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FUNCTIONAL MORPHOLOGY AND EVOLUTION OF
HYOLARYNGEAL APPARATUS IN ARCHOSAURIA

(主竜類の舌喉頭器における機能形態と進化)

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Functional morphology and evolution of hyolaryngeal apparatus in Archosauria

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Archosauria is a large group of vertebrates, including crocodilians, birds, pterosaurs, and dinosaurs, since Mesozoic. Tongue and larynx (hyolaryngeal apparatus) are unique organs of tetrapods with ecological significance. Tongue is adaptive with subsequent modifications for catching prey, tongue projection for food collection, grasping and holding prey, filter-feeding, cropping, manipulating, and swallowing prey. Larynx is an entrance of tracheal passage and also ecologically important in three functions: a barrier to foreign materials entering trachea (airway protection); opening of glottis for respiration (respiratory modulation); and generation and modulation of sound. However, tongue and larynx have never been reported as fossil because it is mainly composed of soft tissue and easily degraded. This dissertation focuses on bones of hyolaryngeal apparatus of Archosauria to know their evolution in terms of anatomy, and function. This project aims to use hyolaryngeal bones, reveal knowledge concerning tongue and larynx, and provide novel huge insights for evolution of Archosauria. The results reveal that hyolaryngeal apparatus have been playing crucial roles in early aquatic adaptation of neosuchian crocodyliforms, and herbivory and vocalization of non-avian dinosaurs.

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I. INTRODUCTION

Background

Tongue and larynx (hyolaryngeal apparatus) are unique organs of tetrapods, which were transformed from gill arch and esophagus in transition from water to land. In the early history of terrestrial vertebrates, tongue is suited for carrying prey item within oral cavity to esophagus without water current (Reilly & Lauder, 1990; Iwasaki, 2002), and composed by epidermal epithelium, hyolingual muscles, and hyoid bones. Larynx is also suited for preventing from water and food items entering into trachea and lung (White 1975; Kirchner 1993). Among tetrapods, tongue and larynx still have been diverse and versatile organs. Tongue is adaptive with subsequent modifications for catching prey, tongue projection for food collection, grasping and holding prey, filter-feeding, cropping, manipulating, and swallowing prey (McLelland 1989; Brainerd & Owerkowicz, 2006; Erdogan & Iwasaki, 2014). Larynx is an entrance of tracheal passage and also ecologically important in three functions: a barrier to foreign materials entering trachea (airway protection); opening of glottis for respiration (respiratory modulation); and generation and modulation of sound (White 1975; Kirchner 1993;

Suthers et al., 2016).

In addition to the ecological importance, hyolaryngeal apparatus does not articulates with other skeletal elements, having a great degree of freedom anatomically. Furthermore, in terms of development biology, hyolaryngeal apparatus is derived from migratory cells, such as, neural crest cells, and migratory muscle precursor cells (Couly et al., 1998; Kuratani, 2017), indicating that it can be easily transformed into different biological designs.

Therefore, hyolaryngeal apparatus might have been evolutionary driver in diverse bodyplan of Archosauria in terms of its ecological importance and evolvability.

However, tongue and larynx have never been reported as fossil because it is mainly composed of soft tissue and easily degraded. Some studies have tried to reveal tongue of extinct tetrapods by morphological evolution of hyoid bones, such as, xenarthran mammals (Pérez et al., 2010), cetacean mammals (Werth, 2007), felid mammals (Weissengruber et al., 2002), proboscidean mammals (Shoshani & Marchant, 2001). While, in extant archosaurs, functional morphology of archosaur hyolaryngeal apparatus remains still unknown because of scarcity of studies. All lingual muscles are

attached to hyoid apparatus or mandible (Erdogan & Iwasaki, 2014; Li & Clarke, 2015), therefore, hyoid morphology is expected to help reconstruction of hyolingual muscles, and its function. This project aims to use hyolaryngeal bones, reveal knowledge concerning tongue and larynx, and provide novel huge insights for evolution of Archosauria.

Literature review

Functional morphology of hyoid bones has been progressively understood, for example, in lungfish (Bemis & Lauder, 1986), salamander (Thexton et al., 1977; Lombard & Wake, 1977; Heiss et al., 2016), turtle (Lemell & Weisgram, 1997; Summers et al., 1998; Natchev et al., 2009), lizard (Smith, 1984; Owerkowicz et al., 1999; Herrel et al., 1998; Herrel et al., 2005), snake (Langebartel, 1968), anteater (Naples, 1999; Endo et al., 2007), howler monkey (Dunn et al., 2015), Clark's nutcracker (Bock et al., 1973), crocodilians (Cleuren & De Vree, 2000), woodpecker (Wang et al., 2011), shoebill (Endo et al., 2013), turacos (Korzoun et al., 2001), hoatzin (Korzoun et al., 2003), Amazonian motmot (Korzun et al., 2004), pigeons (Korzun et al.,

2008), flamingo (Zweers et al., 1995), and waterfowls (Li & Clarke, 2016).

In birds, feeding adaptation of avian tongue was divided to main three categories: collecting of food, intra-oral manipulation, and swallowing of food in the past studies. Here, this study uses six lingual-motion categories: tongue projection, grasping and holding, filter-feeding, cropping, manipulating, and swallowing, following some literatures (Harrison 1964; King & McLelland, 1979; Korzun et al., 2003; Erdogan & Iwasaki, 2014). Specialization in collecting of food in birds is tongue projection, which is adopted for insectivory in woodpeckers and some passerines (Paridae and Sittidae), and for nectarivory in flowerpeckers (Dicaeidae), sunbirds (Nectariniidae), honeyeaters (Meliphagidae), honey-creepers (Drepanididae and Emberizidae), white-eyes (Zosteropidae), humming-birds (Trochilidae), nectar-feeding warblers (Parulidae), orioles (Icteridae), and some flower frequenting lorries (*Trichoglossus*). Specialization in intra-oral manipulation is grasping or holding which is seen in Mergini, porchards (Tome & Wrubleski 1988; Godman & Fisher 1962), penguins (Spheniscidae), shearwaters and fulmars (Procellariidae), loons (Gaviidae), mergansers (Anatidae), eagles and vultures (Accipitidae), cropping in swan, geese,

hoatzin (*Opisthocomus*), some cuckoos (Cuculidae), and motmot (Korzun et al., 2004), filter-feeding in Anatidae and Phoenicopteriformes, and manipulation in Psittacidae and finches (Fringillidae). Specialization in swallowing of food is caudally directed lingual papillae of warblers (Muscicapidae), vireos (Vireonidae), crows (Corvidae), wrens (Troglodytidae), drongos (Dicruridae), and Galliformes. However, non-specialized tongue for tasting, swallowing is usual in many birds such as *Pelecanus*, *Sula*, *Phalacrocorax*, *Anhinga*, *Numenius*, ratites, tinamiforms, some sphenisciforms, tubinarines, Ciconiidae, Threskiornithidae, Bucerotidae, Upupidae, Alcedinidae, Caprimulgidae, gulls (Laridae), plovers (Charadriidae), rails (Rallidae).

The closest extant relatives of birds are crocodylians, which are adapted to aquatic environment. Although some previous studies have described crocodylian hyoid apparatus anatomically, their evolutionary perspective still remains unknown.

In non-avian dinosaurs, the past studies have been largely problematic in identifications and homologies for hyoid apparatus, which are necessary to compare and trace evolutionary trajectories (Colbert et al., 1945; Head et al., 1999; Morschhauser & Lamanna, 2013; Hill et al., 2015; Li & Clarke et al., 2015; Li et al., 2018). It is also lack

of studies for functional morphology.

Problem statement

Functional morphology and evolution of hyolaryngeal apparatus has been largely unknown in both extant and extinct archosaurs although it is ecologically important and highly evolvable organ.

Hypotheses

It should be tested whether hyolaryngeal apparatus has been evolutionary driver in diverse bodyplan of Archosauria. This thesis specifically focuses on four significant evolutionary events in Archosauria: anatomical evolution in modern archosaurs (ch. 1); aquatic adaptation of crocodyliformes (ch. 3); gigantism for herbivory (quadrupedality) in sauropodomorph dinosaurs (ch. 4); and mastication in Ornithischia (ch. 5); and avian-like larynx in non-avian dinosaur (ankylosaur *Pinacosaurus*) (ch. 6).

Hypothesis 1: Hyoid apparatus could be functionally sophisticated and muscle could be reconstructed in Dinosauria

Hypothesis 2: Hyoid modification could provide modern croc-like respiratory adaptation to aquatic environment

Hypothesis 3: Hyolingual apparatus could promote quadrupedality in Sauropodomorpha

Hypothesis 4: Hyoid could be highly correlated with mastication in Ornithischia

Hypothesis 5: Bird-like larynx could appeared in Dinosauria

Materials and methods

This project aims to reveal knowledge concerning the unfossilized soft tissue of ecological importance, tongue and larynx, using their neglected bones, hyoid and laryngeal bones. This will be accomplished by (1) Osteological comparison, (2) Musculature reconstruction, (3) Morphological measurements, and (4) Tracing over trees with model fitting, among both extant and extinct reptiles and birds.

List of institutions for studying materials

AMNH: American Museum of Natural History, New York, USA; **BMNH:** The Natural History Museum, London, UK; **CM:** Carnegie Museum of Natural History, Pittsburgh,

PA, USA; **CMN**: Canadian Museum of Natural History, Ottawa, Canada; **CNHM**: Chungking Natural History Museum, Chongqing, China; **DMNS**: Denver Museum of Natural and Science, Denver, Colorado, USA; **GMNH**: Gunma Museum of Natural History, Tomioka, Gunma, Japan; **HMN**: Museum für Naturkunde der Humboldt Universität, Berlin, Germany; **HoUM**: Hokkaido University Museum, Sapporo, Hokkaido, Japan; **MCZ**: Museum of Comparative Zoology, Harvard University, Boston, Massachusetts, USA; **MMP**: Museo Municipal de Ciencias Naturales Lorenzo Scaglia, Mal der Plata, Buenos Aires, Argentina; **MZSP-PV**: Museu de Zoologia da Universidade de São Paulo; **NM QR**: National Museum, Bloemfontein, South Africa; **NSMT**: National Science Museum, Tokyo, Japan; **ROM**: Royal Ontario Museum, Toronto, Canada; **SMNH**: Smithsonian Museum of Natural History, Washington DC, USA; **YIO**: Yamashina Institute for Ornithology, Abiko, Chiba, Japan; **YPM**: Yale Peabody Museum, New Haven, Connecticut, USA; **ZDM**: Zigong Dinosaurs Museum, Sichuan, China.

II. EVOLUTIONARY ANATOMY OF HYOLARYNGEAL APPARATUS IN ARCHOSAURIA WITH ANATOMICAL NETWORK ANALYSIS

Abstract

Archosauria is a dominant group of vertebrates in terrestrial ecosystem since Mesozoic, and represented by crocodylians, birds, pterosaurs, and dinosaurs. Their adaptive radiation has been studied mainly based on their skeletal elements except hyolaryngeal apparatus (tongue and voice box). Hyolaryngeal apparatus, composed of hyoid and larynx, is a unique feature of tetrapods associated with feeding, respiration, and vocalization and has been playing key roles in the tetrapod evolution. Anatomically, hyolaryngeal apparatus is isolated from the other skeletal elements, and recognized as an independent module. This is supported by the fact that hyoid and its associated muscles are derived from migratory cells in development, such as neural crest cells, and migratory muscle precursor cells. However, because of its ecological importance and weak anatomical constraint, morphology of hyolaryngeal apparatus is largely diverse, and hampers understanding of evolution of hyolaryngeal apparatus in Archosauria. Here

and hampers understanding of evolution of hyolaryngeal apparatus in Archosauria. Here I review the previous studies of hyolaryngeal apparatus, especially anatomical ones, and conducted (i) anatomical comparison for muscular reconstruction and (ii) network analysis for understanding of modular evolution in Archosauria.

Four species of extant archosaurs are dissected (*Crocodylus siamensis*, *Alligator mississippiensis*, *Struthio camelus*, *Gallus gallus*), and some of the past literatures are reviewed. The anatomical comparison shows that m. branchiomandibularis is a synapomorphy of Archosauromorpha (Chelonia, Crocodylia, Neornithes). Ceratobranchial 2 was lost in the basal node of Archosauria. In Crocodylia, none of new hyolingual muscle is retained, indicating that the stem archosaurs likely possessed the muscles seen in crocodylians. Moreover, anatomical network analysis with six network parameters, modular partitioning, and centrality measurements, indicates that hyoid apparatus, especially ceratobranchial, is functionally specialized in Archosauria. These results of extant archosaurs imply that ceratobranchial has important roles in archosaur evolution, and highlight the importance of paleontological approach.

Introduction

Hyoid apparatus is originally derivative of branchial arch complex in fish, and has no articulation with other bones, as well as shoulder girdle, and innervated mainly by cranial nerve VII (facial) and XII (hypoglossal) (Tomlinson 2000), which can be interpreted as an independent module. Modularity in anatomical domain plays key roles in evolution. Therefore, we hypothesized that hyolingual apparatus is a dynamic module, playing key roles in tetrapod evolution.

Modularity is a concept of the animal's body as a set of nested parts within parts, maintaining a level of autonomy to change. Also, modularity enables flexibility because the direction and magnitude of evolutionary change among and within body parts can vary without sacrifice of functions. While, integration is an idea of still growing and adapting in coordinated ways, continuing to gain a central mechanism of evolution (Bateson 1894, Olson & Miller, 1958). These concepts are tightly linked to questions about evolvability and complexity.

Hyoid apparatus are morphologically diverse, which correlates with lingual

function. For example, aquatic crocodylians rise their gular valve to separate oral and pharyngeal cavity (Li & Clarke, 2016). Such morphological specializations are usually assumed to reflect an adaptive evolution in the context of a taxon's feeding ecology. In addition to external/ecological pressures, development may constrain the evolution of limb musculoskeletal anatomy. This potential conflict between selective pressures for locomotive specializations and evolutionary constraints imposed by a shared development has major implications for understanding evolutionary and developmental patterns in archosaur evolution.

To date, however, studies of modularity and integration in archosaurs have focused exclusively on skull data, using morphometric and evolutionary quantitative genetics tools to study phenotypic (co)variation in continuous traits such as skulls and shoulder girdle (Powell et al., 2018; Esteve-Altava et al., 2019). Selection for functional specialization can reduce developmentally-based co-variation. In contrast, modularity and integration among other features of the limb musculoskeletal system, including for example presence/absence of muscles, and physical connections between bones and muscles, has yet to be comprehensively integrated, in part because these features are not

amenable to the same type of quantitative analyses as morphometric traits. In the recent studies, Anatomical Network Analysis has enabled the study of connective patterns (e.g. bone-bone and bone-muscle connections) in an operational and quantitative way, by using mathematical tools based on network theory. Anatomical Network Analysis is useful to test specific hypotheses about the evolution of morphological organization and modularity (Raaskin-Gutman & Esteve-Altava 2014). Significantly, Anatomical Network Analysis uses topological organization and connectivity relationships (e.g. articulations and attachments) between anatomical structures and/or types of tissues (e.g. bones and muscles) in a way that can complement patterns gleaned from morphometric analysis of size and shape.

Here we provide the first comparative anatomical network analysis of the musculoskeletal system of hyolaryngeal apparatus of modern archosaurs, such as, turtles, crocodylians, and birds. We address three hypotheses on the patterns and processes of archosaur hyolaryngeal evolution.

H1) *complexity in bone-bone and muscle-bone network, connectivity in hyolaryngeal apparatus correlates with the functional complexity of the apparatus.* We

predict that crocodylian and bird hyolaryngeal apparatus will have a lower network connectivity than those of turtles because they have a lower functional complexity (Esteve-Altava et al., 2013b). Decreases in number of bone elements are compensated by specialization in function, which is known as Williston's Law (Esteve-Altava et al., 2013b; Williams & Nagy, 2001). In archosaurs, the number of hyolaryngeal apparatus has been changes, such as, loss of ceratobranchial 2 in stem-Archosauria (Li et al., 2018), and acquisition of paraglossal in Neornithes (chapter 6). To test this hypothesis across archosaur hyolaryngeal apparatus, anatomical network analysis is performed and Q-value (strength of modularity) is calculated for its generated network models (Raaskin-Gutman & Esteve-Altava, 2014; Powell et al., 2018; Diogo et al., 2018).

H2) *the evolutionary increase in the number of unique hyolaryngeal muscles in archosaur evolution resulted in a lower average number of muscle-bone connections per structure and therefore in lower anatomical complexity and density of croc and bird hyolaryngeal apparatus compared to those of turtles.* For example, decrease in the number of skull bones in tetrapod evolution (Williston's Law) has been shown to have actually led to an increase in the density of connections and thus of morphological

network complexity in crocodylians and birds. Similarly, we predict negative correlation (i.e. fewer bones -> increase of average bone-bone network density and complexity, e.g. loss of ceratobranchial 2 and acquisition of paraglossal).

H3) *centrality of ceratobranchial is decreasing through the evolution of Archosauria*. Ceratobranchial is the common bony element among archosauromorphs, and attached by many muscles. Morphology of ceratobranchial varies among archosauromorphs, and expected to play important role in the archosauromorph evolution. We compared centrality of paraglossal, basihyal, ceratobranchial, and epibranchial, in order to test whether ceratobranchial shows higher centrality than the other hyoid bones in all the taxa.

Methods

Datasets. Symmetrical adjacency matrices are coded as 1 for presence of bone-bone, bone-muscle, and muscle-muscle contact, while, as 0 for its absence. The coding is based on original dissection of extant archosaurs (*Crocodylus siamensis*, *Alligator mississippiensis*, *Struthio camelus*, *Gallus gallus*) and a review of the past literatures.

