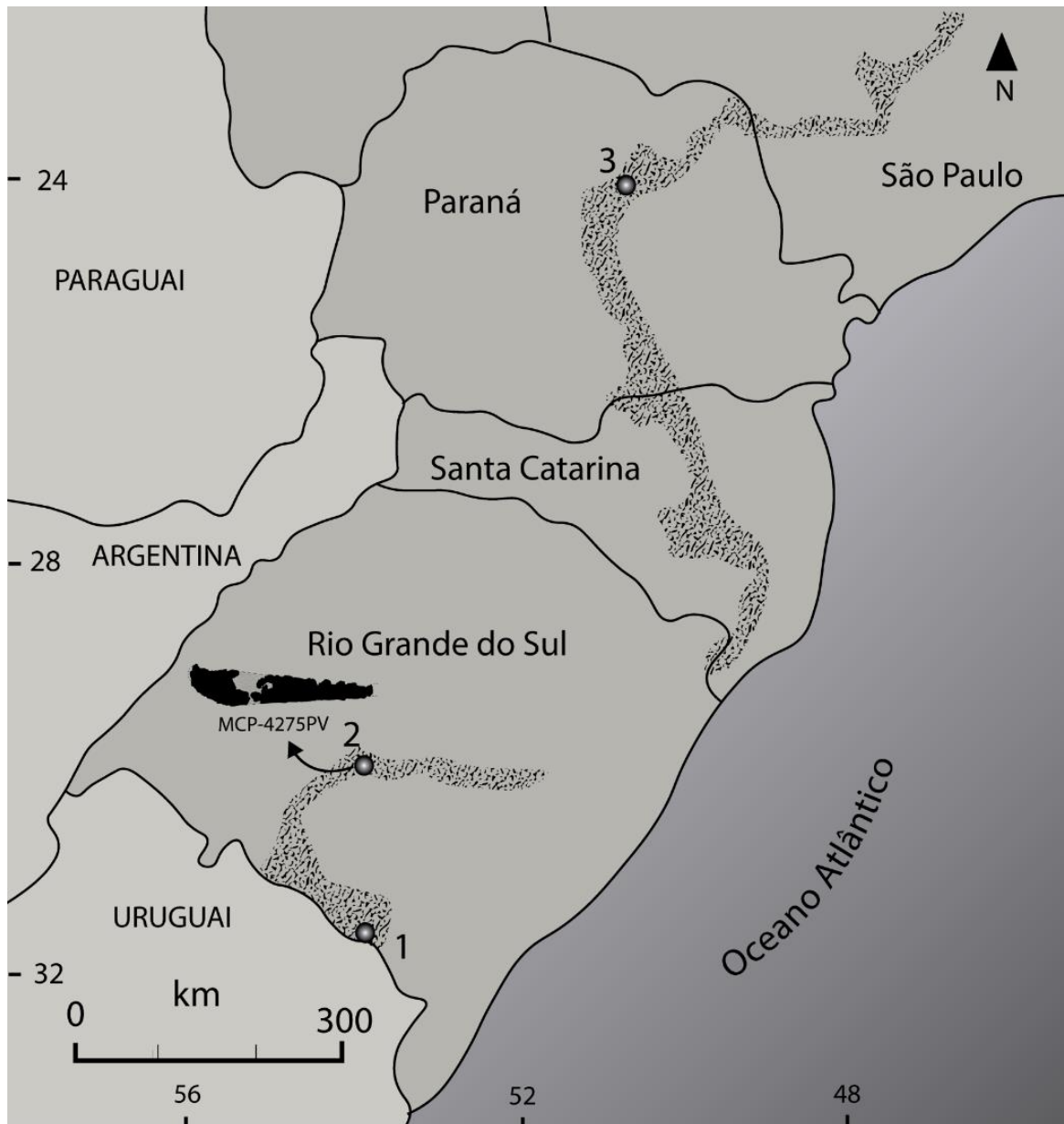
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771 **Figure 4:**



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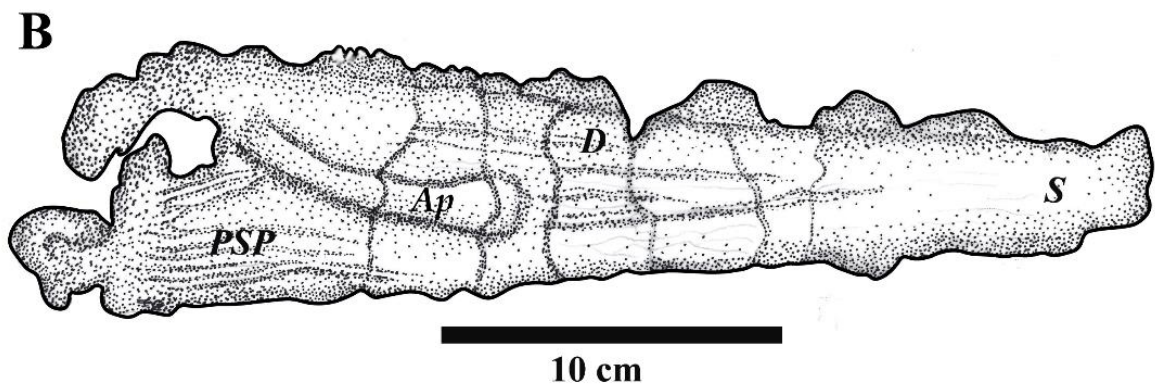
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779 **Figure 5:**



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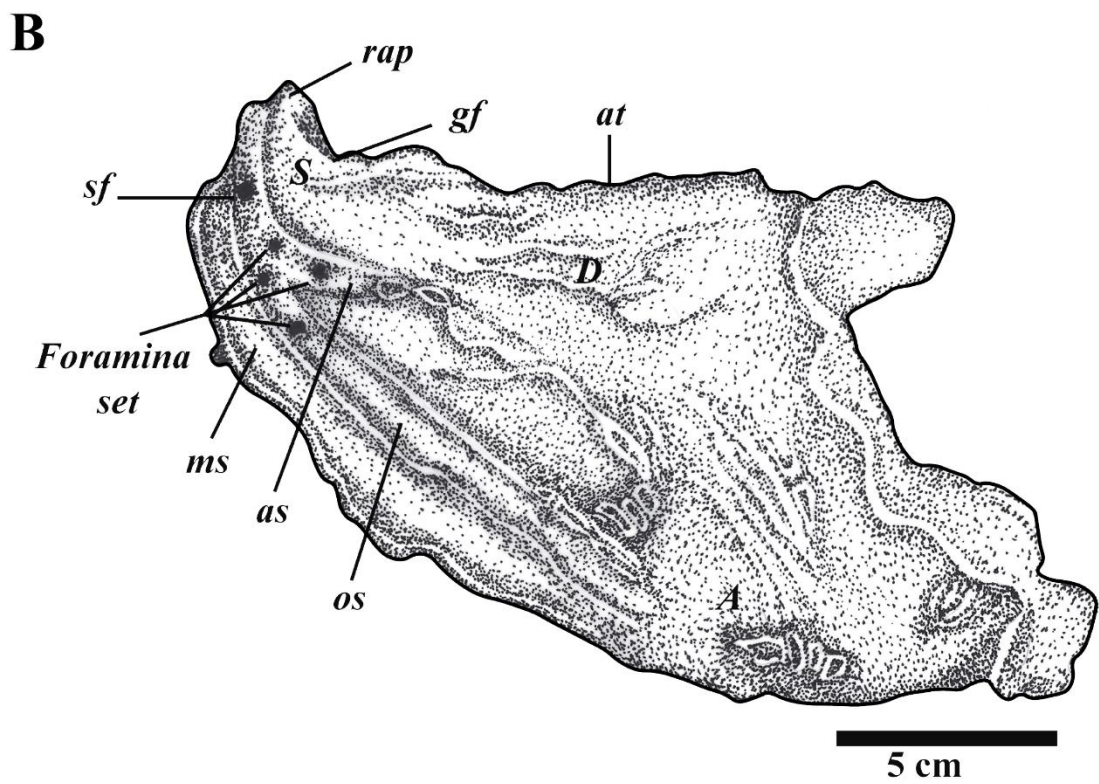
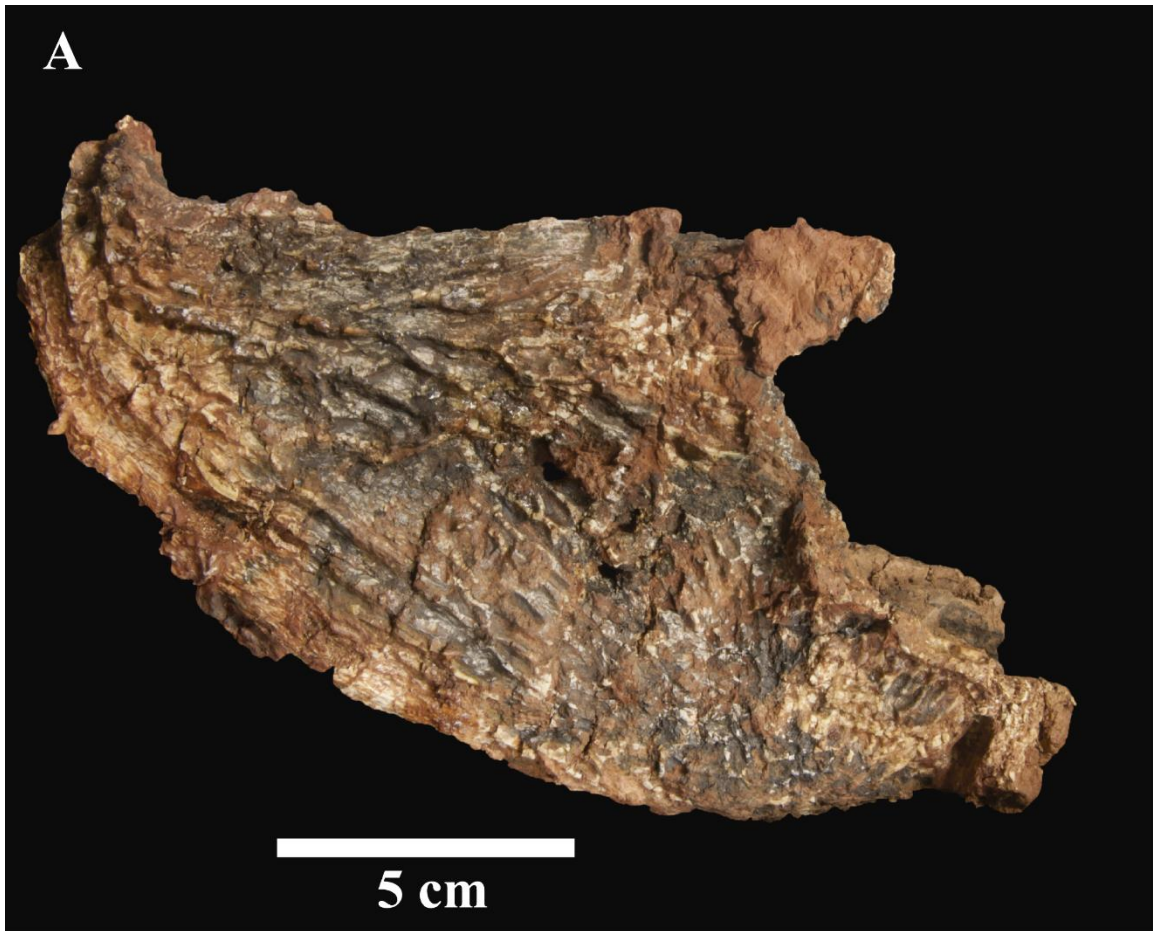
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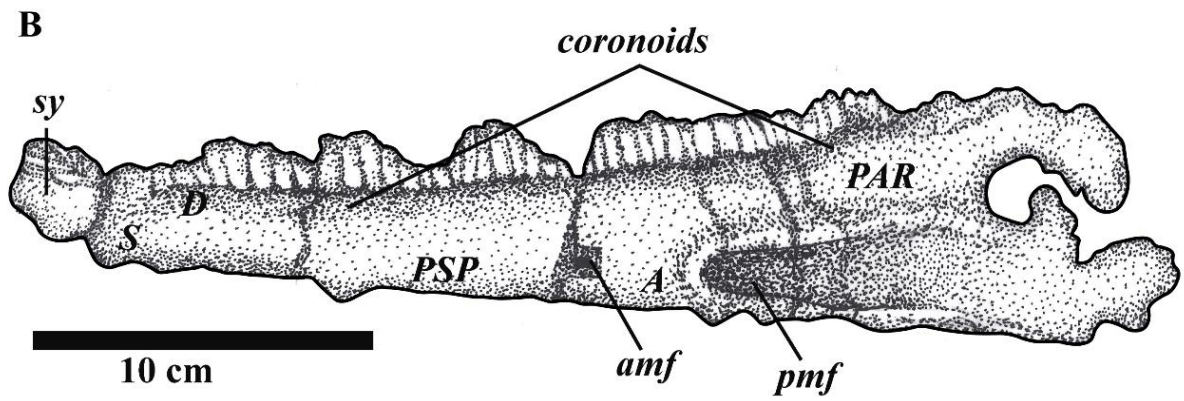
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791 **Figure 7:**



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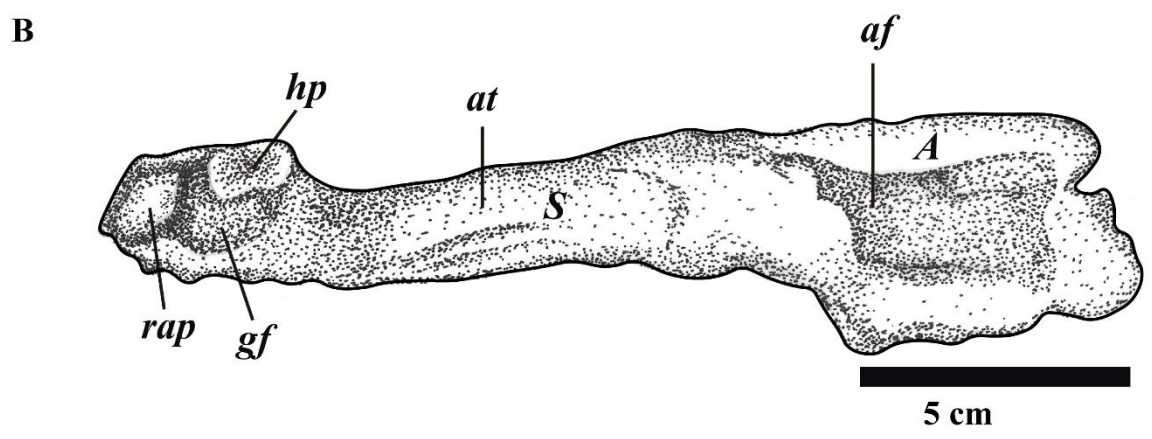
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806 **Figure 8:**



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819 **Figure 9:**



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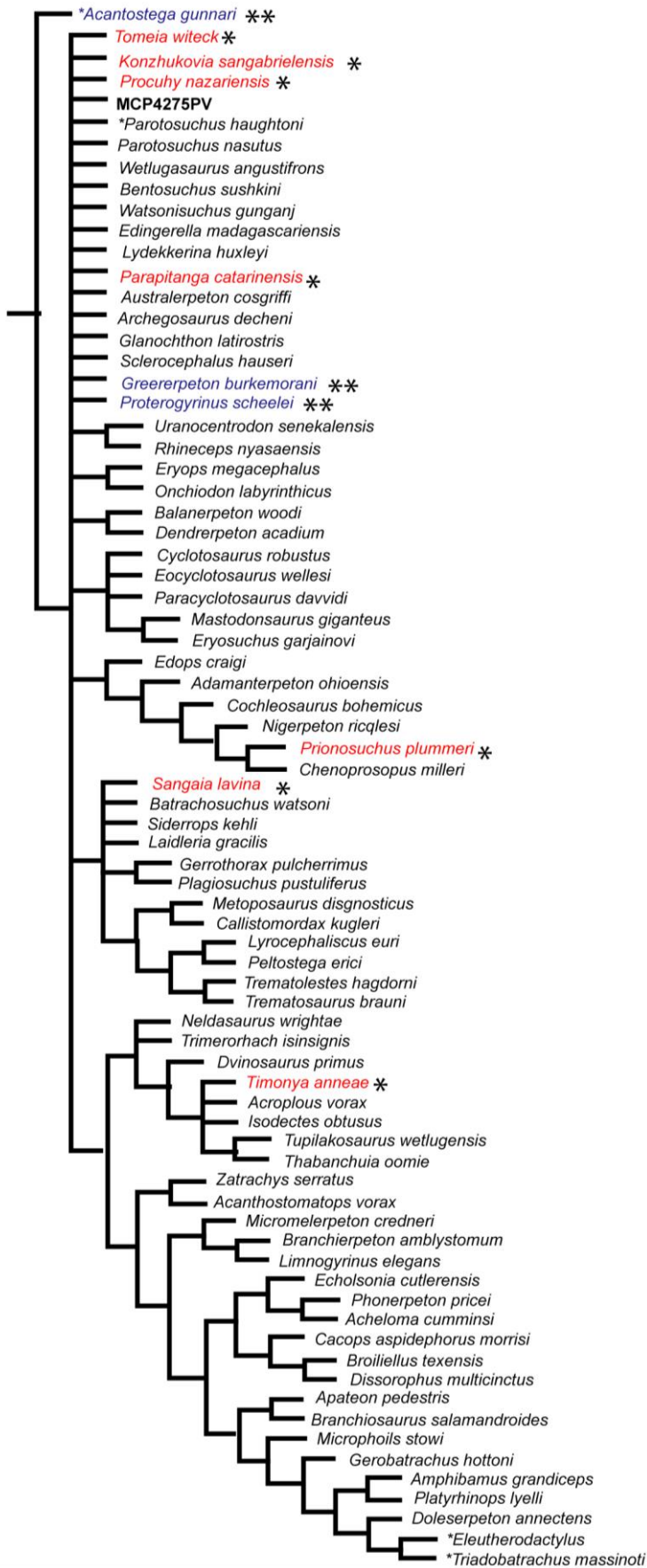
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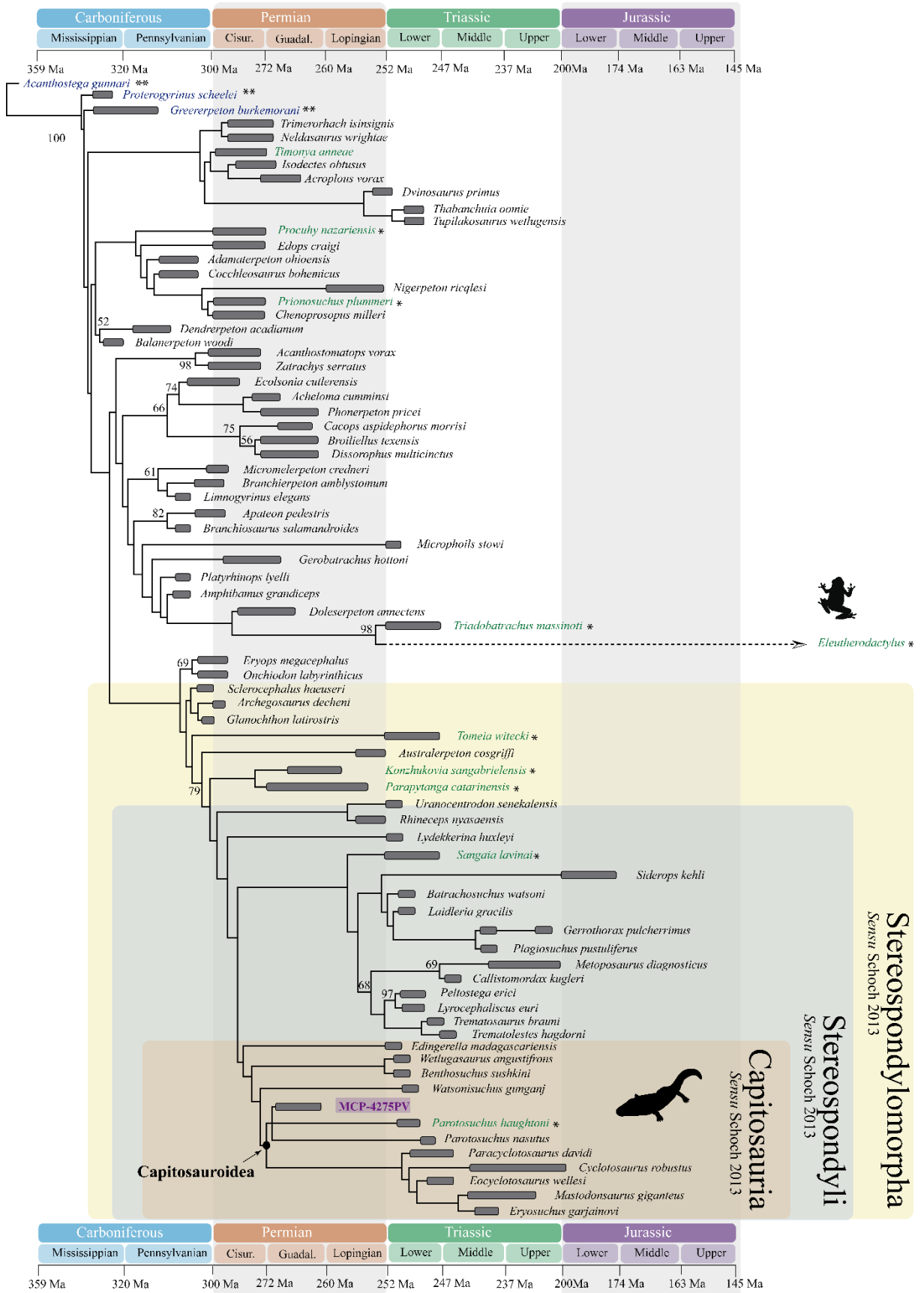
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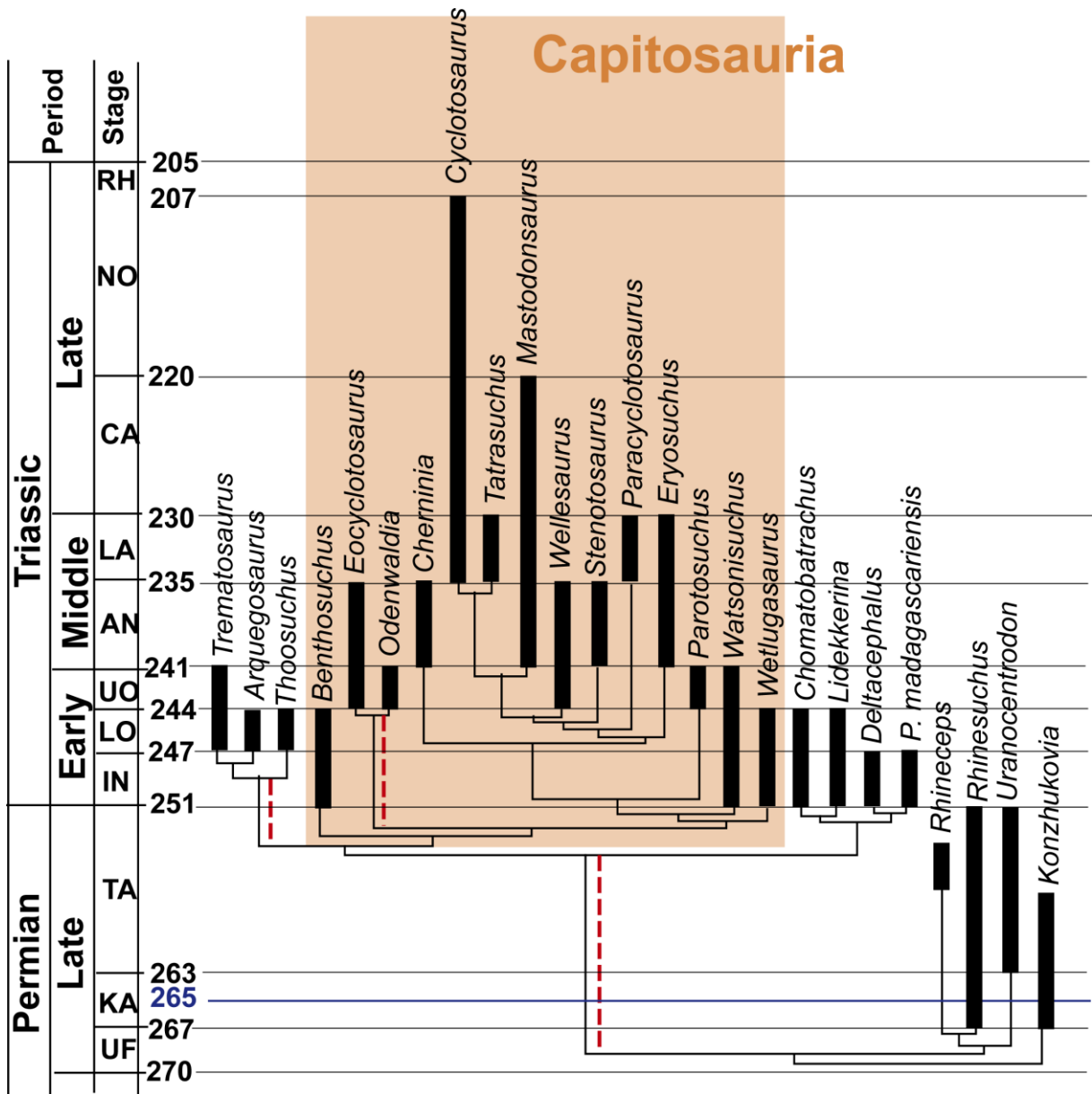


831 **Figure 11:**



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833 **Figure 12:**



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842 **Figure 13:**



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854 **APPENDIX 1. Specific Terminal Taxa - general information and provenance of data**
855 **used for scoring the matrix**

856 **Outgroup:**

857 (1) *Acanthostega gunnari* Jarvik 1952. Data extracted from: Coates (1996), Ahlberg &
858 Clack (1998) and Porro *et al.* (2015). Loc. East of Greenland, Gauss Halvo. Upper
859 devonian.

860 **Material examined personally: AMNH 23102 (Cast).**

861 (2) *Proterogyrinus scheeli* (Holmes, 1984). Data extracted from: Holmes (1984). Loc. Greer,
862 West of Virginia USA, Illinois Basin, Bluefield Formation, Bickett Shale, Early
863 Carboniferous.

864 (3) *Greererpeton burkemorani* Romer 1969. Data extracted from: Smithson (1982) and Bolt
865 & Lombard (2001). Loc. West of Virginia, USA, Illinois Basin, Bluefield Formation,
866 Bickett Shale. Early Carboniferous.

867 **Material examined personally: AMNH 9031 (Cast).**

868 **Ingroup:**

869 (4) *Edops craigi* Romer & Witter 1942. Data extracted from: Romer & Witter (1942). Loc.
870 Texas, USA, Moran e Pueblo Formations. Permo–Carboniferous.

871 (5) *Adamaterpeton ohioensis* Milner & Sequeira 1998. Data extracted from: Milner &
872 Sequeira (1998). Loc. Ohio, USA, Diamond Coal Mine at Linton. Upper Carboniferous.

873 (6) *Cochleosaurus bohemicus* Fric 1885. Data extracted from: Sequeira (2004). Loc. Czech
874 Republic. Upper Carboniferous.

875 (7) *Nigerpeton ricqlesi* Sidor *et al.* 2005. Data extracted from: Sidor *et al.* (2005) and Steyer
876 *et al.* (2006). Loc. Nigeria, West of Africa, Moradi Formation. Upper Permian.

877 (8) *Chenoprosopus milleri* Mehl 1913. Data extracted from: Williston & Mehl (1913). Loc.
878 New Mexico. Permo–Carboniferous.