The matrix is unweighted and undirected for construction of network model of musculoskeletal anatomy of hyolaryngeal apparatus of archosaurs. We analyze skeletal networks and muscular networks separately: skeletal networks include bones and cartilages as nodes, connected by their articulations; muscular networks include muscles as nodes, connected by tendinous joints and fibrous fusions among them. The following indices, network parameters, modular partition, and centrality, are calculated for each taxon.

Network parameters. The matrices are analyzed in a statistical software R with a package “igraph” (Csardi & Nepusz, 2006). Six anatomical network parameters are compared: number of nodes (N), number of connections (K), density of connections (D), average clustering coefficient (C), average shortest path length (L), and heterogeneity (H) of connections. N and K accounts for the number of anatomical structures modeled, anatomical parts and pairwise relations. D is respect to the number of connections, and often used as a proxy for the complexity of a morphological structure because the more connections among parts, the more functional possibilities. C is the good proxy for the number of triangular loops and motifs. L is the proxy for effective proximity among

anatomical network. H is the ratio between the standard deviations of connections each per node and the mean number of connections per node, providing irregularity of network. H is used as a proxy for the anisomerism, which means heterogeneity of connection distribution.

Network modules. Within the network models, the modules are defined with random walk algorithm, as implemented in the function “cluster_walktrap” of igraph. We used random walks of 3 steps for the heuristics of the algorithm, finding groups of nodes (modules) that are more densely connected among them than to nodes outside of the module. The quality of partition is evaluated by the optimization function Q (Newman and Girvan, 2004). Q is closer to 1 if the defined modules deviate from what is expected for a random walk network.

Centrality

Centrality is measure of importance of nodes. Measures of centrality may have different interpretations in anatomical and functional networks (e.g. Honey et al., 2007). For instance, anatomical central nodes often facilitate integration, and consequently enable functional links between anatomically unconnected regions. Such links make central

nodes less prominent, and reduce sensitivity of centrality measures in functional network (Rubinov & Sporns, 2010). In addition, path-measured centrality in functional networks is subject to the same with interpretation caveats as path-measured of integration.

Materials

Anatomical connectivity of archosaurimorphs are examined from the five representative species: *Chelydra serpentina* (Werneburg 2011), *Alligator mississippiensis* (original dissection + Li & Clarke, 2015), *Crocodylus siamensis* (original dissection of HoUM40002), *Struthio camelus* (original dissection of HoUM40003 + Tomlinson 2000), and *Gallus gallus* (original dissection + Homberger & Meyers, 1989).

Topological similarity in hyolingual muscles is examined to suggest hypotheses of homology. Muscle scarring on bones is confirmed to know precise attachment site of muscles and identify osteological correlates. Those anatomical data are analyzed within the framework of the Extant Phylogenetic Bracket approach (EPB), which is based on the principle of parsimony to infer soft tissues in extinct taxa (Witmer 1995a, b, 1997;

Carrano & Hutchinson, 2002). A soft tissue, in this case a muscle, can be interpreted as three different levels of inference (I, II, or III), based on the presence of osteological correlates in both extant bracketing taxa and fossil taxon, one extant taxon and fossil taxon, or only fossil taxon, respectively. In the case that osteological correlates in extant taxa is absent despite presence of soft tissue, the levels of inference can be assigned a “prime” designation (I’, II’, or III’) which is weaker inference than its predecessor. Osteological correlate is defined as characteristic surficial feature (e.g. fossa, tuberosity, spur, flange, and other muscle-related bony structures).

Results

Network parameters

The number of nodes (N) varies, ranging from 25 in *Alligator*, *Crocodylus*, and *Gallus* to 43 in *Chelydra* (Chelonia), and its variation is primarily dependent on the number of bony elements (Table 1). For instance, turtles have a pair of ceratohyal and two pairs of ceratobranchials, and hypoglossum, which are absent in crocodylians and birds.

As well as N, K is the highest in *Chelydra* (64) and the lowest in *Alligator* (31). Density of anatomical network (D) displays a phylogenetic trend which increases from *Chelydra* toward *Gallus*. Contrary to the results of N and K, the D-value of *Chelydra* (0.071) is remarkably lower than the others (0.103 ~ 0.11). Complexity (C) varies among lineages and *Gallus* shows the highest value (0.36), while *Alligator* shows the lowest (0.133). The C-value of *Chelydra* (2.03) is intermediate between Crocodylia (*Alligator* and *Crocodylus*) and birds (*Struthio* and *Gallus*). With respect to the shortest path length (L), *Gallus* (3.53) exhibits the highest value. *Chelydra* shows the lowest D and Q value, and the highest N, K, L, and H values among the archosauromorphs. *Alligator* and *Struthio* exhibit identical values of Complexity with each other. Complexity of *Gallus* is remarkably high compared to others. Heterogeneity of network is high, close to 1.0 in *Chelydra* while it is around 0.6 in *Alligator*, *Struthio*, and *Gallus*. Our network analyses reveal that the musculoskeletal networks in the hyolaryngeal apparatus of a turtle *Chelydra* is less anisomeric (lower H) than *Alligator*, *Crocodylus*, *Struthio*, and *Gallus* although it is higher N, less complex (lower D and C) than the others.

Network modules

Among the specific connectivity modules obtained in the present network analysis, the present study will focus on the modules that include both bones and muscles (Fig. 1), which we can discuss in a more comprehensive functional and evolutionary context. The number of modules is remarkably different among archosaurs, but a detailed examination clearly shows that *Alligator* and *Crocodylus* share a more similar pattern (Fig. 1). *Alligator* and *Crocodylus* display six modules (n= 7) and its laryngeal module is separated into cricoid and arytenoid modules, which is characteristic for both of these crocodylians. The modern crocodylians shows the similar network pattern with each other, including modular partition, and two minor differences in modular contents, which are m. geniohyoideus and m. episternobrachialis. M. geniohyoideus belongs to hyoid module (bh+cb+eb+bhd+bhv+oh+gh) in *Alligator* while it assigns to mandible module (mandible+im+cc+gh) in *Crocodylus*, and m. episternobrachialis belongs to shoulder girdle module in *Alligator* (episternum+coracoid+eb+ebt) while it takes part in hyoid module (bh+cb+eb+bhd+bhv+oh+ebt) in *Crocodylus*. These differences in modular

partitions are due to that *Crocodylus* is distinct from *Alligator* in having a connection between eb and bh. *Struthio* shows five modules, mandible is included in the same module with ceratobranchial. *Gallus* exhibits four modules, which is the least among the studied archosaur species, and largely different from *Struthio* in having a simpler module of skull and mandible (Fig 1.). The common features of *Struthio* and *Gallus* are integration of cricoid and arytenoid modules that are separated in *Chelydra*, *Alligator*, and *Crocodylus*.

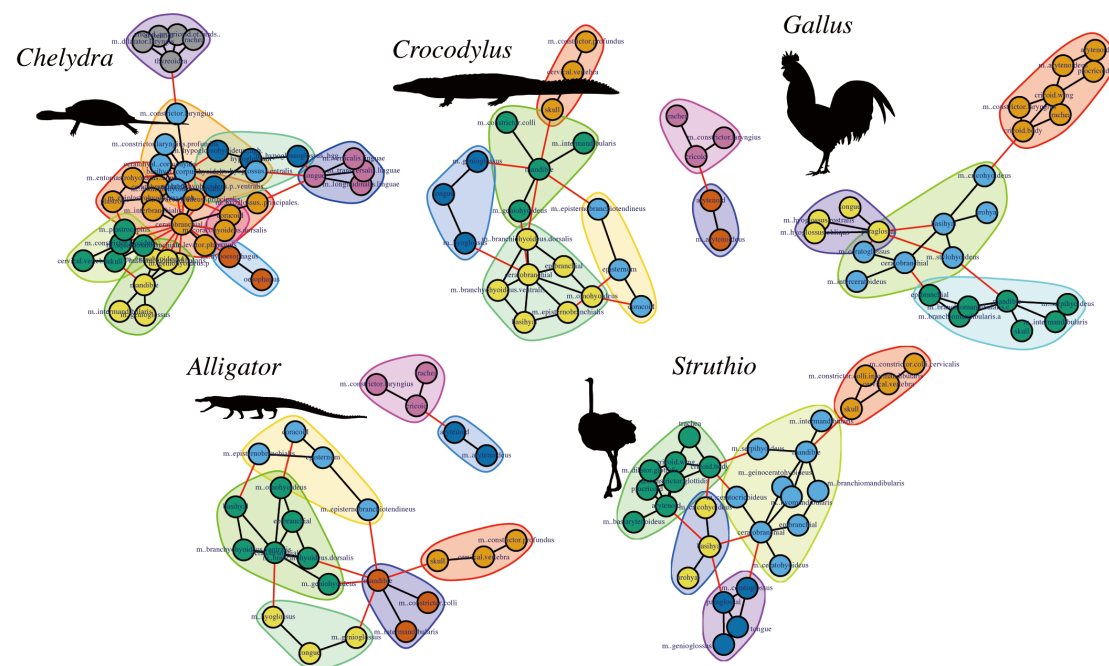


Figure 1. Anatomical networks and modules in *Chelydra*, *Alligator mississippiensis*, *Crocodylus siamensis*, *Struthio camelus*, and *Gallus gallus*.

Anatomical comparison of hyolingual apparatus

M. branchiomandibularis (= m. branchiohyoideus dorsalis) and m. branchiomandibularis ventralis (= m. branchiohyoideus dorsalis) are a synapomorphy of Archosauromorpha (Chelonia, Crocodylia, Neornithes). Acquisition of these two muscles is prior to loss of ceratobranchial 2 in basal node of Archosauria. The loss of ceratobranchial 2 accompanies loss of the attached muscles but the other hyolingual muscles are not changed.

In Crocodylia, none of new hyolingual muscle is retained, indicating that crocodylians shows primitive condition of the muscles in basal archosaurs. In contrast, hyolingual muscles are largely changed in Neornithes. Two muscles are lost (m. branchiohyoideus ventralis and m. episternochoydeus) and one muscle (m. ceratohyoideus (= m. interceratobranchialis)) is retained. Two muscles changed its position of the attachment: origin of m. omohyoideus turned from coracoid to cricoid (cricohyoideus), and that of m. hyoglossus turned from tongue to paraglossal (m. ceratoglossus). In Neognathae, m. hyoglossus is divided into two parts (hyoglossus obliquus and rostralis), and insertion of m. cricohyoideus move from ceratobranchial to

basihyal.

Discussion

The C value of *Chelydra* is higher than the crocodylians, but lower than the birds. The lowest D and Q and the highest N, K, L, and H of *Chelydra* values indicate that the musculoskeletal network of chelonian hyolaryngeal apparatus is complicated, but its modular independence is weakly structured compared to the archosaurs. The number of modules is larger than crocodylians by one, *Struthio* by three, and *Gallus* by four. These are likely due to their ancestral (ceratohyal and ceratobranchial 2) and uniquely derived (paraglossum) bony and cartilaginous elements. Interestingly, *Gallus* possesses the same number of musculoskeletal elements ($N = 25$) with Crocodylia (*Alligator* and *Crocodylus*), but exhibits notably higher complexity ($C = 0.36$),

Modular partition

Modular partition is not largely different between *Chelydra* and two species of Crocodylia (*Crocodylus siamensis* and *Alligator mississippiensis*) (Fig. 2). However,

Neornithes (*Struthio* and *Gallus*) exhibit lower number of modules and different modular partitioning (Fig. 2). Difference in modular partitioning is also present between *Struthio* and *Gallus* although both of them are birds. In *Gallus*, mandible is separated from the hyoid module and basihyal is combined with ceratobranchial into the same module (Fig. 2). These results may attribute to losses of m. genioglossus and m. geniohyoideus which protract hyoid apparatus in *Gallus*. Bipartition of m. branchiomandibularis in *Gallus* contributes to the separation of the mandible from the hyoid module.

Archosauria

- Testudines** (8 modules)
 - Chelydra*
- Crocodylia** (7 modules)
 - Alligator*
 - Crocodylus*
- Neornithes**
 - Paleognathae** (5 modules)
 - Struthio*
 - Neognathae** (4 modules)
 - Gallus*

Figure 2. Modular evolution in a phylogenetic framework of Archosauromorpha.

Modules with the same color representing the same module.

In the introduction this study raised three major questions with implications for our understanding of archosaur evolution. The first concerns the evolution of archosaur complexity: H1) *does the complexity in bone-bone and muscle-bone connectivity in the hyolaryngeal apparatus correlate with the functional complexity, which we predicted would result in decreased network complexity of crocodylian and bird hyolaryngeal apparatus compared to that of turtles.* Some of archosaur hyolaryngeal apparatus are versatile structures that function differently in different ecological contexts. Higher complexity in feeding behavior may lead to less constraint in the evolution of hyolaryngeal apparatus. This would reflect a need to maintain a more versatile, generalized, and thus likely less constrained, anatomy compared to a highly specialized hyolaryngeal apparatus.

Comparison with functional modularity

This study also raised the second hypothesis: H2) *the evolutionary increase in the number of unique hyolaryngeal muscles in archosaur evolution resulted in a lower average number of muscle-bone connections per structure and therefore in lower*

anatomical complexity and density of croc and bird hyolaryngeal apparatus compared to those of turtles. As a result, the average number of connections are much lower in the archosaurs (*Crocodylus*, *Alligator*, *Gallus*, and *Struthio*) than that of *Chelydra*. This result is consistent with the above-mentioned complexity of the network.

Finally, the last hypothesis was that *centrality of ceratobranchial is decreasing through the evolution of Archosauria* (H3). Intriguingly, centrality of ceratobranchial is decreasing while basihyal is increasing in Archosauria as hypothesized. This functional sophistication supports Williston's Law in archosaur hyolaryngeal apparatus, especially in ceratobranchial. Increase of Q-values additionally supports that the connectivity within each isolated module is strong in Archosauria, especially in Neornithes (Table 1). Functional network is likely to be denser than anatomical network, as it will typically contain numerous connections between anatomically unconnected regions in brain (Damoiseaux & Greicius, 2009).

The common ancestor of archosaurs had likely possessed basihyal and ceratobranchial with m. branchiomandibularis, m. omohyoideus (Li et al., 2018). Fossil does not preserve muscle or cartilage basihyal, but there should be m.

branchiomandibularis, m. omohyoideus in the common ancestor of archosaurs. Network analysis is good to evaluate each network independently, and compared with one another regardless of phylogenetic relationships. The ancestral state is hard to discuss because there have been a huge gap between crocodylians and birds. Dinosauria is the key taxon for archosaur evolution. Nevertheless, the anatomical networks show common features between crocodylians and birds, and shed new lights on the modular evolution of hyolaryngeal apparatus in archosaurs despite the difficulty for the fossilization of the soft tissue.

Conclusion

These results show that new quantitative network approaches to study integration and the constraints of evolution, including using network theory to study morphological modularity and integration, can complement more traditional methods such as morphometrics. Such an integrative approach can provide a more comprehensive understanding of the features that define the archosaur lineage, including the evolution of uniquely archosaur traits related to feeding behavior. Ceratobranchial of Archosauria

decreases to one pair, and increases its centrality in the anatomical network. These results support Williston's Law in hyolaryngeal apparatus of Archosauria and highlights functional importance of their ceratobranchials.

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Table 1. Network parameters of hyolaryngeal apparatus of the studied extant archosaurs

	N	K	D	C	L	H	Q (walktrap)	
Sphenodon		23	17	0.067	0		0.954	0.535
Chelydra		43	64	0.071	0.203	3.262	0.934	0.459
Alligator		25	31	0.103	0.133	2.745	0.639	0.48
Crocodylus		25	32	0.107	0.167	2.7	0.668	0.476
Struthio		29	41	0.101	0.243	3.203	0.606	0.542
Gallus		25	33	0.11	0.36	3.53	0.588	0.559

III. A NEW GONIOPHOLIDID FROM THE UPPER JURASSIC MORRISON FORMATION, USA: NOVEL INSIGHT INTO AQUATIC ADAPTATION TOWARD MODERN CROCODYLIANS

ABSTRACT

Goniopholididae is a more basal neosuchian group of the Jurassic and Early Cretaceous, closely related to the derived Neosuchia (Paralligatoridae and Eusuchia). They have flat snout as well as modern crocodylians, being key for the early evolutionary history of crocodylian body plan and their aquatic adaptation. Here we newly describe one of the complete specimens of Goniopholididae from Wyoming, USA, and first report their hyoid apparatus. Phylogenetic analysis reveals that this specimen is a new species, a sister taxon for *Amphicotylus stovalli*, and recognized as the basal-most broad-snouted goniopholidid. Together with posterior extension of internal choana (incomplete secondary palate), shortening and dorsal deflection of ceratobranchial of the new goniopholidid suggests that basal neosuchians could raise gular valve to separate oral cavity and laryngeal region as in extant crocodylians to enable respiration in the water

while external nostrils is above the water surface. This study reveals that modern crocodylian respiratory system had already appeared in the early evolution of Neosuchia prior to postcranial modifications in the evolution toward modern crocodylians. Broad rostrum of the new species also broadens ecological diversity of Goniopholididae as evidence for their success in the freshwater environment of the Late Jurassic.