- 879 (9) *Dendroperon acadianum* Owen 1953. Data extracted from: Holmes *et al.* (1998). Loc.
880 Nova Scotia. Carboniferous.
- 881 (10) *Balanerpeton woodi* Milner & Sequeira 1994. Data extracted from: Milner & Sequeira
882 (1993). Loc. Scotland, East Kirkton Sedimentary Unit. Carboniferous.
- 883 (11) *Trimerorhach isinsignis* Case 1935. Data extracted from: Case (1935). Loc. Texas, USA.
884 Permo–Carboniferous.
- 885 **Material examined personally: AMNH 4565 and 4868.**
- 886 (12) *Neldasaurus wrightae* Chase 1965. Data extracted from: Chase (1965). Loc. Texas, USA.
887 Lower Permian.
- 888 (13) *Isodectes obtusus* Sequeira 1998. Data extracted from: Sequeira (1998). Loc. Ohio, USA,
889 Allegheny Group. Upper Carboniferous.
- 890 (14) *Acroplous vorax* Hotton 1959. Data extracted from: Eglenhorn *et al.* (2008). Loc.
891 Kansas, USA, Council Grove Group. Lower Permian.
- 892 (15) *Dvinosaurus primus* Amalitzkii 1921. Data extracted from: Bystrow (1938). Loc. Russia.
893 Upper Permian.
- 894 (16) *Thabanchuia oomie* Warren 1999. Data extracted from: Warren (1999). Loc. South
895 Africa, Karoo Basin, Beaufort Group. Lower Triassic.
- 896 (17) *Tupilakosaurus wetlugensis* Shishkin 1961. Data extracted from: Shishkin (1961) e
897 Wenerburg *et al.* (2007). Loc. Russia. Lower Triassic.
- 898 (18) *Acanthostomatops vorax* Credner 1883. Data extracted from: Boy (1989) e Witzmann &
899 Schoch (2006). Loc. Germany, Niederhaßlich-Schweinsdorf Formation. Lower Permian.
- 900 (19) *Zatrachys serratus* Cope 1878. Data extracted from: Urban & Berman (2007). Loc.
901 Washington, USA, Washington Formation. Lower Permian.
- 902 **Material examined personally: AMNH 4589 (*Zatrachys serratus*), AMNH 4586, 4587**
903 **and 4873 (*Zatrachys microphthalmus*).**

- 904 (20) *Micromelerpeton credneri* Bulman & Whittard 1926. Data extracted from: Boy (1995).
905 Loc. Southeast Germany. Lower Permian.
- 906 (21) *Limnogyrinus elegans* (Fritsch 1881) Milner 1986. Data extracted from: Milner &
907 Sequeira (2003). Loc. Czech Republic. Upper Carboniferous.
- 908 (22) *Branchierpeton amblystomum* Credner 1881. Data extracted from: Werneburg (1991).
909 Loc. Germany, Döhlener Basin, Niederhaßlich-Schweinsdorf Formation. Lower
910 Permian.
- 911 (23) *Branchiosaurus salamandroides* Fritsch 1875. Data extracted from: Schoch & Milner
912 (2008). Loc. Czech Republic, Nahe Basin. Carboniferous.
- 913 (24) *Apateon pedestris* Meyer 1844. Data extracted from: Schoch & Milner (2008). Loc.
914 Germany. Permo–Carboniferous.
- 915 (25) *Microphoils stowi* Huxley 1959. Data extracted from: Schoch & Rubidge (2005). Loc.
916 South Africa, Katberg Formation. Lower Triassic.
- 917 (26) *Platyrhinops lyelli* (Wyman 1858) Clack & Milner 1994. Data extracted from: Clack &
918 Milner (2010). Loc. Ohio, USA, Allegheny Group. Upper Carboniferous.
- 919 (27) *Amphibamus grandiceps* Cope 1865. Data extracted from: Milner (1982). Loc. Illinois,
920 USA, Carbondale Formation. Upper Carboniferous.
- 921 (28) *Doleserpeton annectens* Bolt 1969. Data extracted from: Sigurdson & Bolt (2010). Loc.
922 Oklahoma, USA. Lower Permian.
- 923 (29) *Dissorophus multicinctus* Cope 1895. Data extracted from: DeMar (1968). Loc. Texas,
924 USA. Permian.
- 925 (30) *Cacops aspidephorus* Williston 1910, *C. morrisoni*, Reisz *et al.* 2009. Data extracted from:
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1298 **APPENDIX 2. Character list**

- 1299 **1.** *Skull (outline)*. Parabolic (0) or triangular with pointed tip (1). (Schoch 2013).
- 1300 **2.** *Skull (height)*. Skull of variable height, but occiput always deeper than snout (0), or
1301 extremely flattened to equal height throughout (1). (Schoch 2013).
- 1302 **3.** *Ornament (elements)*. Reticulate ridges of various sizes (0), isolated pustules (1). (Schoch
1303 2013).
- 1304 **4.** *Ornament (snout)*. Polygons or short grooves (0), or mostly radial, elongated grooves (1).
1305 (Schoch 2013).
- 1306 **5.** *Ornament (general)*. Shallow ridges of variable height (0), high ridges throughout (1).
1307 (Schoch 2013).
- 1308 **6.** *Ornament (intensive growth)*. Elongated ridges ('zones of intensive growth') confined to
1309 snout only (0), or prepineal growth zone established on extended anterior parietal and
1310 postorbital (1). (Schoch 2013).
- 1311 **7.** *Ornament (preorbital)*. Zone of subdued ornament on the medial skull bones adjacent to
1312 the midline suture absent (0), or present (1). (Sequeira 2003).
- 1313 **8.** *Spines*. Absent (0), or present along lateral flank of quadratojugal (1). (Schoch 2013).
- 1314 **9.** *Preorbital region (length)*. Less than twice the length of posterior skull table (0), or more
1315 (1). (Schoch 2013).
- 1316 **10.** *Premaxilla (alary process)*. Absent (0), or present, forming a posterior hook-like
1317 indentation (1). (Milner 1993).
- 1318 **11.** *Premaxilla (prenarial portion)*. Short (0), or very expanded, equaling the length of the
1319 frontal (1). (Schoch 2013).
- 1320 **12.** *Premaxilla (outline)*. Parabolically rounded (0), or box-like and anteriorly blunt (1).
1321 (Schoch & Witzmann 2009a).
- 1322 **13.** *Premaxillary foramen*. Premaxilla and nasal completely sutured (0), or medially bearing an

- 1323 opening separating the two alary processes of the premaxilla (1). (Boy 1972).
- 1324 **14. Premaxillary fontanelle.** Premaxillae with or without small opening (0), or encircling large
1325 fenestra extending posteriorly between the nasals (1). (Boy 1989).
- 1326 **15. Snout (*internarial distance*).** Narrower than interorbital distance (0), or wider (1). (Schoch
1327 2013).
- 1328 **16. Nasal (*width*).** Nasal longer than wide (0), or as wide as long (1). (Schoch 2013).
- 1329 **17. Naris (*position*).** At lateral margin of snout, opening laterally (0), or set well medially,
1330 opening anteriorly (1). (Schoch 2013).
- 1331 **18. Naris (*extension*).** Naris uniform, with oval shaped margin (0), or posteriorly expanded with
1332 distinct anterior and posterior regions giving external overall “key-hole” shape (1). (Polley
1333 & Reisz 2011).
- 1334 **19. Naris (*flange*).** Ventral (inner) side of prefrontal, lacrimal, and nasal smooth (0), or bearing
1335 a complicated bar-like structure (narial flange) permitting contact with the antorbital bar
1336 (1). (Schoch 2013).
- 1337 **20. Nasal (*lateral margin*).** Straight (0), or stepped, with lateral excursion anterior to lacrimal
1338 (1). (Schoch & Witzmann 2009a).
- 1339 **21. Lacrimal.** Present (0), or absent (1). (Schoch 2013).
- 1340 **22. Lacrimal (*lateral suture*).** Parallels medial suture (0), or lateral suture posterolaterally
1341 expanded to give broader preorbital region (1). (Schoch 2013).
- 1342 **23. Lacrimal (*position*).** Extending anterior to orbit (0), or confined to lateral orbit margin (1).
1343 (Schoch 2013).
- 1344 **24. Lacrimal (*posterior extension*).** Restricted to the antorbital region (0), or extending back
1345 lateral to orbit (1). (Schoch 2013).
- 1346 **25. Orbit and naris.** Well separated (0), or separated only by tiny quadrangular lacrimal (1).
1347 (Schoch 2013).

- 1348 **26. Orbit location.** Medial, framed by wide jugals laterally (0), or lateral emplacement, framed
1349 by very slender jugals (1). (Schoch 2013).
- 1350 **27. Orbit margins.** Raised well above skull plain (0), or flush with roof (1). (Damiani 2001).
- 1351 **28. Palpebral ossifications.** Ossifications in orbit restricted to sclerotic ring (0), or numerous
1352 additional ossicles at medial margin of sclerotic ring (1). (Schoch 2013).
- 1353 **29. Pineal foramen.** Present (0), or absent in adults (1). (Schoch 2013).
- 1354 **30. Interorbital distance.** Narrower than or equalling orbital width (0), or wider (1). (Schoch
1355 2013).
- 1356 **31. Frontal-nasal (length).** Frontal as long or longer than nasal (0), or shorter (1). (Schoch
1357 2013).
- 1358 **32. Frontal-nasal (suture).** Level with or anterior to the orbit margin (0), or further posterior
1359 (1). (Schoch 2013).
- 1360 **33. Frontal and Parietal.** Both present as paired ossifications (0), fused into a frontoparietal
1361 (1). (adapted from Laurin & Reiz 1997)
- 1362 **34. Lateral line sulci (adults).** Present (0), absent (1). (Schoch 2013).
- 1363 **35. Sulci (skull roof).** Throughout skull roof if present (0), or confined to circum-orbital region
1364 (1). (Englehorn *et al.* 2008).
- 1365 **36. Infraorbital sulcus.** With simple curve on lacrimal (0), or with pronounced S-shaped
1366 lacrimal flexure (1). (Damiani 2001).
- 1367 **37. Supraorbital sulcus.** Passing entirely through nasal (0), or entering prefrontal and lacrimal
1368 (1). (Damiani 2001).
- 1369 **38. Maxilla.** Excluded from interpterygoid vacuity (0), contacts interpterygoid vacuity (1).
1370 (Laurin & Reiz 1997)
- 1371 **39. Maxilla (anterior margin).** Straight (0), or laterally convex due to enlarged teeth (1).
1372 (Schoch 2013).

- 1373 **40.** *Maxilla (contact to nasal)*. Absent, separated by lacrimal (0), or present (1). (Schoch 2013).
- 1374 **41.** *Prefrontal*. Present (0), absent (1). (Laurin & Reiz 1997)
- 1375 **42.** *Prefrontal-frontal*. Prefrontal substantially longer than frontal (0), or ending at one level
1376 with frontal (1). (Schoch 2013).
- 1377 **43.** *Prefrontal (anterior end)*. Pointed (0), or wide and blunt (1). (Schoch 2013).
- 1378 **44.** *Prefrontal (lateral suture)*. Straight or concave (0), or with marked medial projection of
1379 jugal near the orbit (1). (Schoch 2013).
- 1380 **45.** *Prefrontal-postfrontal*. Sutured (0), or separated by frontal (1). (Damiani 2001)
- 1381 **46.** *Prefrontal (process)*. Prefrontal-lacrimal suture simple (0), or prefrontal underlying
1382 lacrimal laterally to reach the palatine (1). (Schoch 2013).
- 1383 **47.** *Prefrontal-jugal*. Separated by lacrimal (0), or in contact (1). (Schoch 2013).
- 1384 **48.** *Prefrontal-maxilla*. Separated by lacrimal (0), or in contact (1). (Englehorn *et al.* 2008).
- 1385 **49.** *Postfrontal*. Reaches orbit (0), excluded from orbit (1), absent (2). (Laurin & Reiz 1997)
- 1386 **50.** *Posterior skull table (length)*. More than 0.6 times the width (0), or less than that (1).
1387 (Schoch 2013).
- 1388 **51.** *Postorbital*. Reaches orbit (0), excluded from orbit (1), absent (2). (Laurin & Reiz 1997)
- 1389 **52.** *Postorbital (shape)*. Long triangular, wedged deeply between squamosal and supratemporal
1390 (0), or short (1). (Schoch 2013).
- 1391 **53.** *Postorbital (end)*. Posterior end acutely triangular (0), or with finger-like projection (1).
1392 (Sequeira 2003).
- 1393 **54.** *Postorbital*. Not wider than orbit (0), or with substantial lateral process projecting into jugal
1394 (1). (Schoch 2013).
- 1395 **55.** *Postorbital, postfrontal*. Shorter than supratemporal and parietal (0), or as long or longer
1396 (1). (Schoch 2013).

- 1397 **56. *Otic notch***. Semicircular embayment between squamosal and posterior skull table (0), or
1398 straight transverse posterior skull margin without embayment between cheek and table (1).
1399 (Schoch 2013).
- 1400 **57. *Otic notch (position)***. Lateral, expanding along entire cheek to form continuous
1401 unornamented area up to quadrate (0), or slit-like (1), or small and rounded, confined to
1402 dorsomedial part of squamosal (2). (Schoch 2013).
- 1403 **58. *Supratemporal***. Present (0), absent (1). (Laurin & Reiz 1997)
- 1404 **59. *Supratemporal***. Longer than wide (0), or quadrangular, giving a foreshortened posterior
1405 skull table (1). (Schoch 2013).
- 1406 **60. *Supratemporal (width)***. Rectangular, with straight sagittal lateral margin (0), or
1407 posterolaterally constricted by expanded otic notch (1). (Schoch 2013).
- 1408 **61. *Supratympanic flange***. Squamosal continuously ornamented around margin of otic notch
1409 (0), or squamosal having dorsally exposed and ornamented area (supratympanic flange)
1410 stepping abruptly into steeply aligned, poorly ornamented portion (1). (Fröbisch & Reisz
1411 2008).
- 1412 **62. *Semilunar flange***. Supratemporal without ventral projection into otic notch (0), or
1413 supratemporal forming marked ventral flange participating in medial bordering of otic notch
1414 (1). (Schoch 2013).
- 1415 **63. *Jugal***. Reaches orbit (0), excluded from orbit (1), absent (2). (Laurin & Reiz 1997)
- 1416 **64. *Jugal (ventral process)***. No ventral outgrowth (0), or insula jugalis framing subtemporal
1417 window (1). (Schoch 2013).
- 1418 **65. *Jugal (anterior extension)***. Jugal ending at or behind level of anterior orbit margin (0), or
1419 extending anteriorly (1). (Schoch 2013).
- 1420 **66. *Jugal-lacrima***. In contact (0), or separated by orbit or palate bones (1). (Schoch 2013).
- 1421 **67. *Intertemporal***. Present (0), absent (1). (Schoch 2013).

- 1422 **68.** *Intertemporal and postorbital*. Postorbital lateral to postfrontal (0), or expanding medially
1423 to replace intertemporal, contacting parietal (1). (Schoch 2013).
- 1424 **69.** *Tabular*. Present (0), absent (1). (Laurin & Reiz 1997)
- 1425 **70.** *Squamosal-tabular (dorsal)*. Separated by supratemporal (0), or sutured (1). (Schoch 2013).
- 1426 **71.** *Tabular and squamosal*. Forming either squamosal embayment or straight posterior margin
1427 (0), or projecting posteriorly, with tabular extended posterolaterally (1). (Schoch 2013).
- 1428 **72.** *Squamosal (falciform crest)*. Posterior rim of squamosal straight (0), or with convex
1429 projection, referred to as falciform crest (1). (Schoch 2013).
- 1430 **73.** *Tabular (horn)*. Present in some form (0), or entirely absent (1). (Schoch 2013).
- 1431 **74.** *Tabular (extension)*. Tabular horn pointing posteriorly if present (0), or aligned laterally
1432 (1), or sutured with squamosal posterior to otic notch (cyclotosaur condition) (2). (Schoch
1433 2013).
- 1434 **75.** *Tabular (ventral crest)*. Absent (0), or present and shallow (1), or forming a deep ridge that
1435 almost doubles the thickness of the tabular in occipital view (2). These character-states were
1436 ordered. (Schoch 2013).
- 1437 **76.** *Quadratojugal (medial process)*. Absent (0), or present (1). (Schoch 2013).
- 1438 **77.** *Quadratojugal-maxilla*. In contact (0), or separated by jugal (1). (Schoch 2013).
- 1439 **78.** *Quadrate (dorsal process)*. Absent (0), or present (1). (Schoch 2013).
- 1440 **79.** *Posterior skull rim*. Quadrate trochlea posterior to tabular horns (0), or at one level or
1441 anterior (1). (Schoch 2013).
- 1442 Braincase and Occiput
- 1443 **80.** *Occipital flange*. Descending flange of occipital portion of postparietals forming a bulge
1444 (0), or long smooth blades as long as the dermal portion of the postparietal (1). (Schoch
1445 2013).
- 1446 **81.** *Postparietal number*. Two (0), one (1), absent (2). (Laurin & Reiz 1997)

- 1447 **82. *Postparietal-exoccipital*.** No contact (0), or pillar-like dorsal process of exoccipital firmly
1448 sutured to ventral side of postparietal and oblique process of exoccipital sutured with ventral
1449 ramus of tabular (1). (Schoch 2013).
- 1450 **83. *Postfenestral window*.** Large opening, having at least double the width of the foramen
1451 magnum (0), or reduced to a tiny foramen (1). (Yates & Warren 2000).
- 1452 **84. *Quadrate and occipital condyles*.** Quadrate condyles posterior to occipital ones (0), or at
1453 same level (1), or well anterior (2). (Yates & Warren 2000).
- 1454 **85. *Epipterygoid*.** Simple rod-like ascending process (0), or complicated and robust element
1455 with up to six processes (1). (Schoch 2013).
- 1456 Dentition
- 1457 **86. *Dentition (marginal)*.** Heterogenous, varying sizes and distances (0), or homogeneous,
1458 small teeth, equidistant (1). (Schoch & Milner 2000).
- 1459 **87. *Dentition (upper jaw)*.** Conical to slightly curved inwards (0), or caniniform (1). (Dilkes
1460 1990).
- 1461 **88. *Dentition (marginal, tooth bases)*.** Round or oval (0), or forming transversely broadened
1462 ovals (1). (Schoch & Milner 2000).
- 1463 **89. *Palatal tusks (cross-section)*.** Round or oval (0), or laterally compressed and keeled at least
1464 on one side (1). (Schoch 2013).
- 1465 **90. *Dentition (vomer)*.** Tooth patches present at least in small specimens (0), or dentition
1466 entirely restricted to vomerine fangs (1). (Schoch 2013).
- 1467 **91. *Pedicely*.** All teeth formed consisting of a single mineralized conus (0), or at least some
1468 teeth with two separate mineralization centers (pedicellate) (1). (Schoch 2013).
- 1469 **92. *Bicuspidity*.** All teeth with single tip (0), or at least some with bicuspid crowns (1). (Schoch
1470 2013).

- 1471 **93.** *Labyrinthodonty*. Teeth with labyrinth infolding of dentine and enamel at base (0), or never
1472 labyrinthodont (1). (Schoch 2013).
- 1473 **94.** *Transverse tooth row (transvomerine)*. Absent (0), present and transverse (1), V-shaped (2).
1474 (Schoch 2013).
- 1475 **95.** *Additional vomerine fangs*. Vomer with a single pair of fangs at the medial margin of choana
1476 (0), or with additional fangs/fang pairs posteromedially (1). (Schoch 2013).
- 1477 **96.** *Parasphenoid (shagreen)*. Tooth patches present (0), or teeth entirely absent (1). (Yates &
1478 Warren 2000).
- 1479 **97.** *Ectopterygoid (fangs)*. Present (0), or absent (1). (Yates & Warren 2000).
- 1480
- 1481 Palate
- 1482 **98.** *Interpterygoid vacuities*. Slender and slit-like (0), or rounded, oval openings (1). (Schoch
1483 2013).
- 1484 **99.** *Interpterygoid vacuities, pterygoid*. Vacuities rounded bordered by moderately concave
1485 pterygoid (0), or laterally greatly extended at mid-level pushing pterygoid to the margin (1).
1486 (Schoch 2013).
- 1487 **100.** *Anterior palatal opening(s)*. Vomer and premaxilla with continuous suture (0), or
1488 perforated to accommodate symphyseal fangs (1). (Schoch 2013).
- 1489 **101.** *Anterior palatal opening(s)*. Unpaired if present (0), or paired (1). (Schoch 2013).
- 1490 **102.** *Vomer*. Narrow and small (0), or large plate, widely separating choanae (1). (Schoch
1491 2013).
- 1492 **103.** *Vomer (paired anterior depressions)*. Absent (0), or present (1). (Schoch 2013).
- 1493 **104.** *Anterior palatal depression*. Posterior rim round if present (0), or straight transverse (1).
1494 (Schoch & Milner 2000)

- 1495 **105.** *Vomerine ridges*. Absent (0), or present, radiating from vomerine tusks anteriorly (1).
1496 (Schoch 2013).
- 1497 **106.** *Vomerine pit and fontanelle*. Absent (0), or pit present (posterior to mandible) (1), or
1498 fenestra within such pit (2). (Schoch & Rubidge 2005, modified).
- 1499 **107.** *Vomerine septum*. Absent (0), or present (1). (Polley & Reisz 2011).
- 1500 **108.** *Choana (lateral)*. Anterolaterally expanded with triangular outline (0), or oval (1).
1501 (Schoch 2013).
- 1502 **109.** *Choana (medial)*. Medial margin straight or gently convex (0), or anteromedially
1503 expanded giving choana a reniform outline (1). (Schoch 2013).
- 1504 **110.** *Choana (width)*. Elongated oval to slit-like (0), or wide round (1). (Schoch 2013).
- 1505 **111.** *Vomer-pterygoid*. Sutured (0), or separated by palatine (1). (Schoch 2013).
- 1506 **112.** *Vomer (anterior part)*. Anterior portion shorter than behind anterior level of choana (0),
1507 or as long or longer (1). (Schoch 2013).
- 1508 **113.** *Vomer (extension)*. Vomer contacts pterygoid lateral to choana (0), or expanding
1509 posteriorly (1). (Schoch 2013).
- 1510 **114.** *Basipterygoid ramus*. Pterygoid with short, posteromedially curved basipterygoid process,
1511 constricting palatal vacuities posterolaterally (0), or with transversely extended process
1512 producing posteriorly wider vacuities (1). (Schoch 2013).
- 1513 **115.** *Basicranium (contact)*. Joint between basal plate and pterygoid (0), or sutural contact (1).
1514 (Schoch 2013).
- 1515 **116.** *Basicranium, suture*. Suture (if present) much shorter than basal plate, reaching at best
1516 40% its length (0), or suture almost as long as basal plate (1). (Schoch 2013).
- 1517 **117.** *Parasphenoid*. Suturing with exoccipitals (0), or underplating exoccipitals (1). (Schoch
1518 2013).

- 1519 **118.** *Basicranium (carotids)*. Internal carotids entered basicranium ventrally near base of
1520 cultriform process (0), or at posterolateral corner of bone (1). (Shishkin 1968; Boy 1988).
- 1521 **119.** *Parasphenoid plate*. Basal plate sagittally rectangular (0), or quadrangular to wider than
1522 long (1), or much abbreviated, transversely rectangular (2). (Greatest length measured
1523 against shortest width). (Schoch 2013).
- 1524 **120.** *Parasphenoid plate (size)*. Basal plate at level posterior to basicranial joint substantially
1525 narrower than parietals (0), or as wide or wider (1). (Schoch 2013).
- 1526 **121.** *Cultriform process (width)*. Base not wider than rest, clearly set off from basal plate (0),
1527 or merging continuously into plate (1). (Schoch 2013).
- 1528 **122.** *Cultriform process (structure)*. Ventrally flat (0), or with ridge emplaced on broader base
1529 (1), or knife-edged and keel-shaped (2). (Schoch 2013).
- 1530 **123.** *Cultriform process (outline)*. Of similar width throughout (0), or posteriorly expanding
1531 abruptly to about twice the width (1). (Schoch 2013).
- 1532 **124.** *Cultriform process (dentition)*. Main shaft edentulous except for base (0), or with elongate
1533 tooth patch (1). (Schoch 2013).
- 1534 **125.** *Parasphenoid (posterolateral process)*. Posterolateral margin straight (0), or with lateral
1535 wing (1). (Schoch 2013).
- 1536 **126.** *Pterygoid (ventral ornament)*. Palatine ramus of pterygoid smooth (0), or ornamented with
1537 reticulate ridges (1). (Schoch 2013).
- 1538 **127.** *Pterygoid, exoccipital*. No contact (0), or sutured lateral to parasphenoid (1). (Schoch
1539 2013).
- 1540 **128.** *Pterygoid, basioccipital*. No contact (0), or sutured lateral to parasphenoid (1). (Schoch
1541 2013).
- 1542 **129.** *Pterygoid, squamosal*. Entirely sutured (0), or with open fissure (1). (Warren & Black
1543 1986; Englehorn *et al.* 2008).

- 1544 **130.** *Pterygoid (flange)*. Palatine ramus of pterygoid merging continuously into basipterygoid
1545 ramus (0), or broadening abruptly to form transverse flange (1). (Schoch 2013).
- 1546 **131.** *Pterygoid width*. Palatine and quadrate regions forming slender rami (0), or broad shelves
1547 (1). (Schoch 2013).
- 1548 **132.** *Pterygoid, ectopterygoid*. Palatine ramus exclusively formed by pterygoid (0), or with
1549 posteromedial projection of ectopterygoid (1). (Schoch 2013).
- 1550 **133.** *Pterygoid-palatine-ectopterygoid*. Pterygoid contacting both ectopterygoid and palatine
1551 (0), or pterygoid only in contact with ectopterygoid (1). (Schoch 2013).
- 1552 **134.** *Palatine, ectopterygoid*. With simple, transverse suture (0), or palatine with posterolateral
1553 process excluding the ectopterygoid from interpterygoid vacuity and contacting pterygoid
1554 (1). (Schoch 2013).
- 1555 **135.** *Palatine, vomer*. Suture aligned posterolaterally (0), or with medial wing framing the
1556 interpterygoid vacuity anteriorly (1). (Schoch 2013).
- 1557 **136.** *Palatine (laterally exposed palatine, LEP)*. Absent (0), or present (1). (Schoch 2013).
- 1558 **137.** *Palatine, ectopterygoid (ontogeny)*. Maintain their width (0), or become proportionally
1559 wider (1). (Schoch & Witzmann 2009a; recoded).
- 1560 **138.** *Palatine, ectopterygoid (width)*. Much wider than maxilla (0), or as narrow (1).
1561 Amphibamidae. (Schoch 2013).
- 1562 **139.** *Palatine, ectopterygoid (continuous tooth row)*. Absent (0), or present (1). (Schoch 2013).
- 1563 **140.** *Ectopterygoid (length)*. As long or longer than palatine (0), or markedly shorter (1).
1564 (Schoch 2013).
- 1565 **141.** *Ectopterygoid (laterally exposed ectopterygoid, LEE)*. Absent (0), or present (1). (Schoch
1566 2013).
- 1567 **142.** *Ectopterygoid (Y-shaped)*. Ectopterygoid with continuous maxillar suture (0), or Y-
1568 shaped, with posterior half separated from maxilla by a gap (1). (Schoch 2013).

- 1569 **143. *Palate structure.*** In occipital view, pterygoids either sloping continuously ventrolaterally
1570 or flat horizontal (0), or vertically curved ventrally at right angle with basicranium (1).
1571 (Schoch 2013).
- 1572 **144. *Quadrate trochlea.*** Medial bulge only slightly larger than lateral one (0), or being at least
1573 two times longer and twice as wide (1). (Schoch 2013).
- 1574 **145. *Occipital condyle.*** Trilobed, with basioccipital forming ventral part of facet (0), or bilobed
1575 exoccipital condyle with reduced basioccipital contribution (1). (Schoch 2013).
- 1576 **146. *Exoccipital condyles.*** Short and broad base, projecting only with their posterior half behind
1577 the rim of the skull table (0), or almost the complete element posterior to level of occipital
1578 flange (1). (Schoch 2013).
- 1579 **147. *Basioccipital (length).*** Forming a long element posterior to parasphenoid plate (0), or
1580 foreshortened to a narrow posterior rim of the palatal bone (1). (Schoch 2013).
- 1581 **148. *Dentigerous palatal ossicles.*** Absent (0), or present within interpterygoid vacuities (1).
1582 (Schoch 2013).
- 1583 **149. *Postglenoid area.*** Absent or present as very faint outgrowth (0), or longer than glenoid
1584 facet (1). (Schoch 2013).
- 1585 **150. *Postglenoid area (types).*** Type 1 (0), or type 2 (1). (Jupp & Warren 1986).
- 1586 **151. *Postglenoid area (dorsal).*** Plain (0), or with elongated groove (1). (Schoch 2013).
- 1587 **152. *Hamate process.*** Absent (0), present (1). (Writers).
- 1588 **153. *Hamate process.*** Absent (0), or present but lower than postglenoid portion is long (1), or
1589 as high as retroarticular process (2). (Schoch 2013).
- 1590 **154. *Torus arcuatus (Preglenoid process)*** . Labial side of surangular with straight dorsal
1591 margin anterior to glenoid (0), or forming dorsal projection well above the level of the
1592 glenoid articulation (1). (Schoch 2013).