1. INTRODUCTION

Goniopholididae is a group of basal Neosuchia, close to Paralligatoridae and Eusuchia (modern crocodylian clade), and were relatively diverse in freshwater ecosystems of the northern hemisphere during the Jurassic and Early Cretaceous (Buffetaut 1982; Andrade et al., 2011). Some recent phylogenetic studies of neosuchians proposed that Goniopholididae is closer to Eusuchia than to *Isisfordia* and *Susisuchus* (Turner 2015; Turner & Pritchard, 2015), indicating importance in terms of evolutionary history in Neosuchia. Additionally, Goniopholididae is important as the origin of flat and long snout (Foster 2009) and bony secondary palate (Pritchard et al., 2013) in the evolution toward modern crocodylians that survived the Cretaceous-Paleogene mass extinction.

The bony secondary palate of extant crocodylians could date back to Paralligatoridae (Montefeltro et al., 2013). Secondary palate separates oral cavity and narial passage. Huxley (1875) proposed that function of secondary palate is to breathe in holding prey in the mouth, and open mouth under the water. Meanwhile, Langston (1973) suggested an alternative idea that the secondary palate is to avoid weakness of caudal part of palate during strong bite, and several studies additionally support this idea (Busbey 1995; Rayfield & Milner, 2008). However, the choana extends anterior and posteriorly in Goniopholididae, indicating that the mechanical-strength hypothesis is not sufficient to explain the extension of internal nostril in Goniopholididae for acquisition of secondary palate (Pritchard et al., 2013). This study reconsiders gular valve hypothesis that secondary palate is developed for respiratory system with gular valve that is located anterior to choana and posterior end of tongue in extant crocodylians. Rise of gular valve separates oral cavity and laryngeal region, and enables respiration in the water while external nostrils is above the water surface. Examination of palate & hyoid in Goniopholididae is ideal to test gular-valve hypothesis.

Here we newly describe one of the complete specimens of Goniopholididae from

Wyoming, USA, and first report their hyoid apparatus. Phylogenetic analysis is also performed for the new well-preserved goniopholidid specimen to know its phylogenetic position in Neosuchia. Additionally, modern crocodylians are dissected to identify osteological correlates for hyolingual muscles in hyoids, and investigate functional anatomical similarities between fossil and extant crocodylians. Then, palatal and hyoid morphologies are surveyed in the course of aquatic adaptation in Neosuchia toward modern crocodylian lineage.

2. MATERIAL AND METHODS

The new goniopholidid specimen was discovered at Bone Cabin Quarry with *Camarasaurus* skeleton, where the Late Jurassic Morrison Formation is exposed, in Wyoming, USA (McIntosh et al., 1996). The new goniopholidid specimen is stored in Gunma Museum of Natural History (GMNH-PV0000229), Gunma Prefecture, Japan.

The data matrix for the present phylogenetic analysis is composed of 486 characters and 104 taxa, including GMNH-PV0000229, based on Andrade et al. (2011) focusing on Goniopholididae and the analysis is performed on PAUP v. 4.0a (Swofford, 2017).

Following Andrade et al. (2011), *Gracilisuchus* is used as an outgroup and 24 characters are treated as ordered (Cha. 6, 7, 31, 72, 73, 145, 152, 157, 206, 208, 212, 235, 261, 286, 291, 292, 322, 336, 359, 360, 414, 448, 452, 453).

Hyoid musculature anatomy and osteological correlates (e.g. tubercle, process) in GMNH-PV0000229 are assessed by dissection of three modern crocodylians (*Crocodylus porosus*, *Caiman crocodilus*, and *Alligator sinensis*). Hyoid curvature is measured by a ratio of length of dorsal margin of ceratobranchial to its distance. Relative position of anterior and posterior margin of internal choana is quantitatively evaluated with standardization by skull width.

Institutional abbreviation: AMNH American Museum of Natural History, GMNH Gunma Museum of Natural History, SMNS Staatliches Museum für Naturkunde Stuttgart.

3. RESULT

(a) SYSTEMATIC PALEONTOLOGY

Crocodylomorpha Walker 1970

Neosuchia Benton & Clark 1988

Goniopholididae Cope 1875

Amphicotylus Cope 1878

sp. nov.

(a) Etymology

Holotype: GMNH-PV0000229, a well-preserved single individual skeleton, represented by skull, mandible, hyoid (ceratobranchial), vertebra, shoulder and pelvic girdle, fore- and hindlimb, and osteoderms.

Locality: *Camarasaurus* Bone Cabin Quarry, Wyoming, USA, with a *Camarasaurus* specimen (GMNH-PV101, McIntosh et al., 1996).

Stratigraphy: the Morrison Formation

Diagnosis: Goniopholididae with unique combination of the following features; broad rostrum; five subfossae in maxillary depression; anterior projection at posterior margin

of naris; triangular palpebral; lack of crest C in quadrate; postchoanal fossa; perichoanal fossa being wider than nasopharyngeal passage (Ch. 234: 2); posterior border of internal choana at mid-pterygoid (Ch. 237:1).

(b) DESCRIPTION

The new specimen of *Amphicotylus* (Fig. 1) completely preserves skull, mandible, postcranial skeletons, osteoderms, and hyoid apparatus without significant deformation. Missing elements are a coronoid, a left palpebral, a proatlas, some caudal vertebrae, a left radiale, and partial pedal elements. The skull is 43 cm long, one of the largest goniopholidid fossils, and its rostral length (preorbital length) is 26 cm (60% of the skull length), indicating medium rostral proportion. The skull size and the fused sutures of skull and sacral, and caudal vertebra indicate that this individual was mature at death. Axis and cervical, dorsal, and sacral vertebra display incomplete neurocentral fusion. The rostrum projects dorsally like a goniopholidid *Amphicotylus lucasii* (Mook 1942), and is broader than *A. stovalli* (Mook 1964). The orbits are evidently asymmetry because palpebral is preserved only on the right side.

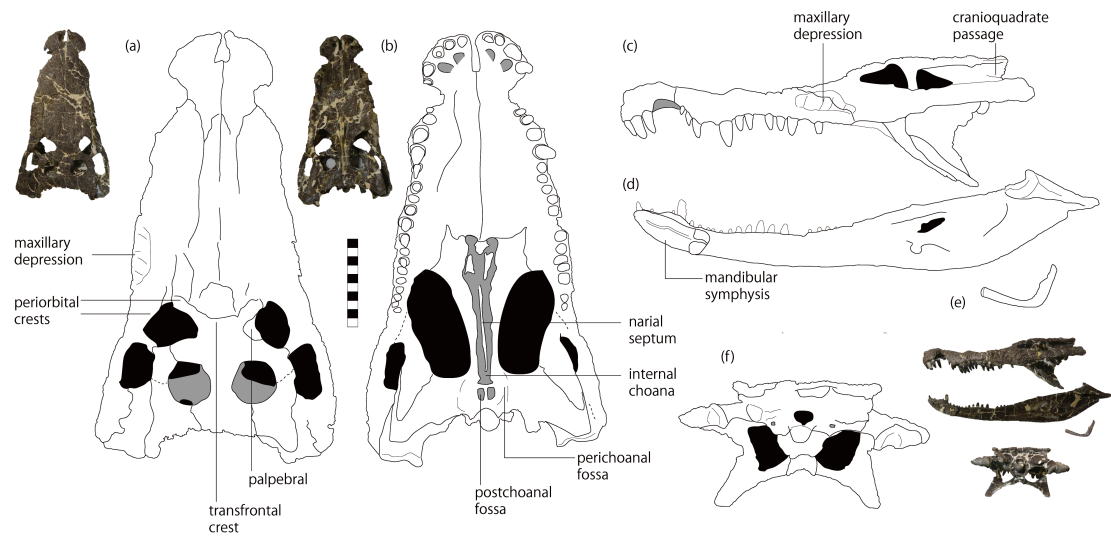


Figure 1. Skull of *Amphicotylus* (GMNH-PV0000229) in dorsal (a), ventral (b), left lateral (c), mandible in left medial (d), ceratobranchial in left lateral (e), and posterior view (f).

The palpebral excludes frontal from the orbital margin, forming subcircular orbit in dorsal view, which is distinct from elliptical shape of *Goniopholis simus* (Andrade & Hornung, 2011). The palpebral is triangular in dorsal view, as in *G. simus*, *Nannosuchus*, *Anteophthalmosuchus hooleyi*, and *Hulkepholis willetti* (Andrade & Hornung, 2011), and the most similar to that of *Anteophthalmosuchus hooleyi* in having a concave lateral margin, small size relative to orbit, and non-extension to lacrimal, but, different in absence of the prefrontal-palpebral contact (Andrade & Hornung, 2011). In dorsal surface, the transfrontal crest of frontal is continuous with the upper periorbital crest of the prefrontal and the lacrimal along the anteromedial margin of the orbit. Lateral to the upper periorbital crest, a lacrimal groove is present in the dorsal surface. The orbits are as large as the supra- and infratemporal fenestrae. Within the supratemporal fossa, the anterior opening of the temporo-orbital (posttemporal fossa) is visible in dorsal view. The caudal end of the paroccipital process has the cranioquadrate passage that opens laterally, which is floored by the medial portion of the quadrate, as in goniopholidids and *Shamosuchus* (Montefeltro et al., 2016). The ventral opening of the nasopharyngeal passage extends anteriorly and posteriorly beyond the suborbital

fenestrae, and is hourglass shape, as in the other Jurassic goniopholidids, such as *Calsoyasuchus*, *Eutretauranosuchus*, *A. stovalli*, and (Tykoski et al., 2002; Smith et al., 2010, Pritchard et al., 2013). The posterior ends of the palatal processes of the maxillae fail to meet in the midline, as in *Calsoyasuchus* (Tykoski et al., 2002), *Sunosuchus junggarensis* (Wu et al., 1995), *Eutretauranosuchus* (Pritchard et al., 2013), and *A. lucasii* (Mook 1942), and palatal shelves of the palatine are not fused and partially contact at the midline as well as *A. stovalli* (Allen 2012), and contrast to *A. lucasii* (Mook 1942). The choanal septum is incompletely preserved, but extends to one centimeter before the end of the nasopharyngeal passage in pterygoid, and seems to be smooth ventrally like basal goniopholidids, such as, *Calsoyasuchus* (Tykoski et al., 2002), and *Sunosuchus junggarensis* (Wu et al., 1995), in contrast to bilateral septal laminae of *Eutretauranosuchus* (Pritchard et al., 2013) and *A. lucasii* (Mook 1942). Posterior to the nasopharyngeal passage, the pterygoid shows postchoanal fossa that is a small shallow depression, rectangular in outline, and not perforated or connected to canals. As similar structure with the postchoanal fossa, parachoanal fossa is present in some notosuchians (*Sphagesaurus* and *Stratotosuchus*) (Montefeltro et al., 2011; Pol et

al., 2014). The postchoanal fossa of GMNH-PV0000229 may not be homologous to parachoanal fossa of notosuchians because of differences in size, morphology, and position. Its function remains equivocal due to lack of analogy in extant crocodylians. Both internal nostril and postchoanal fossa are positioned in a shallow perichoanal fossa, as in modern crocodylians.

Next to the premaxilla and maxilla suture there is a notch for enlarged fourth dentary tooth in the lateral margin, forming axe-head-shaped premaxillae in dorsal view, as in *A. lucasii*, *A. stovalli*, *Goniopholis* spp, in contrast to paddle shape of *Nannosuchus* (Andrade et al., 2011). The naris is placed anteriorly, and anteroposteriorly short (~50% length of rostral axe head), as in *Calsoyasuchus* (Tykoski et al., 2002). The premaxillae entirely encircle the naris, excluding the nasals from its posterior border like goniopholidids such as *Eutretauranosuchus*, *Sunosuchus*, *A. lucasii*, *G. simus*, and *G. kiplingi* (Andrade et al., 2011). The posterior margin of the naris projects anteriorly, resulting in figure-eight narial morphology, as in *A. lucasii* and *A. stovalli* (Mook 1942; Mook 1964; Allen 2012). Lateral to the contact between anterior rami of premaxillae, there is a shallow fossa, like *Eutretauranosuchus*, *A. lucasii*, and *Anteophthalmosuchus*

hooleyi, but not as deep as that of *G. kiplingi*, and *G. simus* (Smith et al., 2010; Andrade et al., 2011). In dorsal surface anteronarial foramen is present between first premaxillary tooth and the naris, similar to *G. kiplingi* (Andrade et al., 2011). The third and fourth premaxillary teeth are the largest among the upper jaw teeth. Two medial pits are present posterior to the first ~ third maxillary teeth for the first and second dentary teeth.

The maxillary depression is present on the laterodorsal surface of the posterior process, as in the other goniopholidids and pholidosaurids (Martin et al., 2016), showing five subfossae, the second being the largest. The number of the subfossae in GMNH-PV0000229 is the same with *G. simus* (Owen 1878; Salisbury et al., 1999), larger than four in *A. lucasii*, and three in *G. kiplingi* (Andrade et al., 2011) and *Anteophthalmosuchus hooleyi* (Martin et al., 2016). Enlarged neurovascular opening is present at bottom of each chamber in *Eutretauranosuchus*, *A. lucasii* and *G. kiplingi* (Andrade et al., 2011), however, only in the second chamber of the left depression of GMNH-PV0000229.

The lacrimal is as long as the prefrontal and the ratio of the anteroposterior

length to the mediolateral width is roughly 3.0, less than that of *G. kiplingi* (about 5.0, Andrade et al., 2011), in contrast to its elongation of *G. simus* and *G. kiplingi* (Owen 1878; Andrade et al., 2011).

In frontal, the width of the anterior process is as large as that of the posterior process (intertemporal bar), which is different from the other goniopholidids, such as, *A. stovalli*, *G. simus*, *Anteophthalmosuchus*, and *Nannosuchus* (Allen 2012; Salisbury et al., 1999; Andrade et al., 2011; Martin et al., 2016; Salisbury 2002). The frontal-postorbital suture is almost straight and simple, unlike *G. simus*, and *G. kiplingi* (Salisbury et al., 1999; Andrade et al., 2011) and the frontal-parietal suture is visible at the intertemporal bar in lateral view, but not in dorsal view.

From the anterolateral corner of the postorbital, very short and robust process projects anterolaterally, as in *G. simus* and *G. kiplingi* (Salisbury et al., 1999; Andrade et al., 2011).

The dorsal surface of parietal is flat, and three times as wide posteriorly as in the intertemporal bar, which is larger than *Anteophthalmosuchus hooleyi* (Martin et al., 2016).

Presence of quadratojugal spine from anterior edge of the ascending process remains ambiguous in GMNH-PV0000229. The posterior end of the quadratojugal does not take part in jaw articular facet of the quadrate, but reaches its lateral side.

The quadrate of GMNH-PV0000229 has an acute edge, separating the dorsal and posteromedial surfaces on the right side, as in *G. simus* (Salisbury et al., 1999), *A. stovalli* (Allen 2012), and *Hulkepholis willetti* (Salisbury & Naish, 2011), while, poorly defined edge on the left side, as in *G. kiplingi* (Andrade et al., 2011). In ventral surface, there are two well-developed crests (A and B): crest A extending along the quadrate-quadratojugal suture, and crest B being positioned medially to crest A, and passing posteromedially toward the quadrate-pterygoid suture (sensu Iordansky, 1973).

A median crest of supraoccipital seems to be absent in the caudal surface, differing from *G. baryglyphaeus* (Schwarz 2002).

The external mandibular fenestra is small, and longer than high, and possess acute posterior corner. The splenial extends to the posterior one-fifth of the mandibular symphysis in GMNH-PV0000229. The participation of splenial to mandibular symphysis is also present in goniopholidids (e.g. *Eutretauranosuchus* Smith et al., 2010,

G. baryglyphaeus Schwarz 2002).

The retroarticular process of articular is posteromedially oriented, and twice as long as the mandibular glenoid fossa.

Dentition

The 3rd and 4th premaxillary teeth are the largest among the tooth row, and the 4th and 5th maxillary teeth are the second largest. The anterior tooth is slightly more slender than the posterior tooth. Low apicobasal ridges run on both lingual and labial crown surfaces. A distinct keel runs both mesial and distal sides of tooth crown.

Hyoid

A pair of ceratobranchials is recovered in GMNH-PV0000229. The left ceratobranchial lacks the dorsal margin of the distal end and the right ceratobranchial is missing the distal portion. The left ceratobranchial is 76 mm long in distance between proximal and distal ends, and its length along the dorsal margin is 99 mm long, which is about 22 % length of the mandible, which is smaller than *Euparkeria* (Ewer

1965), *Geosaurus vignaudi* (Frey et al., 2002), *Simosuchus* (Kley et al., 2010), and *Aplestosuchus* (Godoy et al., 2014), and as long as paralligatorid *Batrachomimus* (Montefeltro et al., 2013) and modern crocodylians (Fig. 2). Ratio of the length of the dorsal margin to the distance is 1.31, as large as eusuchians (Fig. 2). Ceratobranchial is dorsally deflected, more than *Steneosaurus bollensis* (Mueller-Töwe 2006), *Geosaurus giganteus* (Young et al., 2009), and *Simosuchus* (Kley et al., 2010), and as much as paralligatorid *Batrachomimus* (Montefeltro et al., 2013) and eusuchians (Li & Clarke, 2015) (Fig. 2). The distal portion is narrower than the proximal one, and slightly bowed medially. Near the center of the curvature, there is a prominent tubercle in the ventromedial surface, which may bear muscle attachment site for tendon of m. hyoglossus, m. omohyoideus, and m. geniohyoideus. From the posterior one fifth of proximal portion to the distal end, the height is increasing and the dorsal margin is tapering in the cross section. In *Alligator mississippiensis*, proximal end of ceratobranchial is slightly wider than high, limiting dorsoventral motion (Busbey 1989).