- 1593 **155.** *Torus arcuatus (Preglenoid process)*. Present thickening in the dorsal edge (0) dorsal edge
1594 without thickening (1). (Writers).
- 1595 **156.** *Postglenoid process Hook-Like*. Absent (0), present, however poor developed, with
1596 retroarticular process aspx lower than or at the torus arcuatus level (1), present and well
1597 developed, with retroarticular process aspx above the torus arcuatus level (2). (Writers).
- 1598 **157.** *Glenoid fossa and torus arcuatus*. Glenoid fossa lie below the torus arcuatus level (0), or
1599 above the torus arcuatus level (1). (Damiani 1999).
- 1600 **158.** *Meckelian foramen*. Single, longer than high (proportion 2:1) (0), presence of separated
1601 anterior and posterior foramina, both well developed, with length greater than or equal to
1602 its height (1), Single posterior Meckelian foramen, with length greater than or equal to its
1603 height (2). (Schoch 2013).
- 1604 **159.** *PMF center*. Placed anteriorly to the anterior edge of the adductor fossa (0), approximately
1605 below to the anterior edge of the adductor fossa (1), placed posteriorly to the anterior edge
1606 of the adductor fossa. (Jupp & Warren 1986).
- 1607 **160.** *PMF position*. Approximately equidistant between the ventral and dorsal mandibular edge
1608 (0), close to, or on ventral mandibular edge (1). (Jupp & Warren 1986).
- 1609 **161.** *PMF (Posterior Meckelian Foramen)*. Small round or oval opening (0), or elongate
1610 window shorter than the adductor fossa (1), or as long or longer as adductor fossa (2).
1611 (Writers).
- 1612 **162.** *Symphyseal teeth*. No accessory teeth posterior to symphyseal tusks (0), or a transverse
1613 row of such teeth (1). (Yates & Warren 2000).
- 1614 **163.** *Posterior coronoid teeth*. Present (0), or absent (1). (Schoch 2013).
- 1615 **164.** *Anterior, middle coronoid teeth*. Present (0), or absent (1). (Schoch 2013).
- 1616 **165.** *Mandibular osteoderms*. Throat region naked (0), or covered with a mosaic of ventral
1617 osteoderms between mandible and dermal pectoral girdle (1). (Schoch 2013).

- 1618 **166.** *Mandibular sensory canal.* Present (0), absent (1). (Clack 2002).
- 1619 **167.** *Mandibular canal exposure.* Entirely enclosed (0), mostly enclosed (1), mostly
 1620 or entirely open (2). (Clack 2002).
- 1621 **168.** *Oral sulcus of mandibular canal.* Absent (0), present (1). (Clack 2002).
- 1622 **169.** *Accessory sensory canal.* Absent (0), present (1). (Writers).
- 1623 Visceral skeleton
- 1624 **170.** *Stapes (quadrate process).* Absent (0), or present (1). (Schoch 2013).
- 1625 **171.** *Stapes (ventral process).* Absent (0), or present, giving the proximal region two heads (1).
 1626 (Schoch 2013).
- 1627 **172.** *Stapes (shape).* Robust, tetrahedral bone with substantial quadrate process (0), or rod-like
 1628 element with elongated stylus (1), or blade-like (2). (Schoch 2013).
- 1629 **173.** *Stapes (curvature).* Stapes with pronounced dorsodistal curvature (0), or abbreviated
 1630 without such curvature, directed laterally towards vertically aligned otic notch (1). (Schoch
 1631 2013).
- 1632 **174.** *Ceratobranchials.* Bony elements absent (0), present in adults (1). (Schoch 2013).
- 1633 **175.** *Basibranchial.* Bony element absent (0), present in adults (1). (Schoch 2013).
- 1634 **176.** *Hypobranchial elements.* Bony elements absent (0), present in adults (1). (Schoch 2013).
- 1635 **177.** *Branchial denticles.* Conical and attached to small ossicles in groups of 2–10 (0), or free
 1636 and with brush-like end (1). (Schoch 2013).
- 1637 Axial skeleton
- 1638 **178.** *Presacral count.* More than 28 (0), or 23–25 vertebrae (1), or less than 21 (2) (Character-
 1639 states not ordered). (Witzmann & Schoch 2006a). (Schoch 2013).
- 1640 **179.** *Caudal count.* Similar to presacral count or higher (0), or much lower (1). (Schoch 2013).
- 1641 **180.** *Transverse process (orientation).* Short, directed posteriorly (0), or distally extended with
 1642 diapophysis pointing laterally (1). (Schoch 2013).

- 1643 **181.** *Transverse process (length)*. Shorter than dorsal spine is high (0), or markedly longer (1).
1644 (Schoch 2013).
- 1645 **182.** *Neural spine (height)*. As high as distance between zygapophyses (0), or higher (1).
1646 (Witzmann & Schoch 2006a).
- 1647 **183.** *Intercentrum (dorsal view)*. Presacral intercentra opened (0), or closed (1). (Modified from
1648 Yates & Warren 2000). (Schoch 2013).
- 1649 **184.** *Intercentrum (shape in lateral view)*. Wedge-like presacral intercentrum (0), or in cylinder
1650 shape (1). (Modified from Yates & Warren 2000).
- 1651 **185.** *Intercentrum (width)*. Chordal canal wider than intercentrum high (0), narrower (1).
1652 (Witzmann & Schoch 2006a).
- 1653 **186.** *Intercentrum (ventral surface)*. Ventral surface shorter than wide in ventral view, giving
1654 transversely rectangular outline (0), or as long as wide, quadrangular (1). (Schoch 2013).
- 1655 **187.** *Intercentrum anterior surface*. Always concave (0), or convex at least in some presacral
1656 centra (1). (Warren & Snell 1992)
- 1657 **188.** *Parapophysis*. Segmental (0), or intersegmental (1). (Warren & Snell 1992).
- 1658 **189.** *Pleurocentrum (presence)*. Ossified (0), unossified (1). (Witzmann & Schoch 2006a).
- 1659 **190.** *Pleurocentrum(lateral surface)*. As large as that of intercentrum (0), or smaller (1).
1660 (Witzmann & Schoch 2006a).
- 1661 **191.** *Pleurocentrum (ventral extension)*. Wedged between successive intercentra and not
1662 reaching ventral margin of intercentra (0), or pleurocentra ventrally expanded to near each
1663 other (1), or ventrally fused to form a single cylindrical element (2). (Schoch & Rubidge
1664 2005).
- 1665 **192.** *Ribs (length)*. Moderately elongate thoracic ribs curved distoventrally (0), or such ribs
1666 foreshortened without distal curvature (1). (Schoch 2013).

- 1667 **193.** *Ribs (ventral extension)*. Rib heads (tuberculum and capitulum) confluent (0), or clearly
1668 set off and widely separated in mid-trunk region (1). (Schoch 2013).
- 1669 **194.** *Ribs (uncinate blades)*. If present, small and spine-like (0), or extensive and blade-like (1).
1670 (Witzmann & Schoch 2006a).
- 1671 **195.** *Ribs (uncinate spines)*. Short (0), or elongated, as long as shaft (1). (Schoch 2013).
- 1672 **196.** *Cleithrum*. With broadened dorsal head region (0), or a simple rod (1). (Schoch 2013).
- 1673 **197.** *Cleithrum*. Head with slightly convex or straight anterior rim (0), or with pronounced
1674 anterior projection (1). (Schoch 2013).
- 1675 **198.** *Cleithrum*. Dorsal head region confined to anterior rim of scapula (0), or posteriorly
1676 extended to cover dorsal rim of scapula (1). (Schoch 2013).
- 1677 **199.** *Clavicle (ventral blade)*. Wide, triangular, overlapping interclavicle broadly (0), or
1678 slender, with minor overlap (1). (Schoch 2013).
- 1679 **200.** *Interclavicle (length)*. Shorter than posterior skull (0), or substantially longer (1). (Schoch
1680 2013).
- 1681 **201.** *Interclavicle (ontogeny)*. Without major proportional change in ontogeny (0), or
1682 decreasing proportionally relative to skull length (1). (Schoch 2013).
- 1683 **202.** *Interclavicle (central ornamented area)*. Rhomboidal (0), or pentagonal and posteriorly
1684 widest (1). (Schoch 2013).
- 1685 **203.** *Interclavicle (proportions)*. As long as wide (0), or 1.3 times as long as wide (1), or more
1686 than twice as long as wide (2). (Schoch 2013).
- 1687 **204.** *Interclavicle (posterior margin)*. With posterior process (0), or transversely straight (1).
1688 (Schoch 2013).
- 1689 **205.** *Interclavicle (anterior margin)*. Serrated (0), or smooth (1). (Schoch 2013).

- 1690 **206.** *Interclavicle (anterior stylus)*. Anterior portion of interclavicle variably shaped but not
1691 longer than posterior one, as measured by the centre of ornamentation (0), or substantially
1692 longer than posterior one (1). (Schoch 2013).
- 1693 **207.** *Interclavicle (posterior stylus)*. Posterior end rounded or blunt (0), or with elongated stylus
1694 or parasternal process (1). (Schoch 2013).
- 1695 **208.** *Interclavicle, clavicles*. Clavicles broadly separated by interclavicle ventrally (0), or
1696 leaving only narrow stripe of interclavicle in between (1), or in contact and excluding
1697 anterior part of interclavicle from ventral exposure (2). (Schoch 2013).
- 1698 Limb skeleton
- 1699 **209.** *Scapula (glenoid facet)*. Ossified (0), or unossified in adults (1). (Witzmann & Schoch
1700 2006a).
- 1701 **210.** *Scapula (height)*. Maximally two times longer (higher) than wide (0), or dorsally extended
1702 and fully ossified, three times higher than wide (1). (Schoch & Rubidge 2005).
- 1703 **211.** *Humerus (ontogeny)*. Short cylinder in larvae, elongates at slow rate (0), or with
1704 substantial shaft in larvae (1), or very long rod from small stages on (2). (Boy 1972).
- 1705 **212.** *Humerus (adult shaft)*. No shaft proper, humerus blade-like in cross-section (0), or with
1706 short shaft oval in cross-section (1), or shaft elongate and slender, comprising more than
1707 50% of the humerus with rounded cross-section (2). (Schoch 2013).
- 1708 **213.** *Humerus (entepicondylar foramen)*. Present (0), or absent (1). (Schoch 2013).
- 1709 **214.** *Humerus (supinator)*. Present (0), or absent (1). (Yates & Warren 2000).
- 1710 **215.** *Humerus (condyles)*. Distal end at least partially ossified with identifiable condyles (0), or
1711 unfinished without condyles (1), or with fully established condyles (2). (Schoch & Rubidge
1712 2005, modified).
- 1713 **216.** *Humerus (torsion)*. Strong, 70-90° (0), or weak, well below 60° (1) (Witzmann & Schoch
1714 2006a).

- 1715 **217.** *Carpals*. All unossified (0), or all at least some ossified (1). (Schoch 2013).
- 1716 **218.** *Manual digit count*. Five (0), or four (1). (Schoch 2013).
- 1717 **219.** *Feet digit count*. More than five (0), five (1), less than five (2). (Schoch 2013).
- 1718 **220.** *Ilium (shaft)*. Shaft of variable length but laterally flattened (0), or very long and slender
1719 (1). (Schoch 2013).
- 1720 **221.** *Ilium (dorsal end)*. Tip of dorsal end continuous (0), or much broadened (1).
- 1721 **222.** *Ilium (height)*. Shaft more than twice the length of the base (0), or shorter (1). (Schoch &
1722 Rubidge 2005).
- 1723 **223.** *Ilium (orientation)*. Main axis of shaft inclined posterodorsally (0), or vertical (1).
- 1724 **224.** *Ilium (tip)*. Dorsal end two-headed (0), or single-headed (1). (Schoch 2013).
- 1725 **225.** *Pubis*. Unossified (0), or ossified (1). (Schoch 2013).
- 1726 **226.** *Femur*. Intercondylar fossa forming deep and elongated trough (0), or reduced to short
1727 depression (1). (Yates & Warren 2000).
- 1728 **227.** *Femur (trochanter)*. Internal trochanter present as discrete process (0), or reduced to a
1729 shallow crest (1), or greatly enlarged to form a massive projection (2). (Schoch 2013).
- 1730 **228.** *Tarsals*. At least some are ossified (0), or all unossified (1). (Schoch 2013).
- 1731 **229.** *Gastral squamation*. Ossified ventral dermal scales (0), or scales absent (1). (Yates &
1732 Warren 2000).
- 1733 **230.** *Squamation*. Dermal scales oval to spindle-shaped (0), or broad-oval with “microsaur-
1734 type” ornament (1). (Boy 1972).
- 1735 **231.** *Osteoderms*. Absent (0), or present as single row (1), or more numerous to form a carapace
1736 (2). (Schoch 2013).
- 1737 **232.** *Osteoderms (articulations)*. Simple set of osteoderms arranged in one layer if present (0),
1738 or double set of two layers, the ventral one fused to the tip of the neural arch (1). (Schoch
1739 2013).

- 1740 **233.** *Osteoderms (width)*. An intra-dissorophid character: Narrow median osteoderms (0), or
1741 transversely extended plates (1). (Schoch 2013).
- 1742 **234.** *Rib cage*. Trunk narrower than skull or as wide (0), or trunk substantially wider than lateral
1743 margin of cheeks at about mid-level (1). (Schoch 2013).
- 1744 **235.** *Postero-lateral skull corners*: anterior to distal end of tabular horns (1); posterior to distal
1745 end of tabular horns (0). (Damiani 2001).
- 1746 **236.** *Tabular horns*: laterally directed (1); suturing with the squamosal posteriorly (2);
1747 posteriorly directed (0). (Damiani 2001).
- 1748 **237.** *Occipital sensory canal*: present (1); absent (0). (Damiani 2001).
- 1749 **238.** *Frontal*: enters medial border of orbit (1); excluded from medial border of orbit (0).
1750 (Damiani 2001).
- 1751 **239.** *Preorbital projection of jugal*: elongated (1); abbreviated (0). (Damiani 2001).
- 1752 **240.** *Prefenestral division of palate*: elongated (1); abbreviated (0). (Damiani 2001).
- 1753 **241.** *Suture between pterygoid and parasphenoid*: antero-posteriorly elongated (1); short (0).
1754 (Damiani 2001).
- 1755 **242.** *Ectopterygoid*: enters margin of interpterygoid vacuity (1); excluded from margin of
1756 interpterygoid vacuity (0). (Damiani 2001).
- 1757 **243.** *Crista muscularis of parasphenoid*: level with posterior border of pterygoid arasphenoid
1758 suture (1); behind posterior border of pterygoid-parasphenoid suture (0). (Damiani 2001).
- 1759 **244.** *Crista muscularis of parasphenoid*: confluent in midline (1); not confluent in midline (0).
1760 (Damiani 2001).
- 1761 **245.** *Marginal teeth*: strongly antero-posteriorly compressed at base (1); sub-circular or circular
1762 at base (0). (Damiani 2001).
- 1763 **246.** *Denticle field*: absent from pterygoid and parasphenoid (1); present on pterygoid and
1764 parasphenoid (0). (Damiani 2001).

- 1765 **247.** *Posttemporal fenestrae*: triangular (1); narrow and slitlike (0). (Damiani 2001).
- 1766 **248.** *Oblique ridge of pterygoid*: tall, crest-like (1); poorly developed (0). (Damiani 2001).
- 1767 **249.** *Crista muscularis of the parasphenoid*: not visible in occipital view (1); visible in occipital
1768 view (0). (Damiani 2001).
- 1769 **250.** *Basioccipital*: absent (1); present (0). (Damiani 2001).
- 1770 **251.** *Prearticular*: does not suture anteriorly with splenial (1); sutures anteriorly with splenial
1771 (0). (Damiani 2001).
- 1772 **252.** The parietal longer than the supratemporal and much longer than the postparietal (0); the
1773 parietal abbreviated, so that it, the postparietal, and the supratemporal are of similar length
1774 (1). (Fortuny *et al.* 2011).
- 1775 **253.** The postparietal and tabular are shorter than the parietal and supratemporal (0), or they
1776 extend posteriorly to give bones of similar length (1). (Fortuny *et al.* 2011).
- 1777 **254.** The postorbital and prefrontal are widely separated (0), near each other with thin
1778 projections (1), or sutured, excluding the jugal from the orbital margin (2). (Fortuny *et al.*
1779 2011).
- 1780 **255.** Ventrolateral border of the orbit formed by the jugal and lacrimal (0), lateral edge of the
1781 corpus of the palatine exposed dorsally in the lateral margin of the orbit (1). Yates and
1782 Warren (2000).
- 1783 **256.** Postparietal pair less than four times wider, transversely, than anteroposteriorly long (0),
1784 greater than four times wider than long (1). Yates and Warren (2000).
- 1785 **257.** Maxilla and nasal not in contact (0), maxilla and nasal forming a suture (1). Yates and
1786 Warren (2000).
- 1787 **258.** Septomaxilla part of the skull roof forming the posterior nasal margin, or unossified (0),
1788 septomaxilla a large plate of bone forming the floor of the nasal cavity, with limited, if any,
1789 contact with the skull roof at the posterior nasal margin (1). Yates and Warren (2000).

- 1790 **259.** Orbits located about halfway along the skull length (0), orbits located in front of the
1791 midlength of the skull (1), orbits located behind midlength of the skull (2). Yates and
1792 Warren (2000).
- 1793 **260.** Prefrontal excluded from narial margin (0), prefrontal contributing to the narial margin
1794 (1). Yates and Warren (2000).
- 1795 **261.** Skull roof complete between the nostrils (0), medial internarial fenestra at the junction of
1796 the premaxillae and the nasals (1). Yates and Warren (2000).
- 1797 **262.** Pterygoids extend anteriorly to the palatine tusks (0) pterygoids not extending anterior to
1798 the level of the palatine tusks (1). Yates and Warren (2000).
- 1799 **263.** Maxilla and vomer not in contact or in point contact (0), maxilla and vomer forming a
1800 suture (1). Yates and Warren (2000).
- 1801 **264.** Posterior premaxillary teeth of equal size or smaller than the anterior premaxillary teeth
1802 (0), posterior premaxillary teeth larger than anterior premaxillary and maxillary teeth (1).
1803 Yates and Warren (2000).
- 1804 **265.** Maxilla forming most of the lateral border of choanae (0), lateral processes of vomer and
1805 palatine approach one another so as to reduce the maxillary contribution (1). Yates and
1806 Warren (2000).
- 1807 **266.** Absence of a toothrow behind the palatine tusks (0), 4–6 palatine teeth (1), more than eight
1808 palatine teeth (2). Yates and Warren (2000).
- 1809 **267.** Medial margin of the choana without teeth (0), medial margin of the choana with a row of
1810 teeth (1). Yates and Warren (2000).
- 1811 **268.** Palatal surface of the premaxillae smooth (0), rugose, medial tubercle on the palatal
1812 surface of the premaxillae (1). Yates and Warren (2000).

1813 **269.**Prearticular extending anteriorly, at least as far as the level of the midpoint of the middle
1814 coronoid (0), prearticular not extending anterior to the level of the suture of the middle and
1815 posterior coronoids (1). Yates and Warren (2000).

1816 **270.** Posterior Meckelian foramen bordered by the prearticular, postsplenic and angular (0),
1817 posterior Meckelian foramen bordered by the prearticular and postsplenic exclusively (1).
1818 (Yates and Warren, 2000).

1819 **271.** Prearticular not extending posterior to the level of the glenoid (0), prearticular extending
1820 posterior to the glenoid, covering the medial face of the articular (1). Yates and Warren
1821 (2000).

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1835 **APPENDIX 3. Matrix data**

1836 *Acanthostega gunnari*

1837 0?000??000 0000000001 0000000??1 000000?000 010000100? 0001111000 ?000101001
1838 10000?0?0? 0??0?00000 0000010001 101101?100 0?0?0????? ?0?00?100 ?00000?100
1839 00?0??0000 0002100001 0000?01001 ???????000 000000?0?0 0100?0100? ?000?????0
1840 ??00??1000 00011000?? ????-?000 -0-?00??0 ?000-00000 -00102100- 0

1841 *Proterogyrinus scheelei*

1842 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 00?0000000
1843 0000000000 000000000? 0000000000 0000000000 0000000000 0000000000 0000000000
1844 0000000000 0000000001 00001?0000 000000?000 0100000000 0000000000 0000000000
1845 ?000000100 0000000100 000000?00? ?0-?00??10 ?000000000 00?0?1?000 0

1846 *Greererpeton burkemorani*

1847 0000000000 0000000000 0000000001 0000000000 0000100000 000001-000 00?0000000
1848 0010001000 000000000? 0000000001 1000000000 0000000000 0000000000 0000000000
1849 0000000000 0002011001 1000102100 0000100000 0000000000 0000000000 0000000000
1850 ?000000100 0010000100 0000--0000 00-?0000?0 ?000000?01 0001?10000 0

1851 *Edops craigi*

1852 0000000010 1000100000 0000000001 0001000010 0000001000 0010000000 00?0100000
1853 0000001000 0100000000 0000000100 0100100100 0100100001 0000000000 0000000000
1854 0000000?00 0000??0?0? ?00?????01 110000???? ??????????0 000?00000? ??????????
1855 ?10000???? ?01?????00 ?00001000? 00010000?0 ?000?10000 0001?0?0?? 0

1856 *Adamaterpeton ohioensis*

1857 0000001010 1000100000 0000000001 0001000000 0000001000 0010000000 00??100000
1858 000000?000 0100000000 0000000100 0100100100 0100100001 0000000000 0000000000

1859 00000001?0 ?000??021 200?????? ?0000?? ???? ?????? ?????????? ??????????

1860 ?????????? ?01?????? ?0000?000 000100?? ?000?10000 01000001?0 ?

1861 *Cochleosaurus bohemicus*

1862 0000001010 1000100000 0000000011 1001000000 0000001000 0010000000 00?1100000

1863 0000000010 0101000000 0000000100 0100100100 0100100001 0000000000 0000000000

1864 0000000100 0000000001 200??0200? ??000?100 0000000000 0000000000 0000000010

1865 01001?1?00 00100??00 000001000? 000100??0 ?000?00020 0100000000 0

1866 *Nigerpeton ricqlesi*

1867 0000001010 1000100000 0000000001 1001000011 0000001000 0010000000 00??100000

1868 0000001000 0100?00000 0000000101 1100100100 0100100001 0000000000 0000000000

1869 00000001?0 ?000??0?? ?0??0200? ??000???? ?????????? ?????????? ??????????

1870 ?????????? ?01?????? ?000010011 00??01?1?0 ?000?10020 ?1111000?? ?

1871 *Chenoprosopus milleri*

1872 0000001010 1000100000 0000000011 1001000001 0000001000 0010000000 00??100000

1873 0000001000 0100000000 0000000100 0100100100 0100100001 0000000000 0000000000

1874 0000000?00 0000?000?? ?0???????? ?0000???? ?????????? ?????????? ??????????

1875 ?1??????0? 001?????? ?000??00? ?????????? ???0??1020 0????????? ?

1876 *Dendrerpeton acadianum*

1877 0000000001 0010000000 0000000001 0001000000 0000000000 0000000000 00?0000000

1878 0000001000 0101000000 0000000100 0100000100 0001000001 0000000000 0000000000

1879 0000000?00 00000??011 ?00??????1 110000?100 0000000000 0100000000 0000000000

1880 ?101001200 0010000100 000001000? 000100???? ?000010100 11001010?0 ?

1881 *Balanerpeton woodi*

1882 0000000001 0000100000 000000?000 0001000000 0000000000 0000000000 00?0000000

1883 0000001000 0100000000 0000000100 0100000000 0001000001 0000000000 0000000000

1884 0000000?00 0000000021 1001?????1 110000?100 0000000000 0100000000 0000000000

1885 0101001200 0010000100 0000010000 000100???0 ?000000110 010000101- 0

1886 *Trimerorhach isinsignis*

1887 0000000001 0000100000 0001011000 0000000000 0100100000 0000000000 00?0000001

1888 0000001000 0101000001 0001000101 1100000000 0010000001 0100000000 0000000010

1889 0000000?00 0000001021 100??02001 1101110000 0000000000 0000000001 0000000010

1890 ?110110200 0001001100 0000000000 00??0?10?0 ?000000110 011?121010 1

1891 *Neldasaurus wrightae*

1892 0000000001 0000000000 0001011001 0000000001 0000000000 000001-000 00?0000001

1893 0010001000 0101?00001 00000?0101 1100000000 0010000001 0000000000 0000000010

1894 0000000??0 ?000??0000 100??0011? ?????????? ?????????00 1??0????? ??????????

1895 ???????2?? ?01??????0 ?000--0001 ?0??011??0 ?000001?10 011?120??0 0

1896 *Isodectes obtusus*

1897 0000000001 0000010000 0000111001 0000100000 0000100000 000001-000 00?0010000

1898 0010000000 0102?00001 0000010101 1100000000 1000000011 0100000010 0000010000

1899 0000000110 00000001?? ?00??????1 ?10?100000 0000000000 0000000001 0000000010

1900 0111110?10 0011?11?00 0000--0000 00??0????0 ?000100111 01000000?? ?

1901 *Acroploous vorax*

1902 0000000001 0000010000 0000111001 0000100000 0000100000 000001-000 0000011000

1903 001000?010 0102?00001 0000010101 1100000000 1000000011 0000000000 0000010000

1904 0000000?10 00000011?? ?000?????1 ?10????000 0000000000 0??0000001 0000000010

1905 ??1??????0 0011??????0 ?000--0000 00000?10?0 ?000110110 010010000? 1

1906 *Dvinosaurus primus*

1907 0000000001 0000010000 0001011001 0000000000 0000100000 000001-000 0000001101

1908 0000000000 0102000001 0001000101 1100000000 0010000011 1000000010 00000?0010

1909 0000000?10 0000000001 2000?02100 ?20111?000 0000000000 0000000001 0000001010

1910 ?110110?00 0001101?00 000000?000 00?0?0???? ?000000110 0??????00 1

1911 ***Thabanchuia oomie***

1912 0000000001 0000010000 10-0011001 00?0000?00 0000100100 000001-000 00000-1101

1913 0010000010 0102?00001 0000010101 1100000000 1000000?11 1000001110 10100?0000

1914 0000000?10 00000000?? ?0???????? ????1?0?000 0010000000 0000000001 0000001010

1915 ??1???0??? ?0111?1?00 0000??0000 11????00?0 ?00110?111 ?11?10100? 1

1916 ***Tupilakosaurus wetlugensis***

1917 0000000001 0000010000 10-0011001 00?0000?00 00001001?0 ?00001-000 00000-1101

1918 0010000010 0102?00001 0000010101 1100000000 1000000011 1000001110 10100?0000

1919 0000000?10 0000?000?? ?0???????? ????0?000 0010000??0 0????????? ??????????

1920 ?????????? ?01?1????? ?000--0000 10??01???? ?000?01110 01?01000?? ?

1921 ***Acanthostomatops vorax***

1922 0000000111 0011100000 0000000001 1001000000 01001000?1 0100000010 0000101001

1923 0000001010 0101000000 0000000100 0100020000 0001100011 0001000000 0000000000

1924 0000101100 000000?0?? 2000?????1 1100010110 0000000000 0100000010 0000000010

1925 1110110?01 1011?01?10 0000100011 00000????? 1000000020 11000000?? 0

1926 ***Zatrachys serratus***

1927 0000000111 0011100000 0000000001 1001000?00 0100100001 0100000010 0000001001

1928 0000001010 0101?00000 0000000100 0100020000 0001100011 0001000000 0000000001

1929 0000101100 00000?0?? ?0???????? ????0????? ?????????? ?????????? ??????????

1930 ?????????? ??1?????? ?00010000? ?????????? ?000000020 1????????? ?

1931 ***Micromelerpeton credneri***

1932 0000000001 0000000010 0000001100 0000000000 0010110001 0100000000 0100011000

1933 0000011?00 0100?00000 0010100100 0100020000 1001000011 0000000011 0000010000

1934 0000??1?00 00000000?? ?000?????1 110010000 0000000000 1000000010 0000000010

1935 1110010201 0011?11101 000000?100 00???0???? 1000100010 110?011?0? 0

1936 *Limnogyrinus elegans*

1937 0000000001 0000000010 0000001100 00?0000?00 00001100?1 ?100000000 0?00011000

1938 0000011??0 0101?00001 0010000100 0100000000 1001000011 0000000010 00000?0000

1939 0000??1?00 00000?0?? ?00??????1 1110?10000 00????0000 ?000000010 0000000010

1940 111?1?0?0? 0011?11?01 0000?????? ????0???? ?0???????? ???? ????? ?

1941 *Branchierpeton amblystomum*

1942 0000000001 0000000010 0000001100 00?0000?00 00101100?1 ?100000000 0?00011000

1943 0000011?10 0101?00001 0010000100 0100000000 1001000011 0000000010 00000?0000

1944 0000??1?00 00000?0?? ?0???????1 1110110000 00????0000 ?000000010 0000000010

1945 111?1?0?0? 0011?11?01 00000001?0 00??0???? ?000110?00 01???????? ?

1946 *Branchiosaurus salamandroides*

1947 0000000001 0010000010 0000001000 0001000?00 0100110001 0100000010 0?00011000

1948 0000011?10 0101?10001 ?010010100 0100000000 1001000021 0000000010 00000?0001

1949 0100??1?00 00000110?? ?0???????1 1110111200 00????0000 ?100010010 0000000010

1950 22111?0?01 0011?11?00 0000?????? ???? ????? ???? ????? ?