Postcranial skeleton

The 24 presacral vertebrae are almost completely preserved, and composed of nine cervicals, ten thoracics, and five lumbar vertebrae. The presacral vertebra has amphicoelous centrum, without ventral keel (hypapophysis). The sacral vertebrae are almost completely preserved and fused and the sacral ribs are not fused with the ilia.

The two sacral vertebrae are separated with each other. The anterior facet of the first sacral vertebra is twice as wide as high, and the widest among all the other vertebrae.

The second sacral centrum has a concave posterior facet.

The 25 caudal vertebrae come from the anterior to the posterior series and appear to be less than the original number of the caudal vertebrae. The serial number of the caudals is uncertain. All caudal centra are weakly amphicoelous to amphiplatyan.

The scapular blade projects medially, and expands distally, three times as wide as the shaft. Tuberosity is developed dorsal to the scapular glenoid in lateral surface, and in posterior margin of scapular blade, which is attachment site for m. triceps brachii caput scapulare, and m. scapulosternal ligament (or m. scapulaohumeralis caudalis), respectively (Sertich & Groenke, 2010).

The interclavicle is planar, a single element, and lacking the posterior end.

The dorsal surface is slightly inflated, and mediolaterally expanded at the middle.

The forelimb (humerus + ulna + metacarpal III) is as long as the hindlimb (femur + tibia + metatarsal I). The humeri are about 20 cm long, almost the same with femur. The ulna is approximately 80% of the length of the humerus. The olecranon process is slightly higher than the main proximal articular facet. The radius is straight and about 85% of the length of the ulna. The radiale is slightly longer than metacarpals. The radiale possesses a wide proximolateral process, and three articular facets for the radius, the ulna, and the ulnare. The proximal end of the radiale shows the facet for the radius, being wider than the distal end, and more expanded proximolaterally than proximomedially as in *G. simus* (Owen 1878; Salisbury 1999). Posterolateral to the proximal end, the articular facet for the ulna is located on the proximal one-third of the radiale, and facing posterolaterally as in *Crocodylus*.

The metacarpal I is the most robust metacarpal and shorter than the others except metacarpal V, being roughly one-third of the other metacarpal length.

The femur is as long as humerus and both the tibia and fibula are a nearly three fourth of the femoral length.

The 71 osteoderms are marked with pits on the outer surfaces, and their positions are uncertain because of the disarticulation. The osteoderms of GMNH-PV0000229 are variable in size and shape, and distinguished into three morphotypes, wide rectangular osteoderms (n=31), trapezoidal (and hexagonal), and circular one. The rectangular osteoderms are larger than the others and some of them possess an anterolateral process at their lateral edges, as in Goniopholididae (Owen 1878; Buffetaut & Hutt 1980; Wu et al., 1996b; Lauprasert et al., 2007; Martin et al., 2016) and Pholidosauridae (Andrews 1913b; Sereno et al., 2001; Hua et al., 2007). Trapezoidal osteoderms are peripheral and possess a convex lateral edge, while the hexagonal osteoderms are on the center of the ventral shield and sutured to all surrounding osteoderms along the entire margin (Martin et al., 2016). Circular one is without dorsal keel (Wu et al., 1996b). The rectangular ones can be interpreted as median paravertebral dorsal shields, the trapezoidal and hexagonal ones as ventral shield, and the circular ones as accessory osteoderms lateral to the median shields or dorsal to appendicular skeleton, as in some goniopholidids (Wu et al., 1996b; Martin et al., 2016).

(c) PHYLOGENETIC ANALYSIS

The phylogenetic analysis resulted in the most 2592 parsimonious trees. A strict consensus tree of the most parsimonious trees places GMNH-PV0000229 as a member of Goniopholididae. Four synapomorphies support the monophyly of *Amphicotylus stovalli* and GMNH-PV0000229. GMNH-PV0000229 and *A. stovalli* shares apomorphic characters. This clade of *Amphicotylus* is placed outside of the European goniopholidid clade.

One unique character of *Amphicotylus stovalli* (Allen 2012) and *A. lucasii* (Mook 1942) is anterior projection of caudal margin of the naris, forming eight-figure-shaped narial morphology. Also, transversely oriented periorbital crest of jugal and lacrimal characterize *A. stovalli* (Mook 1964). These two characters are shared with GMNH-PV0000229, however, the rostrum of GMNH-PV0000229 is broader than *A. stovalli* (Mook 1964), which cannot be explained by ontogeny because the skull length of GMNH-PV0000229 (43 cm) is almost the same with *A. stovalli* (42 cm. Mook 1964).

(e) HYOID MUSCULATURE AND OSTEOLOGICAL CORRELATES OF
MODERN CROCODYLIANS

All six hyolingual muscles are extrinsic and attach to ceratobranchial. Relative positions of the muscles are similar to each other, suggesting the conservative insertions in Crocodylia at least. The ceratobranchial is dorsally deflected as well as *Amphicotylus*, and there are two muscles near the center of the curvature and four muscles on the distal portion. Near the center of the curvature, there is a prominent tubercle in the ventral surface, which bears muscle attachment site for m. geniohyoideus. In *Crocodylus siamensis*, m. omohyoideus, m. geniohyoideus, and tendon of m. hyoglossus originates from the tubercle that may expand attachment area for those three muscles. Anteriorly, m. hyoglossus is located, which is a lingual muscle extending within tongue. On the distal portion of ceratobranchial, m. omohyoideus originates from its lateral surface and posterior margin. The distal portion of the ceratobranchial is concave laterally in *Crocodylus siamensis*, while, expanded in Alligatoridae. The lateral concavity in *Crocodylus siamensis* is a result of lateral expansion of both anterior and

posterior margin of the distal portion, which may expand attachment area for m. branchiomandibularis anteriorly and m. omohyoideus posteriorly. From the dorsal margin of the distal portion, m. branchiohyoideus dorsalis (m. branchiomandibularis) and ventralis originate, inserting into ventral to splenial and to the last tooth on the medial surface, and lateral margin of the anterior portion of the basihyal, respectively. (In the anterior half of the distal portion, m. geniohyoideus originates, and inserts to the medial surface of the mandibular ramus.) M. branchiohyoideus originates from the anterior margin of distal portion of ceratobranchial to protract and suspend hyoid (Li & Clarke, 2015). Osteological correlates for three muscles, m. hyoglossus, m. geniohyoideus, and m. omohyoideus, are present in modern crocodylians (Fig.). The attachment site for m. omohyoideus is concave in *Crocodylus siamensis*, *Alligator mississippiensis*, and *Tomistoma schlegelii*. By contrast, on the surface of mandible and pectoral girdle, osteological correlates for the hyolingual muscles are absent.

Dissection of this study reveals that dorsal deflection increases moment arm by m. branchiohyoideus ventralis.

4. DISCUSSION

(a) The phylogenetic relationships

GMNH-PV0000229 is placed as the sister taxon of *Amphicotylus stovalli*, sharing four unambiguous synapomorphies: anterior end of frontal is posterior to prefrontal (Ch. 142:0), palatal shelves of palatines are not fully contact at the mid-line (Ch. 213-0), anterior border of internal naris is positioned anterior to suborbital fenestra (Ch. 235-0), internal choana is lanceolated (Ch. 238-1), and anterior process from the ventral margin of external naris (new), but different in having broad rostrum and lack of crest C on ventral surface of quadrate. *A. stovalli* exhibits two autapomorphies: straight lateral border of nasals and rounded anterior margin of palatine. The Cretaceous goniopholidid of North America preserves no cranial elements (Frederickson et al., 2017).

As well as Andrade et al. (2011), Martin et al. (2016) also proposed possible monophyly between pholidosaurids and goniopholidids, based on maxillary depression, presence of both dorsal and ventral shields, dorsal osteoderm with anterolateral process, and amphicoelous vertebra with centra slightly longer than tall. Turner (2015) and

Turner & Pritchard (2015) proposed that Goniopholididae is closer to Eusuchia than to *Isisfordia* and *Susisuchus*. In this study, inclusion of *G. phuwiangensis* places the Goniopholididae closer to “Pholidosauridae + Thalattosuchia” clade than to “Paralligatoridae + Eusuchia” clade. This topology of the tree is only supported in the original results of Andrade et al. (2011), unlike most of the past studies supporting that Goniopholididae is a sister clade of “Paralligatoridae + Eusuchia” clade (Montefeltro et al., 2013; Adams 2013).

(b) Gular valve and dorsal deflection of ceratobranchial

In Crocodyliformes, dorsal deflection of ceratobranchial is present in Eusuchia, Paralligatoridae, and Goniopholididae, indicating its origin at the basal Neosuchia (Fig. 2, 4). ANOVA reveals that a significant difference between neosuchians and non-neosuchians in curvature ($p < 0.0001$), relative size ($p = 0.0002$), and posterior margin of internal choana ($p = 0.002$). Thalattosuchians are marine crocodyliforms and taxonomically close to Neosuchia, but shows no morphological similarity with modern crocodylians (e.g. *Steneosaurus bollensis* and *Geosaurus*

giganteus. Mueller-Töwe 2006; Young et al., 2009).

The dissection of the hyoid apparatus reveals that m. branchiohyoideus ventralis can pull up anterior portion of basihyal to raise ventral fold of gular valve (Fig. 3) which are transverse folds between oral cavity and pharynx (Putterill & Soley, 2006). Dorsal deflection of ceratobranchial increases moment arm of this muscle, and is present in *Amphicotylus* (GMNH-PV0000229) and modern crocodylians (Fig. 2). Osteological correlate for m. branchiohyoideus ventralis is ambiguous because its attachment site is not preserved, however, presence of osteological correlates for three other muscles indicates the same muscular structure with modern crocodylians.

Ventral fold of gular valve rises and covers dorsal fold to separate oral cavity and pharynx, then connect choana and glottis, and enable breathing in semi-submerge when only external nares is above the water surface (Putterill & Soley, 2006). Previously, the appearance of valves was unknown in their evolutionary history because such a soft tissue is hardly fossilized. However, dissection and morphology of hyoid bones prove that neosuchians could raise gular valve.

(c) Palatal evolution and ceratobranchial shortening

In addition to the dorsal deflection, ceratobranchial is short in Goniopholididae, Paralligatoridae, and Eusuchia (Fig. 2). Ceratobranchial shortening of the neosuchians indicates the posterior location of the base of their tongue. Therefore, when gular valve rises from the base of tongue, internal choana (secondary palate) is supposed to be positioned posteriorly to separate pharynx from oral cavity as seen in modern crocodylians (Huxley 1875; Busbey 1995; Salisbury et al., 2006).

Interestingly, goniopholidids show narial passage extending posteriorly to pterygoid, and the derived ones (Fig. . e.g., *Goniopholis simus*, Owen 1878; *G. kiplingi*, Andrade et al., 2011) complete bony secondary palate like modern crocodylians (Salisbury et al., 1999; Pritchard et al., 2013). Therefore, there has likely been gular valve system in Goniopholididae.

A remaining issue is that basal goniopholidids lack bony floor for narial passage and seems not to complete the system without soft tissue covering the ventral floor. The soft tissue is conceivably present, which covers the anterior portion of the ventral opening of the nasopharyngeal passage in the basal goniopholidids, as in

incisive foramen and suborbital fenestra of palate of modern crocodylians although there is no evidence of osteological correlate of such a soft tissue. Besides, in modern birds, relatives of crocodylians, palates are covered in soft tissue, such as, emu (J. Y. pers. obs.), commorants and gannets (Bang 1971), hoatzin (Korzun et al., 2003a), parrots, and cockatoos (Homberger 1980, 2001; Redd et al., 2012). Also, the nasal septum extends to the posterior end of the nasal passage in goniopholidids (GMNH-PV0000229, *Amphicotylus lucasii*, and *Eutretauranosuchus*), which likely supports palatal floor (Pritchard et al., 2013), and decreases each diameter of airway to reduce turbulence that interferes transport of the air on nasal passage, according to the principle of Reynolds number. Those lines of evidence indicate that the anterior portion of the opening was covered by soft tissue and the posterior end was genuine choanal opening in goniopholidids.

However, there have been the other three explanations previously proposed for their secondary palates other than gular-valve-acquisition hypothesis (Huxley 1875): (i) biomechanical strength of palate (Langston 1973), (ii) enlargement of oral cavity (Salisbury et al., 2006), and (iii) head buoyancy with paranasal sinus (Jankowski 2013).

First, we reject hypothesis (i), biomechanical strength, because, as indicated by Pritchard et al. (2013), the anterior portion of the nasopharyngeal passage is not ossified ventrally in basal goniopholidids (e.g. GMNH PV0000229, *Sunosuchus* spp.), which is mechanically weak in *Alligator* (Daniel & McHenry, 2001) despite that goniopholidids show similar cranial shape (platyrostrum) being expected to exhibit stress with modern crocodylians. Second, cranial buoyancy hypothesis (iii) is lack of supportive evidence so far. These functions (i) and (iii) maybe secondarily gained in Neosuchia (Busbey 1995; Jankowski 2013). However, hypothesis (ii), enlargement of oral cavity, is consistent with shortening of ceratobranchial which is positioned posterior to tongue and unable to extend anterior to base of immobile tongue (Clueren & De Vree, 2000), because the posterior shifts of choana and tongue base can increase capacity for holding and crushing of food items. The co-occurrence of shortening and dorsal deflection in GMNH-PV0000229 cannot resolve which valve or oral enlargement (ii) preceded in the early history (Table 1). The hypothesis (ii) is plausible as given that soft tissue covers the opening of nasopharyngeal passage as well as gular valve hypothesis. It still remains unknown which gular valve or enlargement of oral cavity was the primary driving force

for the posterior extension of nasopharyngeal passage because more basal neosuchians preserve no transitional ceratobranchial that is lack of either transformation.

(d) Aquatic adaptation in Neosuchia

Goniopholididae is the semiaquatic neosuchians, characterized by the oldest croc-like bodyplan (e.g. platyrostrum). Platyrostrum is resistant for mediolateral bending stress than oreinirostrum (tall rostrum) (Pierce et al., 2008), while, palate is not adapted mechanically. At the same time, they also retained a new unique respiratory system (gular valve) as in modern crocodylians.

The following three lines of evidences, the posterior extension of the nasopharyngeal passage, the shortening, and the dorsal deflection of ceratobranchial, suggest gular valve raising system in goniopholidids and paralligatorids, as well as modern crocodylians (Fig. 4). Secondary palate and gular valve enable crocodylians to completely isolate its oral and narial cavities for submerge (Ferguson 1981), and adapt to aquatic environment.

Emergence of the novel ceratobranchial morphologies in Goniopholididae is

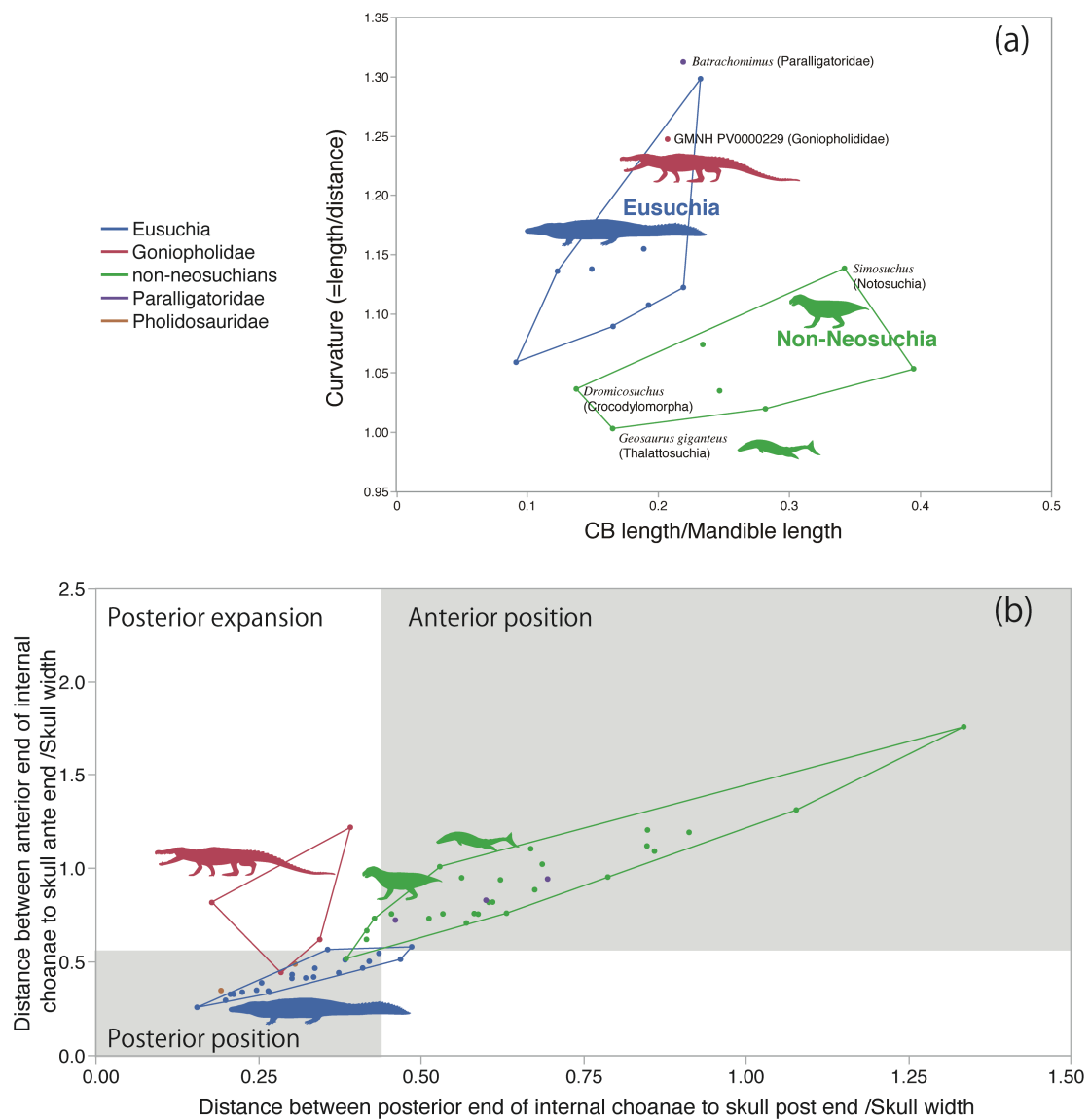


Figure 2. Relationship between curvature and relative length of ceratobranchial (a).