1951 *Apateon pedestris*

1952 0000000001 0010000010 0000001000 0001000000 0110110001 0100000010 0?00011000

1953 0000011?10 0101?10001 ?000010100 0100000000 1001000021 0000000011 0000010001

1954 0100??1?00 00000110?? ?0???????1 1110111200 00??00000 2100010010 0000000000

1955 22111??201 0011?11100 00001?01?? ????????? ?00?0???? ????????? ?

1956 *Microphoils stowi*

1957 0010000001 0000000010 0000001100 0001000000 0010110001 0100000000 0000011001

1958 0000011110 0101000000 0000101100 0100020010 1001000021 0001000011 0010010101

1959 0000101100 0000011010 2000?????1 111011?210 0000000000 1100010010 0000000000

1960 ?211001200 0010010100 000001?100 00??0010?? ?000100?10 010010000? 0

1961 *Platyrrhinops lyelli*

1962 0000000001 0000000010 0000001100 0001000000 0000110001 0100000001 0100011000

1963 0000011100 0100010000 0100000110 0100000010 1001000021 0001000001 0000010101

1964 0000101100 0000000000? ?0???????1 1110?1?2?0 0000000000 1100010010 0000000000

1965 2211001?01 001?000?10 0000000000 00??0????? 1000010?00 010000100? ?

1966 *Amphibamus grandiceps*

1967 0000000001 0000000010 0000001100 0001000000 0010110001 0100000011 0100011000

1968 0000011100 0100?10000 1110001110 0100010010 1001000021 00010000?1 0010010101

1969 0000101?00 00000000?? ?0???????1 111011?2?0 0000000000 2100010010 0000000000

1970 2211001?00 00100?0?00 0000010000 00??00????? ?000010?0? 01000000?? ?

1971 *Doleserpeton annectens*

1972 0000000001 0010000010 0000001100 0001000000 0010110001 0100000010 0100011000

1973 0000011100 0100010000 1110001110 0100010010 1001000021 0000000001 0010010101

1974 0000101100 00000??0?? ?00???????1 1110?0?200 0000000000 2100010010 0000000000

1975 ?211201?00 0010000??0 0000010100 0?0100001? 1000110000 11000101?? ?

1976 *Dissorophus multicinctus*

1977 0000000001 0000000010 0000001?01 0001000000 0010110001 0100000010 1100011000

1978 0000011110 010200000? 000001?100 01000?0000 1001100010 0000000001 0000010000

1979 0000101?00 00000??0?? ?00???????1 1100?0?210 0100000000 0100000110 0000000001

1980 ?211201?01 1110000??0 1110100100 0??0?1??? ?000110?00 0??0??????? 1

1981 *Cacops aspidephorus morrisoni*

1982 0000000001 0010000010 0000001?00 0001000000 0010110001 0100000010 1100011000

1983 0000011110 0100000000 000001?100 0100020000 1001100010 0000000001 0000010000

1984 1000101100 00000?0?? ?00??????1 1100?0?210 0100000000 0100000110 0000001001
 1985 ?211201?01 1110000?0 1100?????? ?????????? ?????????? ?????????? ?
 1986 *Broiliellus texensis*
 1987 0000000001 0000000010 0000001100 0001000000 0010110001 0100000010 1100011000
 1988 0000011110 0101?0000? 000001?100 01000?0000 1001100010 0000000001 0000010000
 1989 ?000101?00 00000?0?? ?00??????1 1100?0?2?0 0100000000 0100000110 0000000001
 1990 ?21?20??01 111000??0 1110?????? ?????????? ?????????? ?????????? ?
 1991 *Acheloma cumminsi*
 1992 0000000001 0000000110 0000001?00 1001000000 0010110001 0100000000 1100011000
 1993 0000011110 0100001000 0000000100 0100021000 0001100010 0000000001 0000010000
 1994 1000101?00 00000?0?? ?00??????1 1100?0?2?0 0000000000 0100000110 0000000001
 1995 ?210201?01 1110000?0 100001010? 0??01???? ?000000101 1??1?????? ?
 1996 *Phonerpeton pricei*
 1997 0000000001 0010000110 0000001?00 0001000000 0010110001 0100000000 1100011000
 1998 0000011110 0100001000 000001?100 0100011000 0001100010 0000000001 0000010000
 1999 1000101?00 00000?021 100??????1 1100?0?2?? ??00000000 0??00001?0 ?????????01
 2000 ?21020??01 1110000?0 1000010101 00?0?0??1?? 1000100101 100100101? 0
 2001 *Ecolsonia cutlerensis*
 2002 0000000001 0000000110 0000001?00 00?1000?00 00101100?1 ?100000000 1100011000
 2003 0000011110 0100?0100? 0000000100 0100011000 0001100010 0000000001 0000010000
 2004 0000101?00 00000?0?? ?0????????? ???0?????00 0000000000 0100000110 ?000000001
 2005 2210201?01 1110000?00 2000110100 00?00????? 1100100101 01?1?0??10 0
 2006 *Onchiodon labyrinthicus*
 2007 0000000001 0100100000 0100000001 1001000010 0000101001 0000001000 0000101000
 2008 0000001000 0100?00000 0000000100 0110000001 0001100111 0010000000 0000001000

2009 0000101100 00000000?1 ?000?????1 1100100100 0100000000 0001000000 1000000000
 2010 0110201?01 1110020?00 0000000000 000000???? 1000000020 000100101? 0
 2011 *Eryops megacephalus*
 2012 0000000001 0100100000 0100000001 1001000010 0000101001 0000001000 0001101000
 2013 0000001000 0100000000 0000000100 0110000001 0001100111 0010000000 0000001000
 2014 0000101100 00000000?? ?0???????1 110010?100 0100000000 0001000000 1000000001
 2015 ?110201?01 1110020?00 000001001? 0?????????0 ?000000?20 0?????????? ?
 2016 *Sclerocephalus haeuseri*
 2017 0000000001 0100100001 0000000001 0000000011 0000001000 0000001000 0000101000
 2018 0000101000 0100000000 0000000100 0110000000 0001000111 0000000000 0000000010
 2019 0000101100 0000000021 1000?????0 1100100100 0100000000 0001000001 0010000000
 2020 0110001?00 0010020?00 0000000000 00??0110?? 0100001?00 000100010? 0
 2021 *Glanochthon latirostris*
 2022 0000000011 0100100001 0000000001 0000000001 0000001000 0000001000 0000101000
 2023 0000101000 0100?00000 0000000100 0110000000 0001000111 0000000000 0000000010
 2024 0000101100 0000000021 1000?????0 1100100100 0100000000 0001000001 0010000010
 2025 0110100?00 00110?1?00 0000000001 00?00???? 1000001000 000101010? 1
 2026 *Archegosaurus decheni*
 2027 0000000011 0100100001 0000000001 1000000001 0000001000 0000001000 0000101000
 2028 0000101000 0100000000 0001000100 0110000000 0000000111 0000000000 0000000010
 2029 0000101100 0000000021 100??02110 1100100100 0100000000 0001000001 0010000010
 2030 0111110?00 00110?1?00 000000?001 0000000010 ?000001020 00010111?? ?
 2031 *Australerpeton cosgriffi*
 2032 0000000011 0100100000 0000000000 0000000001 0000001000 0000001000 0001101000
 2033 0000101000 0100?00000 000?000101 1100000000 0000000111 0000000000 0000000010

2034 0000101?00 0000000001 10101021?? ???0?0?100 0100000000 0001000001 0010000010
 2035 ??10??0?0? ?01?????00 0000010001 1000010110 0000001?20 0100021100 ?
 2036 *Parapytanga catarinensis*
 2037 ??0??????? ?????????? ??????00?0 ?????????? ?????????? 0????????? ?????????? ??????????
 2038 ?????1????? ?0?0?0???? ?????????? ???11010? 0??0?00?? ?????????? ???101??? ??????????
 2039 ??????????1 110??????? ?????????? ??????00?1 ?0???1?01 ?????????? ???0?0?00 ??????????
 2040 1?00?????0 ?????????? ?????????? ?
 2041 *Rhineceps nyasaensis*
 2042 0000000011 0000000000 0000001001 1000000?01 0001001000 0001002000 0001101000
 2043 0100201000 0100000100 0001000101 1100000000 0001100111 0000100000 0000000010
 2044 0000101?00 0001000001 1001?02??1 1100?0?01 0000000000 000?0?0?01 00101000??
 2045 ?????????? ?1??????0 0000000000 10000?0110 0100001020 1100021100 0
 2046 *Uranocentrodon senekalensis*
 2047 0000000011 0000000000 0000001001 1000000?01 00010010?0 ?001002000 0001101000
 2048 0100201000 0100000100 0001000101 1100000000 0001100111 0000100000 0000000010
 2049 0000101?00 00010?0?? ?0???????1 1100100001 0000000000 0000000001 0010100000
 2050 ?111110?00 00101?0?00 0000010??? 1?00???1?0 ?00??0???? ?????????? ?
 2051 *Lydekkerina huxleyi*
 2052 0000000001 0000000000 0000001001 0000010001 0000001000 0001002000 0001101001
 2053 0100101010 0101010101 0001001101 0100000000 1001100111 0000110000 0001000010
 2054 0000101?10 0001001021 1001?021?1 1100???1?1 0000000000 0000000001 0010100000
 2055 ?11000?01 0010120?00 0000100000 1?0000?10 1100001?00 ?100011?10 1
 2056 *Peltostega erici*
 2057 1010110001 0000000000 ???011001 00000???0? ???0?0???0 ?000102000 00????1001
 2058 0100?0?000 0101?101?1 000????001 110000010? ?001111100 1000001010 1????0?0??

2059 0000111??? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????
2060 ?????????? ?????????? ?????????? ?????????? ?????????? ?

2061 ***Laidleria gracilis***

2062 1110000001 0000000000 10-0011001 0000001001 0010001100 000011-000 000?0-1001
2063 1010?0?010 0112?10101 0000011101 1100000000 1001110111 1000010010 0010100010
2064 0000101?1? 000????0?? ?0????????? ???0???2?1 001100001- 00000???01 0????0????
2065 ?1111????? ?1?????00 2001010100 11?01???? ?000-00?00 01001200?? ?

2066 ***Siderops kehli***

2067 0000000001 0000011000 10-0011001 0000001001 0000101100 000011-000 00010-1001
2068 0100?00010 0102010101 0000011101 0100000000 1001110111 1000011000 1110100010
2069 0010111?11 0000000021 1000?02??1 1100???201 000000000? 0000000001 0010100010
2070 ?111110?00 0011111?00 0000110000 11?011??? 0100-01?10 0100121?01 1

2071 ***Batrachosuchus watsoni***

2072 0000000001 0000011000 10-0011001 000000?001 0000101100 000011-000 00010-1001
2073 0010?00010 0102?10101 0000011101 0100000000 1001110111 1000011010 1110100010
2074 0010111?11 00000000?? ?0???????0 1200?????? ?????????? ???00?00? ??????????
2075 ?????????? ?1???????0 000?100000 111001?0?0 ?100-01010 01001000?? 1

2076 ***Plagiosuchus pustuliferus***

2077 0110000001 0000010000 0000011000 0100000001 00101010?1 ?00001-010 0001001001
2078 0010?00010 0112?10101 0001011100 0100000000 1001110111 1000001000 1110100010
2079 0010111?11 00000010?? ?00?0????? ???1??0211 001100011- 0000001001 0101100110
2080 ?110100?00 0011111?00 100110?100 11?01???? 100-001?1- 0100100010 1

2081 ***Gerrothorax pulcherrimus***

2082 0010000001 0000010000 0000011000 0100000001 0010101001 000001-010 0001001001
2083 0010?00010 0112010101 0001001100 0100000000 1001110121 1000011000 1110100010

2084 0000111?11 000000000? ?0???????0 1201110211 001100011- 0000001001 0101100100
 2085 ?110100?01 1110111?00 20011?0100 11?????01?? 1110000010 010001101? 0
 2086 *Edingerella madagascariensis*
 2087 0000000001 0000000000 0000001001 0000010001 0000001000 0001002000 0001101001
 2088 0100100010 0101010101 0001000101 0100000000 1001110111 1000010000 0001100010
 2089 0000101?10 01010010?? ?1???????1 11000????1 0000000000 001?000001 0010100110
 2090 ?111110??? ?1??????10 0000100110 101?1100?1 ?110001?20 01100210?? ?
 2091 *Watsonisuchus gunganj*
 2092 0000000001 0000000000 0000001001 0000010001 0000001000 0001002000 0001101001
 2093 0100100010 0100010101 0001010101 0100000000 1001110111 1000010000 0001100010
 2094 0000101?10 01010??0?? ?1???????1 11000????? ?????????? ?????????? ??????1????
 2095 ?????????? ?1???????0 ?000100111 1111111111 ?001001?20 01100210?? ?
 2096 *Benthosuchus sushkini*
 2097 0000000011 0000000000 0000001001 0000011001 0000001000 0001002000 0001101001
 2098 0100100010 0101010101 0002001101 0100000000 1001111111 1100010000 0001100010
 2099 0000101?10 0101000001 1100?02111 110???????1 0000000000 001?000001 0010110110
 2100 ?110110?00 001?11???? ?000101011 1010100111 1000001?20 0110021010 1
 2101 *Trematosaurus brauni*
 2102 0000110011 0000000000 0000011001 0000011001 0000001000 0000102000 0001001001
 2103 0100100010 0101?10101 0000001101 1100000000 1001111111 1200001000 1010100010
 2104 0000101?10 0112000001 1100?????1 110??????? ?????????? ??????????01 00201101??
 2105 ?????????? ?1???????0 ?000110001 1110001111 0000001?10 0110011010 1
 2106 *Trematolestes hagdorni*
 2107 0000110011 0000000000 0010011000 0000011001 0000000100 0000102000 0001001001
 2108 0100100010 0101?10111 0000001101 1100000000 1001111111 12000010?0 1010100010