Relationship between relative positions of anterior and posterior margins of internal choana (b).

simultaneous with platyrostrum, and preceded several other known changes for crocodylian aquatic adaptation, such as, complete bony secondary palate, vertebral procoely, great range of mediolateral vertebral motion, and flexible tetraserial dorsal shields (Salisbury & Frey, 2000; Salisbury et al., 2006; Molnar et al., 2015; Fronimos & Wilson, 2017). This implies that the hyoid apparatus played a key role in early evolution of Neosuchia.

Other ceratobranchials of extinct pseudosuchians are not similar to that of neosuchians, even in marine ones. A basal pseudosuchian *Qianosuchus* is possibly aquatic (Li et al., 2006; Nesbitt et al., 2011), and different from neosuchians in possessing long, slender, and straight ceratobranchial. A basal-most phytosaur *Diandongosuchus* of Triassic (Stocker et al., 2017) also shows difference from Neosuchia in having straight and short ceratobranchial relative to its mandible. Derived phytosaur *Mystriosuchus* (Gozzi & Renesto, 2003) shows slender ceratobranchial. In marine crocodyliform thalattosuchians, such as *Steneosaurus bollensis* (Mueller-Töwe 2006), *Geosaurus vignaudi* (Frey et al., 2002), and *G. giganteus* (Young et al., 2009), absence of gular valve rising is indicated by lack of ceratobranchial dorsal deflection

(Fig. 4). Secondary palate is unnecessary for aquatic reptiles due to absence in aquatic turtles and snakes, and non-neosuchian pseudosuchians. Crocodylians are lip- and cheek-less reptiles, therefore, closure of gular valve prevents from water entering to body cavities, and helps their respiration while the mouth is underwater. In Neosuchia, paralligatorid *Batrachomimus* is closely related to Eusuchia, and shows a different form of bony secondary palate from eusuchians in which a vomer septum reaching to the palatal shelves and forming palate with palatines (Montefeltro et al., 2013). This suggests that incomplete secondary bony palate is a common feature of basal neosuchians and bony secondary palate is independently retained among neosuchians. Interestingly, the ceratobranchial of *Batrachomimus* is short and dorsally deflected like goniopholidids and eusuchians (Fig. 2), indicating presence of the similar system in *Batrachomimus*. In more basal lineage of crocodylomorphs, *Mahajungasuchus* is a sister taxon to Neosuchia and exhibits the basal-most bony secondary palate (Turner & Buckley, 2008), but it is unknown whether internal choana was preceded to ceratobranchial modification due to its lack. In sum, valve rise may have been retained in only neosuchians, advantageous for their habitat shift to aquatic environment, and

have been passed down to modern crocodylians. Choristoderan *Champsosaurus* (ROM71400) is similar to non-neosuchian in having elongate ceratobranchial without dorsal deflection.

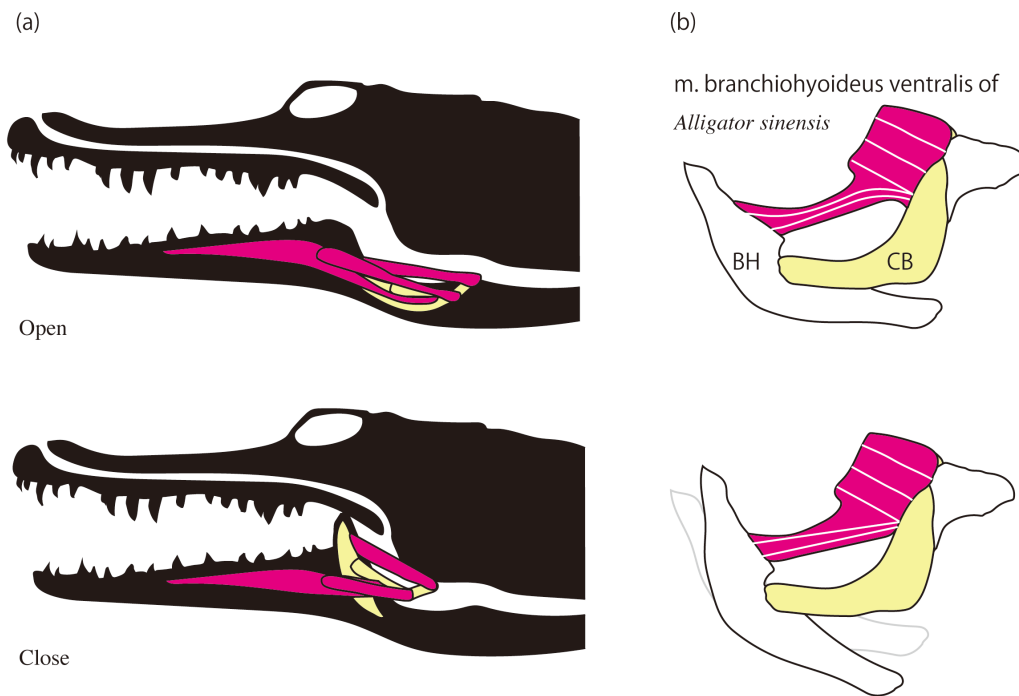


Figure 3. Schematic illustration of valve closing with contraction of four muscles (a). M. branchiohyoideus ventralis in modern crocodylian (*Alligator sinensis*) (b).

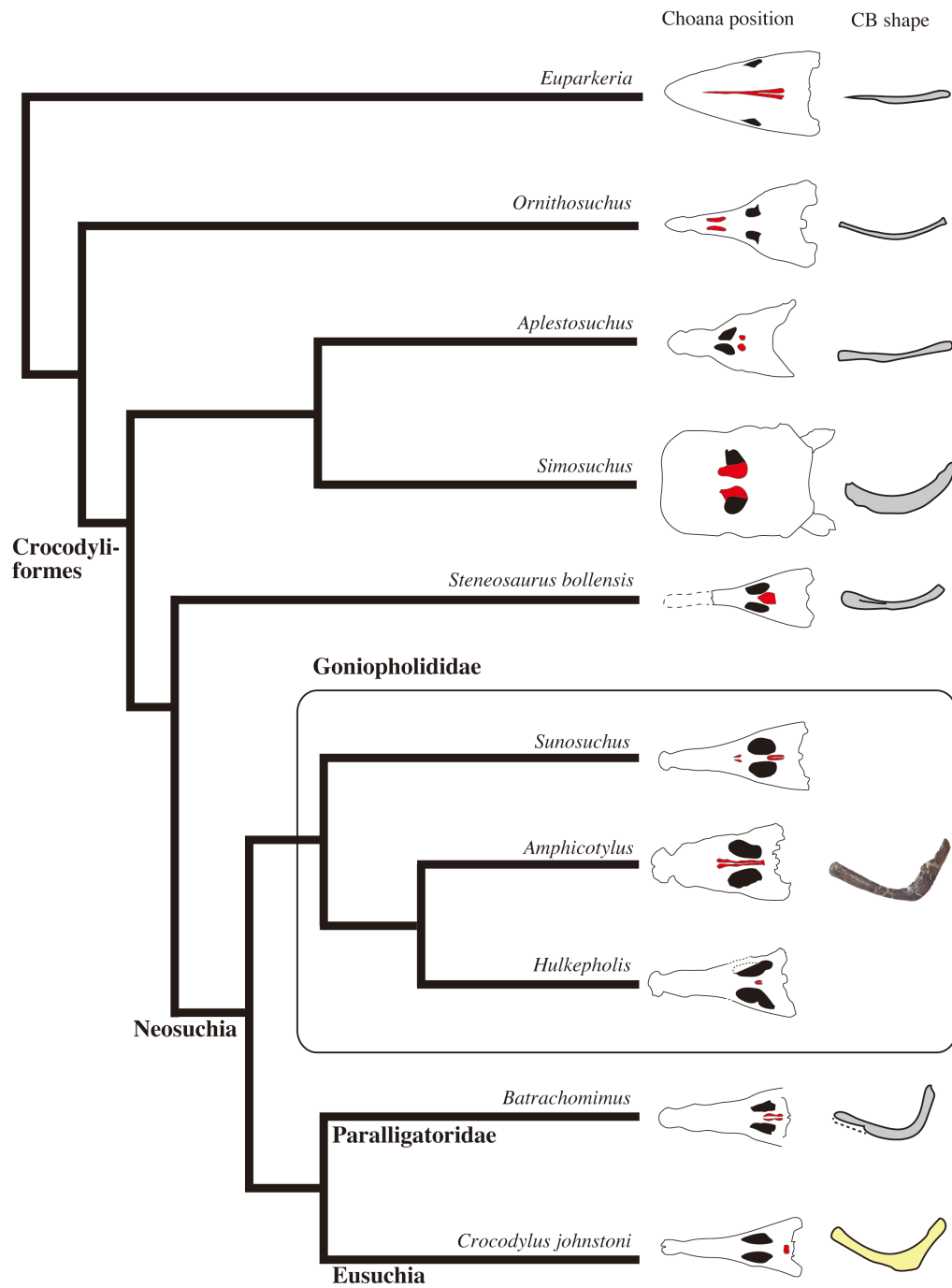


Figure 4. Phylogenetic relationships of Goniopholididae and transformation of internal choana and ceratobranchial.

(e) Paleoecology of Goniopholididae

The Late Jurassic Morrison Formation yielded abundance of goniopholidids, such as, *Eutretauranosuchus* (Mook 1967; Smith et al., 2010), *Amphicotylus stovalli* (Mook 1964), *A. lucasii* (Cope 1878), and this new specimen (GMNH-PV0000229). GMNH-PV0000229 is characterized by broad rostrum compared to the other coeval crocodyliforms. In modern mesorostrine crocodylians, flat and broad rostrum is suited for feeding on large and agile prey (McHenry et al., 2006). Therefore, the broader rostrum than the other goniopholidids of the Morrison Formation suggests that GMNH-PV0000229 habit different ecological niche that fed on large and agile animals from them within the sympatric freshwater environment. Broad rostrum is absent in basal goniopholidids, but present in some of the derived goniopholidids from Europe, such as, *Goniopholis simus*, *G. kiplingi*, and *Anteophthalmosuchus hooleyi* (Andrade et al., 2011; Martin et al., 2016). The broad rostrum of new *Amphicotylus* (GMNH-PV0000229) suggests rostral diversification in North American goniopholidids. Abundance of semiaquatic goniopholidids and their rostral diversification may be achieved by successful aquatic adaptation with acquisition of gular valve and secondary

palate.

CONCLUSION

Presence of gular valve has been postulated in basal neosuchians (Salisbury et al., 2006), and yet to be proven. The shape, size, and osteological correlates for the hyolingual muscles in the ceratobranchial fossil suggest presence of hyoid rotation for rising gular valve in basal neosuchians as well as modern crocodylians. Tongue of crocodylians is lack of intrinsic muscle (Ferguson 1981b), fused to buccal floor, and immobile (Clueren & De Vree, 2000), instead, they retained new functions in their hyoid apparatus.

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IV. EVOLUTION OF HYOID APPARATUS IN SAUROPODOMORPH DINOSAURS: CERATOBANCHIAL MODIFICATIONS IN A TRANSITION FROM BIPEDALITY TO QUADRUPEDALITY

ABSTRACT

Sauropod dinosaurs were the largest terrestrial animals eating plants in Mesozoic. Their unique bodyplan, represented by small head, long neck, large trunk, and robust four legs, is result of adaptation for bulk herbivory, and facilitates higher energy-efficient feeding and consumption of lower nutrient plant contents. This study describes a hyoid element (ceratobranchials) of Sauropodomorpha, and conducted comparison within their evolutionary framework in both qualitative and quantitative approaches. The results show dorsal deflection, ventromedial tubercle, and dorsolateral shelf of ceratobranchial were retained in Sauropodiformes simultaneously with their quadrupedality and prior to other unique ecomorphological traits, such as, elongate neck, reduction of tooth row, and loss of cheek. Muscular reconstruction reveals the three morphological changes of ceratobranchial are indicative of dorsal rotation of basihyal, anterior projection of hyoid

apparatus, and enough mass of tongue muscle (m. hyoglossus), which facilitates their bulk feeding, as in modern large herbivores like giraffes. This early evolutionary changes of hyoid apparatus might have promoted gigantism for herbivory in Sauropodiformes and their adaptive radiation.

INTRODUCTION

Herbivory is multifactorial and related to some adaptive changes in body plan morphologically and physiologically, such as tooth, cranial kinesis, and digestive tract (Sander et al., 2014). Tongue increases bite mass and also facilitates the selection of soft plant parts such as leaves for better quality of bites (Hongo & Akimoto, 2003; Searle & Shipley, 2008; Pretorius et al., 2016).

In the Triassic, sauropodomorphs retained large digestive tract, large body holding it, and elongate neck to reach food items with less movement for less energetics. Such a body plan is unique among vertebrates and some of them weighted over 40 t, which are the largest terrestrial animals through the history of life (Sander, 2013). Tongue is a unique feature of tetrapod vertebrates (Iwasaki 2002), and specialized for

herbivory in some modern tetrapods, such as giraffes (Pretorius et al., 2015), and anseriform birds (e.g. goose, duck, and swan) (McLelland, 1979). In large herbivorous mammals, tongue increases bite mass and also facilitates the selection of soft plant parts such as leaves for better quality of bites (Hongo & Akimoto, 2003; Searle & Shipley, 2008; Pretorius et al., 2016). Anseriform birds utilize lingual up-down motion to “masticate” plant materials, working together with serrated beak (Durant 2013). Lingual motion plays an important role in herbivorous terrestrial tetrapods (Zweers et al., 1995), but its evolutionary course remains poorly solved. In gigantic sauropodomorphs, their elongate neck accompanies their light and small skulls, limiting bite mass at once. Assuming that, increase of bite mass is hypothesized to be achieved by active lingual motion in gigantic sauropodomorphs.

Understanding of gigantism of the herbivorous dinosaurs has potential to inform not only paleoecology of individual taxa but also selection pressure involved in the evolution of maximum body size of animals ultimately. Sauropod body plan is unique among vertebrates and some of them weighted over 40 t, which are the largest terrestrial animals through the history of life (Sander, 2013). Interestingly, their

ecological niches were variable (*Plateosaurus* with fleshy cheek Galton 1985; specialized grazer *Nigersaurus* Sereno et al., 2007; insular dwarf *Europasaurus* Sander et al., 2006; wide and sharp rostrum shapes, Whitlock, 2011).

Some specialized lingual motions are achieved by its corresponding morphological change in hyoid apparatus (e.g. anteater, Naples 1999). This study hypothesizes that sauropodomorphs retained morphological changes in lingual apparatus for their herbivory although it is unclear whether hyoid is strongly large and curved for tongue raising and projection, or small and straight for swallowing large amount of food items. To address this hypothesis, two continuous indices, curvature and relative size of ceratobranchial, are measured.

MATERIALS & METHODS

The osteology of 12 taxa was examined and two taxa (*Giraffatitan* HMN S66 and *Tapuiasaurus* MZSP PV807) are described here. Two indices are measured: ratio of length to distance of dorsal margin of ceratobranchial (= tortuosity), and ratio of ceratobranchial length to mandible length. In order to trace morphological

transformation in sauropodmorph evolution, a supertree is constructed based on a variety of recent phylogenetic analyses (Cabreira et al., 2015; Wang et al., 2017; D’Emic 2012; Wilson 2016). In evolutionary model analysis, this study employs R packages ‘phytools’ v. 3.6.1 (Revell 2012) and ‘paleotree’ v. 2.0 (Bapst 2012). Time-scaled tree were produced using three methods ‘All Branches Additive’ (aba), which a million years are added to each branch, ‘Minimum Branch Length’ (mbl), which sets all branches to one million years at least, takes time from earlier branch and give it to later branch, and ‘Equal’ which equilibrate time distributed on the tree by adding time to the root of the tree and adjusting zero-branch length by borrowing time from earlier branches to give to later branches (Bapst 2012). Four different evolutionary models (Brownian motion (BM), Ornstein-Uhlenbeck (OU), Early burst (EB), and Trend models) were evaluated to fit in at the best by Akaike Information Criterion (AIC) weight over the twelve models removing zero to three basal taxa (Table 2).

The musculature reconstruction of hyoid apparatus is based on dissection of three crocodylians (*Alligator sinensis*, *Caiman crocodilus*, *Crocodylus siamensis*), two paleognaths (*Struthio camelus*, *Dromaius novaehollandiae*), a chicken (*Gallus gallus*

domesticus), two waterfowls (*Anas penelope*, *Cygnus olor*), and the literatures (Schumacher 1973; Ghetie 1976; Huang et al., 1999; Li & Clarke, 2015, 2016). These extant archosaurs are representatives of the extant phylogenetic bracket to reconstruct muscle attachment sites in hyoid fossils. Using the EPB (Witmer 1995a), each muscle was categorized into four levels of inference based on the presence or absence, and the degree of certainty of the extant archosaurs. Level I inference indicates that a muscle group is present in both groups of extant relatives, and osteological correlates for that muscle group are present in both groups too. Osteological correlates are established as processes or tubercles, surficial texture such as scarring, or discrete surface coinciding with attachment sites. Level I' inferences indicate that a muscle group is present in both groups but osteological correlates are absent in one group or both. Level II inferences indicate that a muscle group is present in one group and osteological correlates are present. Level II' inferences indicate that a muscle group is present in one group but osteological correlates are absent. In some previous studies, Level III and III' have been employed for musculature reconstruction, however, these are ignored in this study because those are defined by a lack of soft-tissue group in both groups and less robust to

infer existence. Comparison of origin and insertion sites of muscles in birds and crocodilians help to find the possible sites in dinosaurs, however, if sites of muscle differed between birds and crocodilians, further evidence is required for more plausible reconstruction. To account for independent loss of muscles in crocodilians, a generalized description of lepidosaur musculature was used to determine the possible basal condition (Romer 1944; Russell & Bauer, 2008; Jones et al., 2009; Abdala & Diogo, 2010).

Institutional abbreviation

AMNH, American Museum of Natural History, New York, USA; **CM**, Carnegie Museum of Natural History, Pennsylvania, USA; **HMN**, Museum für Naturkunde; **MCZ**, Museum of Comparative Zoology, Harvard University; **MZSP**, Museu de Zoologia da Universidade São Paulo, Brazil; **NM**, National Museum, Bloemfontein, South Africa; **ULBRA**: Museu de Ciências Naturais, Universidade Luterana do Brasil, Canoas, Brazil; **ZDM**, Zigong Dinosaur Museum, Sichuan, China,

RESULTS

Description

Giraffatitan brancai

Janensch (1935) described a pair of ceratobranchial of *Giraffatitan brancai* (HMN S66), which is composed of complete left element and distal end of right one. The articular surface of the anterior end is concave with a pit and divided into two condyles, which is absent in other sauropodomorphs. The left ceratobranchial is strongly deflected and tallest at the proximal two thirds and the anterior ramus is longer than the posterior ramus. The anterior ramus bears medial groove along the ventral margin. The distance between both ends is 40 cm, being the largest ceratobranchial among dinosaurs. In the lateral side, there is a shelf along dorsal margin (Fig. 1), as seen in ceratobranchial of *Tomistoma schlegelii*.

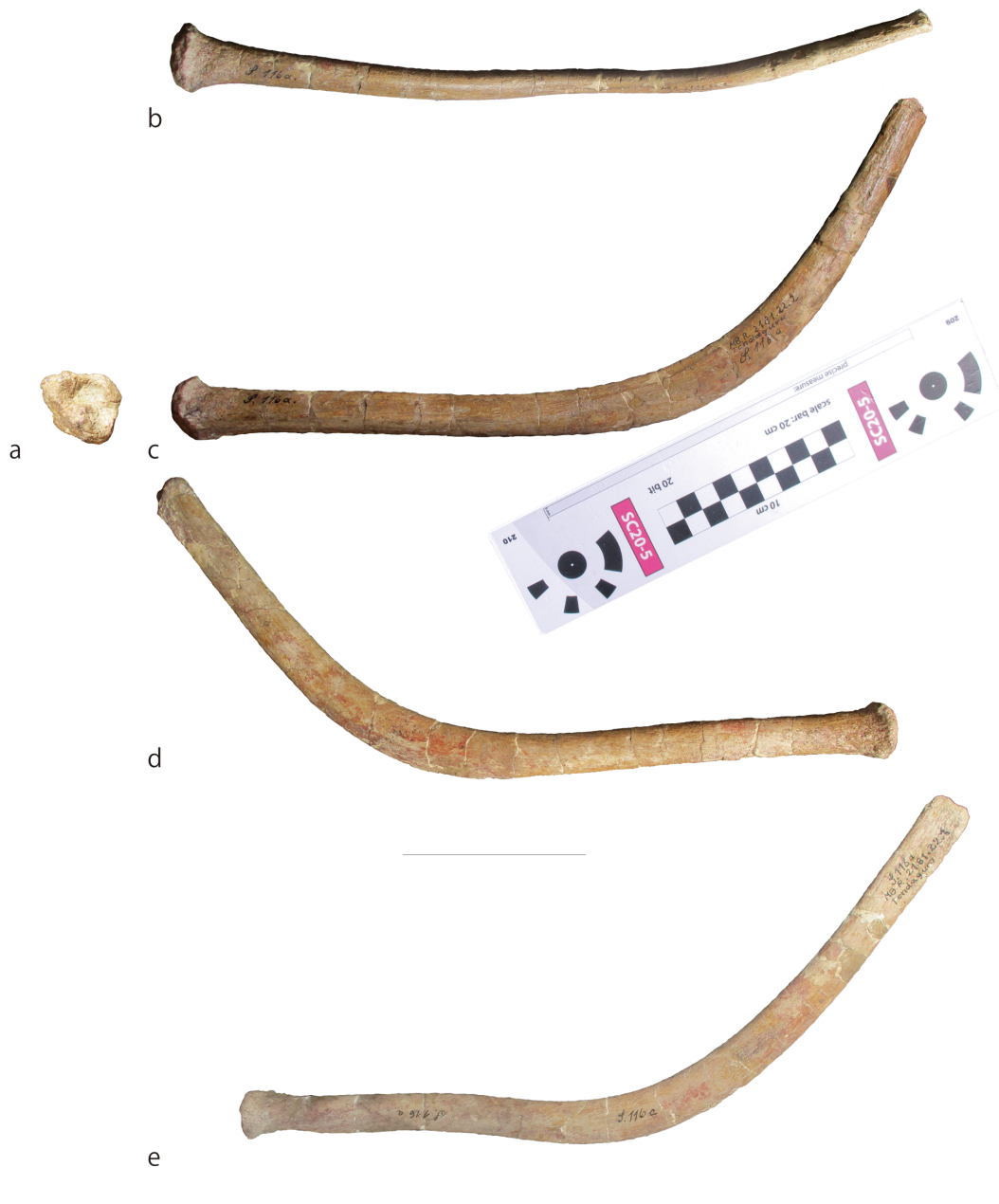


Figure 1. Ceratobranchials of *Giraffatitan brancai* (HMN S66). A left ceratobranchial (HMN S66 MB.R.2181.22.2) in proximal (a), dorsal (b), lateral (c), and medial view (d). A right ceratobranchial (HMN S66 MB.R.2181.22.4) in medial view (e) Scale bar = 10 cm.

Tapuiasaurus macedoi (MZSP PV807)

A titanosaur *Tapuiasaurus macedoi* (Zaher et al., 2011) was discovered from the Aptian Quiricó Formation of Brazil, with a well-preserved pair of ceratobranchials. A left ceratobranchial lacks proximal end, while a right ceratobranchial is completely preserved. Ceratobranchial of *Tapuiasaurus* is dorsally deflected, possessing medial groove (Fig. 2), as well as *Europasaurus* (Marpmann et al., 2014). Medial grooves are discontinuously distributed in proximal portion, middle curvature point, distal portion. The proximal portion is slightly expanded to the shaft, and higher than wide. Lateral surface of middle part is smooth, unlike lateral shelf of *Giraffatitan brancai*. In distal portion, lateral groove is present as well as crocodylians such as, *Gavialis gangeticus*, and *Tomistoma schlegelii*, which is attachment surface for m. branchiomandibularis.



Figure 2. *Tapuiasaurus macedoi* (MZSP PV807). *In situ* preservation of ceratobranchial with skull and jaw (a). A skull, a jaw, and a right ceratobranchial (b). A right ceratobranchial in proximal (c), medial (d), and lateral view (e). A left ceratobranchial in proximal (f), lateral (g), and medial view (h). Scale bar = 10 cm.

Relative size, and curvature

Length of ceratobranchial relative to mandible is ranging from 0.37 to 0.59, not variable through their evolutionary history although their relative size data is not satisfactory for quantitative evaluation. The conservative size variation of ceratobranchial suggests that relative position of tongue was anterior half of mandible and have not been largely changed, in contrast to decrease in neosuchians (chapter 3).

On the evolution of Sauropodomorpha, dorsal deflection of ceratobranchial is first occurred in *Melanorosaurus*, and continuously possessed in more derived sauropodomorphs (Fig. 3). For Sauropodomorpha, BM model was the best to describe the curvature evolution in all three branch-scaling models (aba, equal, and mbl). However, excluding *Buriolestes*, and *Melanorosaurus*, the trees fit into the OU model, except the ABA scaling tree without *Buriolestes* (Table 1). Exclusion of *Buriolestes*, *Melanorosaurus*, and *Plateosaurus*, demonstrates that Sauropodiform ceratobranchial curvature fits in OU model for the ABA and MBL trees, while it fits in BM model for the equal tree (Table 1). The results were insensitive to the branch scaling method and elimination of the selected terminal taxa. These results support that ceratobranchial

curvature has not evolved in the basal sauropodomorphs, but moderately had an optimum value in Sauropodiformes. Ancestral state reconstruction demonstrates that curved ceratobranchial have been retained in Sauropodiformes during Norian of Triassic.

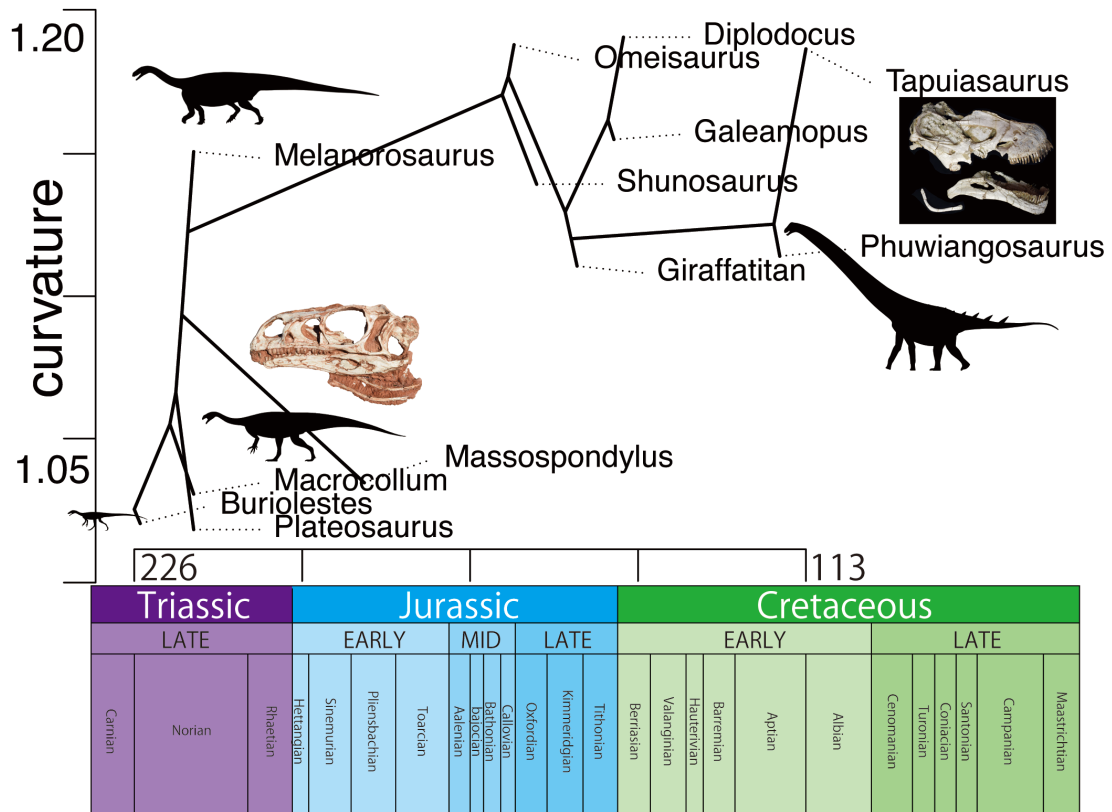


Figure 3. Ceratobranchial curvature evolution in Sauropodomorpha

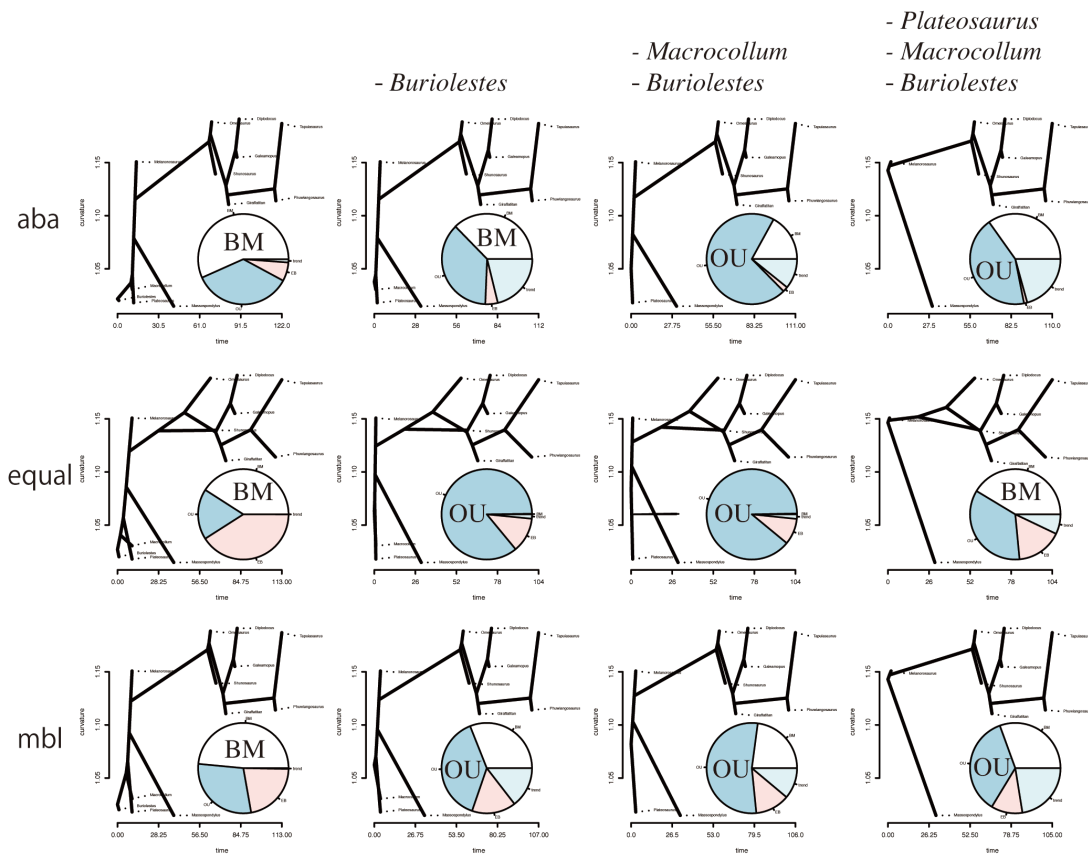


Figure 4. Ceratobranchial curvature of Sauropodomorpha in time-calibrated phylogenetic trees. Branch scaling models are aba (upper row), equal (middle), and mbl (lower). Each column showing removed taxa from the tree. Each circle consisting of AIC weights for four models: Brownian motion (white), Ornstein-Uhlenbeck (dark), Trend (faint blue), and Early burst models (pink). Sauropodiformes displaying a moderate trend toward an optimum value with small variation.

Osteological correlates and muscular reconstruction

Some sauropodiforms show distinctive osteological correlates on surface: (1) medial expansion on the ventral margin around the middle deflected point, (2) lateral shelf around dorsal margin, and (3) lateral groove in distal portion. Medial groove is present in ceratobranchials of *Shunosaurus*, *Europasaurus*, and *Tapuiasaurus*. Lateral shelf is present in ceratobranchial of *Giraffatitan*. Lateral groove is present in *Tapuiasaurus*.

M. hyoglossus (= m. ceratoglossus)

Medial expansion is present crocodylians (e.g. *Crocodylus niloticus*) and a chelonian (e.g. *Chelydra*), and consequently forms a medial groove above the expansion. For them, this is the attachment site for m. hyoglossus. In some birds, m. ceratoglossus attaches to the groove in distal portion of *Cygnus columbianus*, suggesting that it is osteological correlate (chapter 3). This muscle homologous to m. hyoglossus of crocodylians, chelonians (Werneburg 2011, Schumacer 1973, Li & Clarke 2015). Level of inference is I because the medial expansion of ceratobranchial is marked as attachment site for m. hyoglossus in crocodylians and turtles, and m. ceratoglossus in some birds.

M. branchiomandibularis (= m. branchiohyoideus dorsalis)

M. branchiomandibularis originated from epibranchial in neognath birds, and epibranchial cartilage in non-tinamid paleognath birds (e.g. *Struthio*, *Dromaius*). In Crocodylia, m. branchiohyoideus dorsalis originates from dorsal margin of distal portion of ceratobranchial and inserts into mandible (dorsal to coronoid). The functions of the muscle in crocodylians are protraction and suspension of hyoid (Li & Clarke, 2015). Lateral groove is present in distal portion of ceratobranchial of *Tapuiasaurus* and its level of inference is I'.

M. geniohyoideus

M. geniohyoideus is present in crocodylians and turtles, and attaches to lateral side around middle part of ceratobranchial. The osteological correlate is marked in *Alligator sinensis* and *Tomistoma schlegelii*. This muscle is absent in birds (Bonga-Tomlinson 2000; Baumel & Witmer, 1993). M. geniohyoideus attaches to the lateral surface of ceratobranchial 1 in chelonians (Werneburg 2011) and leave osteological correlates as a

tubercle. Moreover, in *Sphenodon* m. geniohyoideus 2 inserts into the anterior edge of the central portion of the first ceratobranchial (Jones et al., 2009), and likely homologous to each other based on attachment position. The presence in crocodylians, chelonians, and *Sphenodon* indicates that m. geniohyoideus is a level of inference II for the sauropodomorph *Giraffatitan*.