2109 0000101110 01120??011 2100?????1 11011??101 0000100000 0010100001 0020110110
 2110 0111110?10 00111111?10 0000000001 1110001111 0000001?10 011011001? 1
 2111 ***Lyrocephaliscus euri***
 2112 1000110001 0000000000 0000011001 0000011?01 01100010?0 ?000102000 0001101001
 2113 0100101000 01010101?1 0002000001 1100000100 1001111100 1200001010 1110100010
 2114 0000111??? ?????????? ??????????1 11????????? ?????????? ?????????? ?????????? ??????????
 2115 ?????????? ???010000 1110001111 ?000001010 01101110?? ?
 2116 ***Callistomordax kugleri***
 2117 0000110001 0000001000 0010011000 0000011001 0000000100 0000102000 0001001001
 2118 0100100011 0101?10111 0000001101 1100000000 1001111111 12000010?0 1110100010
 2119 0001111?10 0112010001 1100?????? ?11?0001 0010111001 0010100001 0010110210
 2120 0110110?10 00111111?10 0000110000 11?0111?1 1000001?10 0110010010 1
 2121 ***Metoposaurus diagnosticus***
 2122 0000110001 0000001000 0010011001 0000011001 0000000000 0000102000 0001001001
 2123 0100100011 0102010111 0001011101 1101000000 1001110111 1000011000 1110100010
 2124 0001111110 0112111011 1100?021?1 11001??101 1010111101 0010000001 0010110210
 2125 ?110110?00 0011101?10 0000010001 1110011111 1000001?10 0100111010 1
 2126 ***Wetlugasaurus angustifrons***
 2127 0000000011 0000000000 0000001001 0000010001 0000001000 0001002000 0001101001
 2128 0100100010 0100010101 0002001101 0100000000 1001110111 1000010000 0001100010
 2129 0000101?10 01010000?? ?1???????1 110?0????? ?????????? ??????????0? ??????1????
 2130 ?????????? ?1???????0 ?000100011 1010001111 ?000001?20 01100210?? ?
 2131 ***Eryosuchus garjainovi***
 2132 0001000011 0000000000 0000000000 0000011001 0010001000 0001002000 0001101001
 2133 0101100010 0101110101 0001011101 0101000000 1001110111 1000000000 0001100010

2134 0000101?10 1202101011 2100?????1 110?0???01 1000000001 0011000001 0010110110
 2135 ?111110?00 001??????0 ?000110100 1010010111 1000001020 0110021010 1
 2136 *Paracyclotosaurus davidi*
 2137 0001000011 0000000000 0000001001 0000010001 0010001000 0001002000 0001101001
 2138 0102100010 0101010101 0001011101 0101000000 1001110111 1100001000 1001100010
 2139 0000101?10 02020??0?? ?100?????1 11000??001 1000000001 0011000001 0010110110
 2140 ?111110?00 00111?1?00 0000100110 1110111111 ?111001?20 01000210?? ?
 2141 *Eocyclotosaurus wellesi*
 2142 0001000011 0000000000 0000001001 0000011001 0010001000 0001002000 0001101001
 2143 0102100010 0101010101 0001011101 1101000000 1001110111 1100011000 1001100010
 2144 0000101?10 02020010?? ?1???????1 110?0????1 1000000001 001?000001 0010110110
 2145 ??11?1???? ?1?1?????0 ?00011001? ?????????? ?000001?20 0????????? ?
 2146 *Cyclotosaurus robustus*
 2147 0001000011 0000000000 0000001001 0000010001 0010001000 0001002000 0001101001
 2148 0102100010 0101010101 0001011101 0101000001 1001110111 1100011000 1001100010
 2149 0000101?10 0202101011 110???????1 110?0????1 1000000001 0??0??01 0010110110
 2150 ?11111???? ?1?1?????0 ?000110110 1011011011 0001001020 0110121000 1
 2151 *Mastodonsaurus giganteus*
 2152 0001000011 0000000000 0000001000 0000011001 0010101000 0000002000 0001101001
 2153 0101100010 0101110101 0001011101 1101000000 1001110111 1100001000 1001100010
 2154 0000101?10 1202001000 2100?02111 110?0???01 1010000001 0011000001 0010110100
 2155 ?110110200 00111112?0 0000110101 1010011111 0000001020 0110121000 0
 2156 *Parotosuchus nasutus*
 2157 0000000011 0000000000 0000000001 0000010001 0010001000 0001002000 0001101001
 2158 0100100010 0100010101 0001011101 0101000000 1001110111 1000010000 0001100010

2159 0000101?10 01011010?? ?1???????1 110?0????? ?000?????0? 0???????0? ?????1????

2160 ?????????? ?1???????0 ?00011011? ?????????? ?001001?20 0????????? ?

2161 ***Parotosuchus haughtoni***

2162 000000?01? ???000000 0000000?01 0000010001 00101?1000 0001002000 00?1101001

2163 0100100010 0100110101 0001?11101 010?0??000 1???????1? ?000100?0 010110?010

2164 00?01?1?10 0?01001021 1110002111 110??????? ?0000?0?? ?????????? ??????????

2165 ?????????? ?????????? ???100111 10111?01?1 0111001?20 0110011010 0

2166 **MCP-4275PV**

2167 ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????

2168 ?????????? 000??????? ?????????? ?????????? ?????????? ?????????? ?????????? ?001??1021

2169 211000211? ?????????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????

2170 ?????????? ?????????? ?????????? ?

2171 ***Sangaia lavinai***

2172 1000000001 0000000000 ???00?0?0 00000?1?01 0000001000 000011-000 000?001001

2173 1010?0?010 0101?10101 000?01?10? ?100000000 1001110111 1000010010 000?000010

2174 0000101??? ?????????? ?????????? ???0????? ?????????? ?????????? ?????????? ??????????

2175 ?????????? ???10000? ?????11?1 ?110001010 0????????? ?

2176 ***Procuhy nazariensis***

2177 0?01?????0? ???1????? ?????0?01 ?00??????? 0???0???00 001?1?000 ?0???0000

2178 ?000????? ?00?0????? ?0?0????? ?????????? ?????????? ?????????? ?????????? ??????????

2179 1????110?? ?100????? ?????????? ?????????? ?????????? ?????????? ?????????? ??????????

2180 ???1000?? ?????????? ?00?0?01? ?????????? ?

2181 ***Prionosuchus plummeri***

2182 0?010???1? 10000000?1 0???0????? ???0?0?01 ?????????? ?????????? ??????????

2183 ?????????? ?????0?000 00000????? ?11?000100 ?1????????? ?????????? ??????????

2184 ?????????? ?????????? ?????02??? ?????????? ?????????? ?????????? ?????????? ??????????

2185 ?????11??? ?????????? ?????0????? ??????1??? ?10?00?? ?

2186 ***Timonya anae***

2187 0?010?00? ??????1??? 0?????1?01 ??????????0 0?????00?1 ??????1-000 ?00?011-01

2188 ??0??0?? ????0??00? ?0?????1?0 -????????? 1?????0?? ???????00? ?0??1??0? ??????????1?

2189 ???1011??? 1?0??????? ????1??0?? ?0?????0? ?????????? ????1??0?? ?????????? ??????????

2190 ?????0????? ??????????0 ?????????? ?????????? ?

2191 ***Gerobatrachus hottoni***

2192 0000000001 00?0000010 0000001?00 0001000100 0?10110001 0100000?0 0?00011000

2193 0000011?00 0101?00001 ?0100??110 01000?00?0 1001000??? 000?000000 0010010101

2194 0000101?00 0000??0?? ?0????????? ???0?0?210 0000000000 ?10001001? ??????????

2195 ?211201??? ?010??0??0 0000100100 00????????? ?000-0?00? ?????????? ?

2196 ***Triadobatrachus massinoti***

2197 00??0??00? ?????????? 1---??1000 ?01?????1?- 1?0---?11 1-----01-- ?-1-----1- -?---0?1-- 1-?0-

2198 ----? ??????1-11? ?????????? ??????0?? 120?101-0? ?---??---- --??1????? ?0-?01????

2199 ?0????????? ?1???1?211 0????????? ??????????- -----01 ?10?0?1?10 0110?0??0 0?0--0-?0 -

2200 -??0????? ?--?--?01 ?????????? ?

2201 ***Eleutherodactylus orcei***

2202 000?0??001 0011100110 1---0?1000 ?-1?????10- 1-----11 1-----?1-- ?-1-----1- -1---10?-- 1-?1-

2203 1---? 111??1-11? 100??10?? 1?1??1?1? 101?101-?? 0---?0---- --??1??00 00-????????

2204 ?00????????? ???????211 ??????0??0? ??????1??1- -----?? ???????1210 ??11??01?? ???0--0-?0 -

2205 -?00????? ?--?--?0? ?????????? ?

2206 ***Konzhukovia sangabrielensis***

2207 0?010?0010 0100?00001 001000?0?? ?0?0?00001 0?0?0?10?? 0????????? ?01?0????

2208 ?????????? ???????0110 00010?01?? 01?????100 10?????0? ?????????? ?001??101

- 2209 ?0?????? ???? ????? ???? ????? ???? ????? ???? ????? ???? ?????
- 2210 ??????? ??????1? ?0??1???? ????0?1020 01110211?? ?
- 2211 ***Tomeia witecki***
- 2212 ??00??00?? ????????? ????000?? ????????? 0??01?1?0? ?????010?? 100?????01
- 2213 ?00?????0? 0110????? ?00?????? ????????? ??????0?1? ?????10?0? ????????? ???? ?????
- 2214 ???0?1??0? ????????? ????????? ????????? ????????? ????????? ????????? ?????????
- 2215 ????1?01?? 0?1??1011? 1???????? ???????00 ?

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Preliminary anatomy of a large sized temnospondyl amphibian from the Permian of Brazil

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Temnospondyl amphibians are an important component of the Permian tetrapod fauna of Brazil, well represented by the Rio do Rasto Formation. Despite the worldwide diversity of temnospondyls, their fossil record in South American is still scarce. For the Brazilian Permian, just four taxa are recognized: *Prionosuchus plumeri*, *Australerpeton cosgriffi*, *Bageherpeton longignathus* and *Parapytanga catarinenses*. The specimen MCP-4275PV, a hemimandible, comes from the Posto Queimado outcrop (Fm. Rio do Rasto, Paraná Basin), in the municipality of São Gabriel, RS. The morphology and the phylogenetic relationship of the specimen are currently under evaluation. The morphological study aims to use CT-Scan imagery of the specimen to access sutural contacts of the bones, as well as the analysis of internal morphology. A preliminary study of the material indicates that the jaw belongs to a large taxon with proportional small tooth and arc jaw with a short symphysis. These characteristics allow the exclusion of MCP-4275PV from taxa such as *Prionosuchus plumeri*, *Australerpeton cosgriffi* and *Bageherpeton longignathus* since these have a long symphysis and proportionally bigger teeth. MCP-4275PV also distinguishes from *Prionosuchus* as it lacks the “Y” shaped jaw profile of the later. The total length of the specimen, over 500mm long, indicates that MCP-4275PV was a large sized temnospondyl, although not as long as *Prionosuchus*. A meticulous anatomical description and phylogenetic study of MCP-4275PV will contribute to our knowledge of amphibian diversity in the Permian of Pangea. Permian tetrapod diversity is a key element to build stratigraphic correlations between putative synchronous units from Brazil (e.g. Fm. Rio do Rasto), Africa (Karoo Supergroup) and Eurasia (Russian Platform).



PALEO RS 2015
4 a 6 de dezembro - São Gabriel, RS



UM NOVO TEMNOSPÔNDILO DE GRANDE PORTE PARA O PERMIANO DO RIO GRANDE DO SUL

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Uma nova espécie em potencial de um anfíbio temnospôndilo de grande porte é apresentada para o Permiano do Rio Grande do Sul. O espécime (MCP-4275PV), uma hemimandíbula preservada em dois segmentos, provém do afloramento de Posto Queimado, nas proximidades do município de São Gabriel (RS). A hemimandíbula tem comprimento aproximado de 50 cm, indicando que esta espécie superava em tamanho a maior parte dos temnospôndilos brasileiros conhecidos. Análises filogenéticas preliminares, implementadas por meio de programas de uso corrente (TNT, PAUP), partiram de versão adaptada de uma matriz previamente publicada (66 táxons, 217 caracteres). Os resultados mostram que MCP-4275PV consistentemente surge como grupo irmão do capitosaurio *Parotosuchus*. No entanto, esse resultado, além de possuir baixa resolução e suporte entre os Stereospondyli, não dá à monofilia de Capitosauria. Entre as características compartilhadas com vários táxons desse grupo, estão o tipo de área pós glenóide (consistente com PGA tipo I), forame meckeliano posterior bem desenvolvido, padrão de dentição mandibular decrescente anteroposteriormente, coronóides sem dentes, entre outras características. O novo temnospôndilo é potencialmente um dos mais antigos representantes entre os Capitosauria, cujo registro é limitado quase que totalmente para o Triássico. MCP-4275PV também amplia a distribuição espacial do grupo, representando potencial uso na correlação de faunas entre a Formação Rio do Rasto e unidades permianas do Supergrupo Karoo (África do Sul) e da Plataforma Russa (Europa Ocidental), além de diversas unidades sul-americanas. A futura implementação de CT-scan deverá permitir acesso detalhado à anatomia do espécime, uma codificação mais completa de MCP-4275PV na matriz, bem como o refinamento destes resultados filogenéticos prévios. [CNPq]

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Number: 59th Annual Meeting

Year: 2015

Location: Cardiff

Hosted By: Cardiff University and Amgueddfa Cymru – National Museum Wales

Organised By: Caroline Buttler, Lesley Cherns and Lucy McCobb

A new large-sized temnospondyl from the Permian of southern Brazil

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Although the temnospondyl known diversity is substantial, the current knowledge of South American taxa is lacking. Remains of a large-sized temnospondyl from the Rio do Rasto Formation (Middle–Late Permian) of Southern Brazil represents a putative new taxon that may shed light on temnospondyl evolution and palaeobiogeography. The specimen MCP-4275PV is a hemimandible of ~50 cm in length, indicating that this specimen exceeded the majority of Brazilian temnospondyl taxa in size, only surpassed by the Late Permian *Prionosuchus*. Meaningful characters include a type I postglenoid area (PGA), hamate process and coronoids devoid of teeth, proportionally small but numerous dentary teeth. The short and posterodorsally-oriented retroarticular process parallels the morphology of certain Crocodylia, highlighting biomechanic similarities between these different tetrapod groups. Preliminary phylogenetic analysis (TNT, PAUP; 66 taxa, 217 characters) consistently places MCP-4275PV as the sister-group of *Parotosuchus*, a capitosaur genus currently known from Laurasian territories, South Africa and Antarctica. If confirmed as a *Parotosuchus*, MCP-4275PV will expand the presence of the genus to South America. Furthermore, it will represent possibly the oldest capitosaur, a group almost entirely restricted to the Triassic. The future use of CT-scanning should provide access to new morphological data and the refinement of current results.