M. omohyoideus

M. omohyoideus is likely lost in plateosaurian sauropodomorphs because it is originate from coracoid. For protraction of hyoid, constriction of such a muscle is not reasonable in their elongate neck. In addition, osteological correlates for m. omohyoideus is absent in Saurpodomorphs, which is present in modern crocodylians as a lateral concave surface in *Crocodylus siamensis* and *Tomistoma schlegelii*, and ridge separating from attachment site of m. geniohyoideus in *Alligator sinensis* and *Caiman crocodilus* (chapter 3). Level of inference is II because this muscle is only present in crocodilians and turtles, and osteological correlate can be recognized in those extant taxa. Absence of the osteological correlate in Sauropodomorpha suggests true absence of m.

omohyoideus in this clade.

M. ceratohyoideus (*m. interceratoideus*)

M. ceratohyoideus is only present in Paleognathae (Bonga-Tomlinson, 2000), and appears to be homologous to *m. interceratoideus* of Neognathae. Insertion of this muscle is marked as medial groove in some birds (chapter 5), and absent in crocodylians. Level of inference is II.

M. genioceratohyoideus

M. genioceratohyoideus is only present in Paleognathae, which originates from ceratobranchial and inserts into mandibular symphysis (Boga-Tomlinson 2000).

Presence of this muscle is ambiguous in Dinosauria, but likely retained only in

Palaeognathae based on comparisons with other extant archosaurs. Level of inference is II'.

DISCUSSION

Dorsal deflection of ceratobranchial

Dorsal deflection of ceratobranchial have not been changed in the course of sauropodiform evolution, despite that sauropodomorphs exhibit diverse array of ecomorphologies, such as rostrum shape (Sereno et al., 2007; Whitlock 2011), tooth shape, size, and replacement (refs; Whitlock 2011), neck elongation and mobility (Stevens & Parrish 1999, refs). This indicates that morphology of ceratobranchial is not related to ecological niches. Furthermore, this morphological transition advanced other eco-morphological characters associated with herbivory, such as, obligate quadrupedality (Yates et al., 2003), tooth-tooth occlusion, and neck elongation (Fig. 5). This also occurs in insular-dwarf sauropod *Europasaurus*, and precedes obligate quadrupedality, a character of sauropodomorph gigantism, in the evolution of sauropodomorphs, indicating its size-independence. These facts suggest that the dorsal deflection is attributed by the basic feeding mechanism in Plateosauria (*Plateosaurus* + more derived sauropodomorphs).

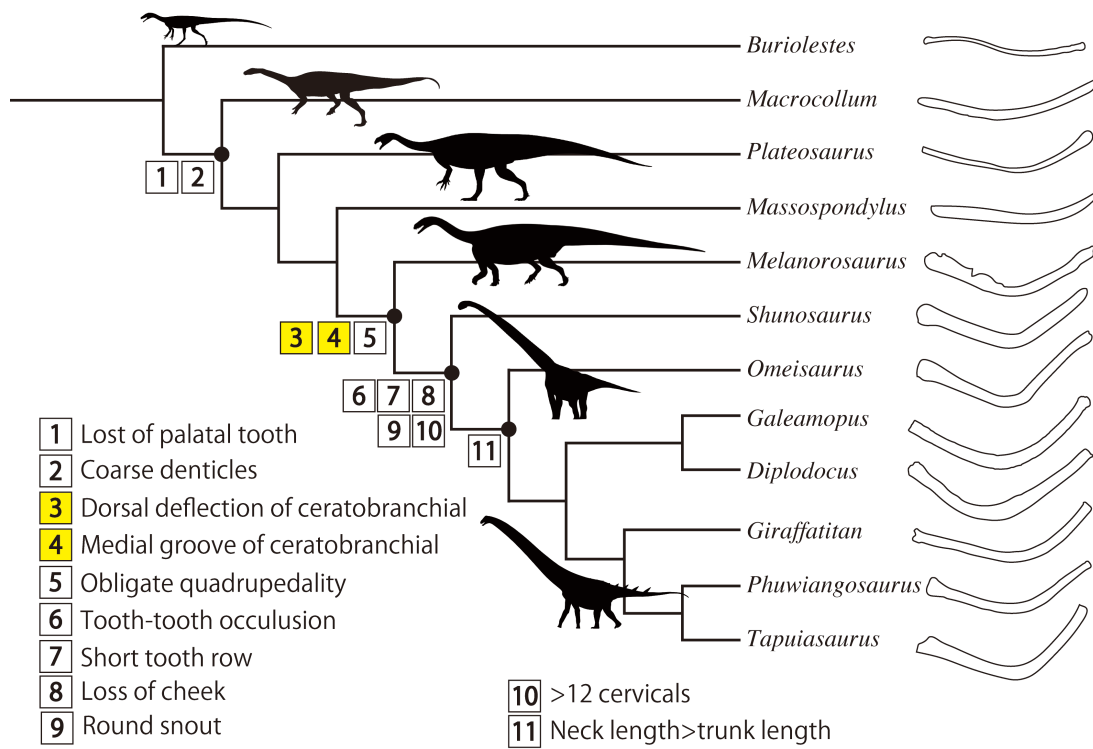


Figure 5. Morphological evolution of ceratobranchial in sauropod phylogeny with other eco-morphological transformations.

Anatomical evolution of ceratobranchial and the relevant muscles

Osteological features of sauropodomorph ceratobranchial are dorsal deflection in Sauropodiformes; medial groove in *Plateosaurus*, *Shunosaurus*, *Europasaurus*, *Giraffatitan*, and *Tapuiasaurus*; and a shelf on lateral side along dorsal margin in *Giraffatitan*. Basal sauropodomorphs, (e.g. *Plateosaurus*, and *Massospondylus*) have straight ceratobranchial, but sauropodiforms (e.g. *Melanorosaurus*) exhibits dorsal deflection. The dorsal deflection of ceratobranchial was occurred at the basal node of Sauropodiformes in Norian when dinosaurs have diversified and radiated. Dorsal deflection of ceratobranchial is also present in derived crocodyliforms (Li & Clarke, 2015; chapter 3) and some ornithischian dinosaurs (chapter 5), but, in contrast, they Sauropodiformes does not exhibit shortening of ceratobranchial relative to mandible. The oldest and basal-most presence of medial groove of ceratobranchial is sauropodomorph *Plateosaurus* of Norian, which is shared among Plateosauria. Medial groove is also present in some birds, and crocodylians (chapter 3), but its anatomical interpretation is different. A shelf on lateral side along dorsal margin is present in *Giraffatitan*, which is an insertion for m. geniohyoideus as

seen in crocodylians. The shelf is also present in False gharial (*Tomistoma*) indicating that the surficial morphology is a osteological correlate for m. geniohyoideus. The dorsal deflection and presence of medial groove is simultaneously retained in the evolution of Sauropodomorpha. Sauropodiforms have maintained dorsal deflection of ceratobranchial although they have exhibited variety of rostrum shape (Serenio et al., 2007; Whitlock 2011), tooth shape, size, and replacement (Upchurch et al., 2004; Whitlock 2011), neck elongation and mobility (Stevens & Parrish 1999; Taylor & Wedel, 2013). This indicates independence of the ceratobranchial morphology from minor difference in ecological niches on Sauropodiformes. In addition, this morphological transition was simultaneous with obligate quadrupedality (Yates et al., 2003), and advanced other eco-morphological characters for herbivory, such as, tooth-tooth occlusion, broad rostrum, and increase of cervical vertebra (Wilson et al., 2004; Button et al., 2017) (Fig. 4). This also occurs in insular-dwarf sauropod *Europasaurus* (Emanuel Tschopp pers. comm.), indicating its size-independence. In terms of snout shape, *Plateosaurus* and *Melanorosaurus* share narrow V-shaped snout, while, eusauro pods show relatively broad U-shaped snout, suggesting that snout shape

is irrelevant to dorsal deflection of ceratobranchial. These facts suggest that the dorsal deflection is attributed by the basic feeding mechanism in Plateosauria.

Plateosaurus have buccal emargination (medial inset of tooth row relative to eminence of coronoid process) in dentary, and, together with large lateral foramina of maxilla, may have possessed cheek (Galton 1985). Similarly, cheek maybe developed in some sauropodomorphs (Upchurch et al., 2004). In addition, *Plateosaurus* possibly have secondary palate for separating chewing and breathing like mammals (Galton 1985).

While, cheek is unlikely present in Sauropoda because of apparent lack of possible osteological correlates (Upchurch et al., 2004). Presence of soft tissue covering tooth crown base is suggested in sauropod *Camarasaurus* (Wiersma & Sander, 2016).

Whether cheek was present or absent in *Plateosaurus* and other basal sauropodomorphs, dorsal deflection of ceratobranchial is seen in cheekless sauropodiforms, suggesting that dorsal deflection is not related to cheek or oral processing. Development of spatulate tooth, tooth-tooth occlusion, a reduced tooth row, broad snout, and inferred loss of cheek, would have facilitated a wider gape (Barrett & Upchurch, 2007). Basal sauropodiform *Melanorosaurus* have narrow, long, V-shaped rostrum, shallow

mandibular ramus, long retroarticular process, absence of tooth-tooth occlusion, and buccal emargination, similar to other sauropodomorphs like *Plateosaurus* (Yates 2007). These features indicate presence of cheek, limited gape, and simple cropping with little oral processing in *Melanorosaurus* as well as *Plateosaurus* (Galton 1985; Yates 2007).

Lingual motion and paleoecology of sauropodomorphs

Osteological correlates for m. hyoglossus, m. geniohyoideus, and m. branchiomandibularis are suggestive of distinctive lingual motion. Lingual motions of Archosauria can be categorized into projection, filter feeding, cropping, manipulation, holding, and swallowing (McLelland, 1979). Sauropodomorph ceratobranchial is about a half length of mandible, as usual as other dinosaurs, indicating that resting position of tongue is not largely shifted. For water intake (drinking or filter feeding), retraction of tongue is used in modern birds, such as flamingo (Zweers et al., 1995). Their long neck must be taken into account for drinking (e.g. elephant). Muscles for tongue retraction are m. omohyoideus, and m. episternobrachialis in crocodylians (Li & Clarke, 2015), and m. stylohyoideus, m. serpihyoideus, in birds (Hemberger 2017). The tongue

retraction muscles of crocodylians insert into pectoral girdle (Li & Clarke, 2015), which is lost in birds, possibly due to cervical elongation. Therefore, for swallowing, hyoid is hypothesized to be small and straight for taking large amount of food items. Dorsal deflection of ceratobranchial is suitable morphology for hyoid rotation and protraction by m. branchiomandibularis, and suggest that rotation or protraction of hyoid is likely present in lingual motion of sauropodiformes.

Diet of *Plateosaurus* is still unknown due to absence of direct evidence (e.g. gut content). Strict herbivory is not appropriate for basal sauropodomorphs, as well as osteophagy and ingestion of invertebrates of modern herbivores (Bredin et al., 2008). According to muscle reconstruction, cranium of *Plateosaurus* exhibits structural efficiency and force transmission to maintain relatively high jaw closure speed, suggesting its omnivorous diet (Button et al., 2016). The diet of *Plateosaurus* is inferred to be plants because of its lanceolate teeth with coarse denticles (Barrett & Upchurch, 2007). Manus of *Plateosaurus* is useful for grasping (Mallison 2010), indicating that basal sauropodomorph which is facultatively quadrupedal employ forelimb for feeding. Body mass increased in the least clade including *Plateosaurus* + sauropods (Rauhut et

al., 2011; Sander et al., 2011; Benson et al., 2014), which may has been crucial for fully herbivorous diet in Sauropodomorpha.

In some herbivorous birds (some anseriforms and *Opisthocomus*), keratinized epithelium is present within mouth, and work with mobile tongue (Korzun et al., 2003a), but sauropodomorphs may not employ tongue raising within keratinized oral cavity for digestion, because ceratobranchial is dorsally deflected in variety of oral tissue (e.g. tooth morphology and position, and cheek) in sauropodomorphs. Meanwhile, tongue projection is employed for larger intake mass in large modern herbivore, Giraffidae, (Pretorius et al., 2015), and may be employed in sauropodiforms similarly. Therefore, tongue protraction appears to exist in sauropodomorphs, and its occurrence was prior to other herbivore traits, such as increasing the number of cervical vertebra, obligate quadrupedality, broad snout, and tooth-tooth occlusion, and simultaneously or early occur with obligate quadrupedality in their evolution. This study sheds light on evolution of tongue in extinct animals, which has been rarely unknown.

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Table 2.

Taxa	Specimen. Reference	CB length / ML	CB Tortuosity
<i>Buriolestes</i>	ULBRA-PVT280. Cabreira et al., 2016	0.562	1.02
<i>Macrocollum</i>	CAPPA/UFSM0001b Müller et al., 2018	0.594	1.03
<i>Lufengosaurus</i>	CUP2038a.		
<i>Xixiposaurus</i>	ZLJ0108. Sekiya 2010		
<i>Plateosaurus</i>	HMN XXIV. Galton 1985	0.599	1.018
<i>Plateosaurus</i>	HMN MB 1927. Galton 1985		
<i>Plateosaurus</i>	UT 1. Galton 1985		
<i>Massospondylus</i>	BP/1/4376. Gow et al., 1990. Juvenile.	0.519	1.015
<i>Massospondylus</i>	BP/1/4779. Gow et al., 1990. Subadult.		
<i>Massospondylus</i>	BP/1/4934. Gow et al., 1990. Adult.		
<i>Xingxiulong</i>	LFGT D0002. Wang et al., 2017	na	
<i>Melanorosaurus</i>	NM QR3314. Yates 2007	0.366	1.15
<i>Sarhsaurus</i>	MCZ8893. Rowe et al., 2010	na	na
<i>Shunosaurus</i>	ZDM T5401. Zhang 1988	0.467	1.139
<i>Omeisaurus</i>	Dong et al., 1983	na	1.188
<i>junghsiensis</i>			
<i>Brontosaurus</i>	YPM1980. Marsh 1883	unconfirmed	unconfirmed
<i>Galeamopus</i>	SMA 0011. Tschopp & Mateus, 2017	1.155	na
<i>pabsti</i>			
<i>Camarasaurus</i>	CM11338. Gilmore 1925. Juvenile.	na	na
<i>lentus</i>			
<i>Europasaurus</i>	DFMMh/FV. Marpmann	na	na

	et al., 2014		
<i>Europasaurus</i>	DFMMh/FV. Marpmann	na	na
	et al., 2014		
<i>Europasaurus</i>	DFMMh/FV. Marpmann	na	na
	et al., 2014		
<i>Giraffatitan</i>	HMN S66. Janensch 1935	na	1.111(L)/1.087 (R)
<i>Abydosaurus</i>	DNM16488. Chure et al., 2010	na	na
<i>Phuwiangosaurus</i>	P.W.5-25. Martin et al., 1999	na	1.114
<i>Tapuiasaurus</i>	MZSP PV807 Zaher et al., 2011	0.435	1.187

V. HYOID APPARATUS OF ORNITHISCHIAN DINOSAURS

Abstract

Ornithischia is a large group of herbivorous dinosaurs of Mesozoic. Each family (Ornithopoda, Ceratopsia, Ankylosauria) has been specialized their plant-eating strategy in a variety of adaptations. This study provides detailed descriptions of ceratobranchials of *Psittacosaurus*, *Protoceratops*, *Styracosaurus*, *Plesiohadros*, and *Pinacosaurus*, and quantitative comparisons in the course of ornithischian evolution. The results demonstrates that ceratobranchial have been slightly curved in stem ornithischians, then curved further in neornithischians, and shortened and secondarily straight in ceratopsians. Furthermore, ornithopods show distinctive morphological structures which are osteological correlates for m. branchiomandibularis and m. geniohyoideus, while ceratopsids show another structure which is osteological correlates for m. geniohyoideus. Neornithischian and ankylosaur ceratobranchials are likely to be suited for dorsoventral motion of hyoid apparatus, while ceratopsian ceratobranchials are limited to anteroposterior motion. Ornithischians share some herbivorous features (e.g. dental battery, and broad edentulous rostrum), however, hyoid bones are

morphologically diverse within them for different feeding strategy.

Introduction

Ornithischia is an extinct group of herbivorous dinosaurs and have been evolutionarily successful during Mesozoic (Fastovsky & Smith, 2004). Ornithischians were ancestrally herbivorous and specialized their plant-eating strategy in each sub-clade (Norman et al., 2004). They have retained many notable features for plant digestion, such as beak (Mallon & Anderson, 2014), predentary bone (Nabavizadeh & Weishampel 2016), dental tissue complexity (Erickson et al., 2012, 2015), dental battery, jaw mechanics (Mallon & Anderson, 2015). The previous studies could have studied only skull, jaw, and dental elements, but another cranial element, hyoid apparatus, have never been studied in terms of function and evolution although its presence has been known in the fossil specimens.

Tongue increases bite mass and also facilitates the selection of soft plant parts such as leaves for better quality of bites, as seen in Giraffidae and Sauropodiformes (Hongo & Akimoto, 2003; Searle & Shipley, 2008; Pretorius et al., 2016; chapter 4).

Moreover, anseriform birds utilize lingual up-down motion to “masticate” plant materials, working together with serrated beak (Durant 2013). Lingual motion plays an important role in herbivorous terrestrial tetrapods (Zweers et al., 1995). In plant-eating saurischian dinosaurs, Sauropodomorpha, ceratobranchials were dorsally deflected with the acquisition of quadrupedality and highly mobile hyoid apparatus was likely a result of trade-off from free mobile forelimb (chapter 4). In terms of efficiency of collecting food, ornithischians have modified rostral structure and morphologies, such as, development of bills, and acquisition of predentary, differing from sauropodiforms. As well as sauropodomorphs, many of ornithischians also retained giant body size later in their evolution, such as ceratopsians, hadrosauroids, ankylosaurs, and stegosaurs (Benson et al., 2014), therefore, efficiency of collecting food are hypothesized to be require for those giant ornithischians. The present study aims to reveal functional morphology of hyoid apparatus and its evolution in ornithischian dinosaurs. In order to do it, this study provides detailed descriptions of new ceratobranchial specimens of *Psittacosaurus*, *Protoceratops*, and *Styracosaurus* and quantitative comparisons within 27 ornithischian specimens in the course of ornithischian evolution.

Materials and Methods

This study newly describes ceratobranchials of three ceratopsians, which have been never reported: *Psittacosaurus*, *Protoceratops*, *Styracosaurus*.

Ceratobranchial morphologies are quantitatively examined: (1) curvature (ratio of dorsal marginal length to distance between proximal and distal ends), (2) relative size (length ratio of dorsal margin of ceratobranchial to mandible), (3) aspect ratio of height to width of proximal end, and (4) robustness (ratio of mid-height to dorsal marginal length). Software R v. 3.0. with packages “paleotree” (Bapst 2012) and “phytools” (Revell 2012) was employed to analyze the ancestral state estimation and evolutionary rates of the ornithischian tree with the 27 studied specimens which contain *Lesothosaurus*, six thyreophorans (e.g. *Scelidosaurus*, *Stegosaurus*, and *Pinacosaurus*), *Thescelosaurus*, seven ceratopsians (e.g. *Psittacosaurus*, *Styracosaurus*) and twelve ornithopods (e.g. *Theiophytalia*, *Edmontosaurus*). (Fig. 1). Time-scaled tree were produced using three methods ‘All Branches Additive’ (aba), which a million years are added to each branch, ‘Minimum Branch Length’ (mbl), which sets all branches to one

million years at least, takes time from earlier branch and give it to later branch, and ‘Equal’ which equilibrate time distributed on the tree by adding time to the root of the tree and adjusting zero-branch length by borrowing time from earlier branches to give to later branches (Bapst 2012). Four different evolutionary models (Brownian motion (BM), Ornstein-Uhlenbeck (OU), Early burst (EB), and Trend models) were evaluated to fit in at the best by Akaike Information Criterion (AIC) weight over the twelve models removing zero to three basal taxa (Table). The temporal range for each taxon was referred to PBDB (Paleobiology Database: <https://www.paleobiodb.org>).

The musculature reconstruction of hyoid apparatus is based on dissection of three crocodylians (*Alligator sinensis*, *Caiman crocodilus*, *Crocodylus siamensis*), two paleognaths (*Struthio camelus*, *Dromaius novaehollandiae*), a chicken (*Gallus gallus domesticus*), two waterfowls (*Anas penelope*, *Cygnus olor*), and the literatures (Schumacher 1973; Ghetie 1976; Huang et al., 1999; Li & Clarke, 2015, 2016). These extant archosaurs are representatives of the extant phylogenetic bracket to reconstruct muscle attachment sites in hyoid fossils. Using the EPB (Witmer 1995a), each muscle was categorized into four levels of inference based on the presence or absence, and the

degree of certainty of the extant archosaurs. Level I inference indicates that a muscle group is present in both groups of extant relatives, and osteological correlates for that muscle group are present in both groups too. Osteological correlates are established as processes or tubercles, surficial texture such as scarring, or discrete surface coinciding with attachment sites. Level I' inferences indicate that a muscle group is present in both groups but osteological correlates are absent in one group or both. Level II inferences indicate that a muscle group is present in one group and osteological correlates are present. Level II' inferences indicate that a muscle group is present in one group but osteological correlates are absent. In some previous studies, Level III and III' have been employed for musculature reconstruction, however, these are ignored in this study because those are defined by a lack of soft-tissue group in both groups and less robust to infer existence. Comparison of origin and insertion sites of muscles in birds and crocodilians help to find the possible sites in dinosaurs, however, if sites of muscle differed between birds and crocodilians, further evidence is required for more plausible reconstruction. To account for independent loss of muscles in crocodylians, a generalized description of lepidosaur musculature was used to determine the possible

basal condition (Romer 1944; Russell & Bauer, 2008; Jones et al., 2009; Abdala & Diogo, 2010).

Institutional abbreviation

AMNH, American Museum of Natural History, New York, USA; **CM**, Carnegie Museum of Natural History, Pennsylvania, USA; **CMN**, Canadian Museum of nature, Ottawa, Canada; **MCZ**, Museum of Comparative Zoology, Harvard University, Massachusetts, USA; **IGM**, Institute of Geology, Mongolia; **ROM**, Royal Ontario Museum Ontario, Canada; **RTMP**, Royal Tyrrell Museum of Paleontology, Alberta, Canada; and **YPM**, Yale Peabody Museum, USA.

Result

Psittacosaurus (IGM100/1930)

Psittacosaurus (IGM100/1930) preserves a pair of ceratobranchials with small fracture.

The ceratobranchial is slightly curved, and the distal portion is oriented dorsomedially.

In dorsoventral view, the middle shaft is curved laterally. Ceratobranchials bear

striations on the lateral side, which maybe muscle attachment scar. The relative sizes of ceratobranchial (56 mm) to mandible (124 mm) are 0.45, to post-rostrum (71 mm) are 0.79, and to skull width (114 mm) are 0.49.

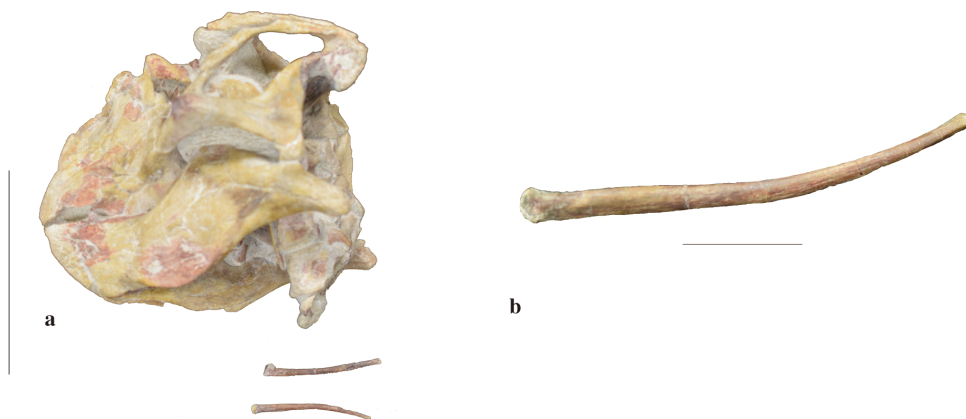


Figure 1. *Psittacosaurus mongoliensis* (IGM 100/1930). Skull, jaw, and a pair of ceratobranchials in lateral view (a). A left ceratobranchial in lateral view (b). Scale bar = 10 cm.

Protoceratops (IGM100/3502)

Protoceratops (IGM100/3502) preserves a pair of ceratobranchials and the left is complete, while, the right is lack of proximal portion. In dorsoventral view, the ceratobranchial is curved medially in proximal portion, and laterally in distal portion, forming loosely sigmoid outline. The proximal end of the ceratobranchial is pointed in the ventromedial corner, expanding ventromedially, and [as wide as high]. The ratio of maximum to minimum width in the proximal end is 1.32. The shaft is higher than wide in the cross section, like crocodylians, derived ornithopods, neoceratopsians, sauropods. The distal portion of the ceratobranchial bear both medial and lateral grooves, as in modern crocodylians and birds. The medial groove is deeper than the lateral one. Relative size of ceratobranchial to mandible is 0.46, and to skull width is 0.45.

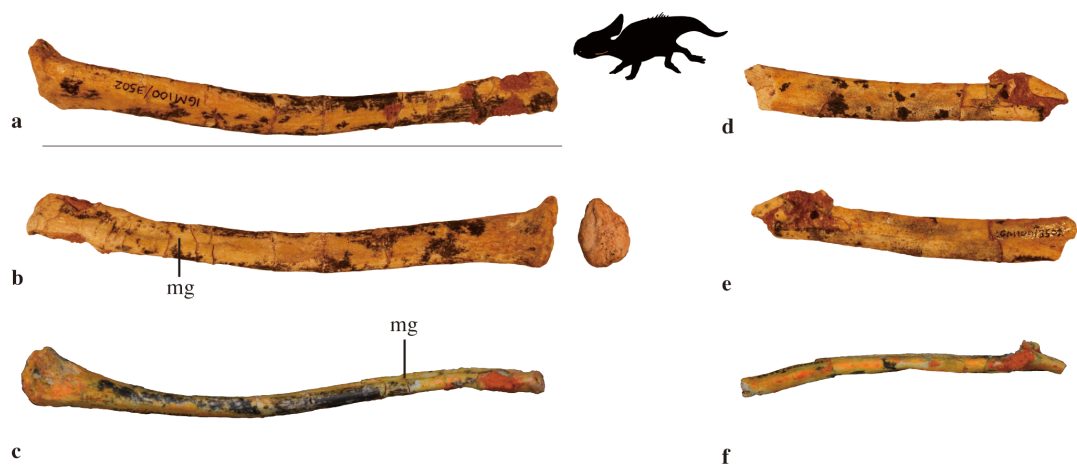


Figure 2. A pair of ceratobranchials of *Protoceratops* (IGM100/3502). A left ceratobranchial in lateral view (a), medial (b), and dorsal view (c). A right ceratobranchial in lateral (d), medial (e), and dorsal view (f). Scale bar = 10 cm.

Styracosaurus (CMN344)

Ceratobranchials are robust and short, about 30 % length of the mandible. The shaft is straight unlike ornithopods and ankylosaurs. The medial surface is slightly concave. The proximal end is expanded, as in other ceratopsids such as, *Centrosaurus*, *Arrhinoceratops*, and *Pachyrhinosaurus*. The proximal end is higher than wide. The middle shaft bears a ventrolateral tubercle as in *Centrosaurus* (ROM767). The distal end is circular in distal view.



Figure 3. Skull and ceratobranchial of *Styracosaurus* (CMN344) (a). A right ceratobranchial in proximal (b), medial (c), distal (d), ventral (e), and lateral view (f).

Scale bar = 10 cm.

Plesiohadros (MPC-D 100/745)

Ceratobranchial is elongate, slightly curved, robust proximally, and slender distally. The proximal end is triangular, slightly wider than high in proximal view, and medially expanded relative to the shaft. From the top of the proximal end, a proximal ridge runs down toward the middle of the medial surface of the shaft. On the mid shaft, a dorsal crest is positioned dorolateral to the proximal ridge. The surficial striations of the dorsal crest are likely to be attachment site for *m. geniohyoideus*. Medial to the proximal ridge, the middle shaft bears a low ridge on the medial surface. Ventral to this medial ridge, the ventral surface bears longitudinal striations that are less ambiguous than the dorsal crest, which is likely to be attached by *m. hyoglossus*. The distal portion of the ceratobranchial is dorsally deflected, bearing a low ridge on the dorsal surface and a shallow groove on the ventral surface. The dorsal ridge of the distal portion is formed by both lateral and medial grooves. The lateral grooves runs from a distal half of dorsal crest through the large part of the distal portion. These surficial features of the distal portion are indicative of muscle attachment sites, such as *m. branchiomandibularis* for the dorsal ridge, and *m. omohyoideus* (or *m. sternohyoiedus*)

for the ventral groove. These distinctive morphologies of the ceratobranchial indicate its large development of hyolingual musculatures, such as, m. geniohyoideus, hyoglossus, branchiomandibularis, and omohyoideus, compared to other non-hadrosauroid dinosaurs. Plesiohadros clearly shows surficial features compared to other ornithopod ceratobranchials (Fig. 5)



Figure 4. A right ceratobranchial of *Plesiohadros* (IGM100/745) in proximal (a), ventral (b), distal (c), medial (d), dorsal (e) and lateral view (f). dc, dorsal crest; mc, medial crest. Scale bar = 10 cm.



Figure 5. Ornithopod ceratobranchials. *Theiophytalia* YPM 1887 (a), *Tenontosaurus* OMNH 58340 (b), *Protohadros* SMU 74582 (c), *Brachylophosaurus* CMN 8893 (d), *Velafrons* CPC59 (e), and *Edmontosaurus* ROM 64076 (f). Scale bar = 5 cm.

Curvature analysis

On the evolution of Ornithischia, dorsal deflection of ceratobranchial is occurred in Neornithischia and Ankylosauria, while straight in Ceratopsia (Fig. 6). Acestrally, ceratobranchial is slightly curved in basal ornithischians, as seen in *Lesothosaurus* (Fig. 5), then there are two trends in ornithischian ceratobranchials: dorsal deflection and straightening. For Thyreophora, *Scelidosaurus* displays slightly-curved ceratobranchial, however, *Stegosaurus* shows straight ceratobranchial and ankylosaurs exhibit curved ceratobranchials. In Neornithischia, ceratopsians retained straight ceratobranchials, while ornithopods have retained curved ceratobranchials. These bipolarizations of ornithischian ceratobranchial are supported by evaluation of AIC weights which shows that OU model was the best describe the curvature evolution in all three branch-scaling models (aba, equal, and mbl) (Table 1).

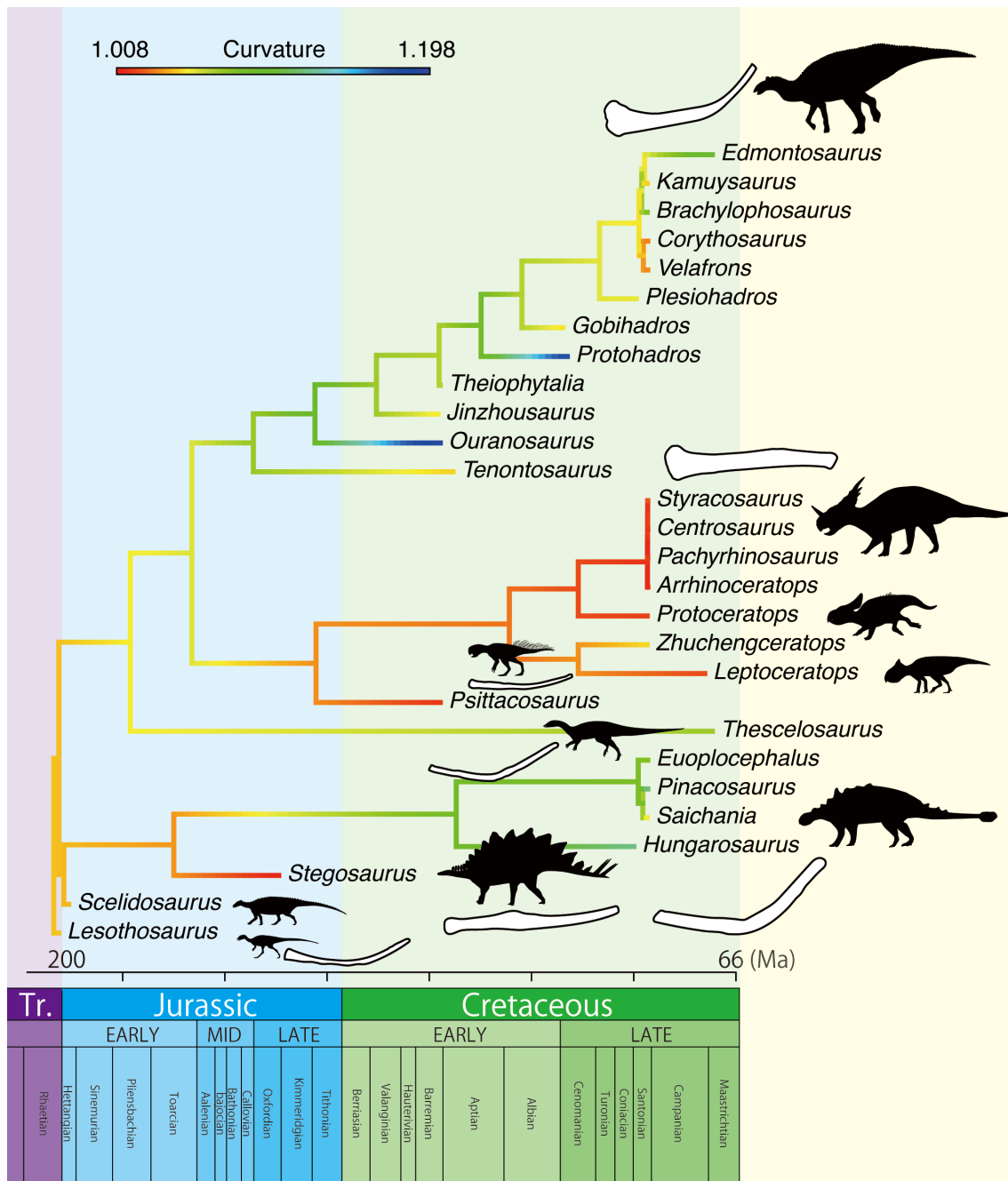


Figure 6. Evolution of curvature in ceratobranchials of Ornithischia. Ceratobranchials depicted in representative terminal branches, placing its proximal end on the left. Curved ceratobranchials retained in Ankylosauria and Neornithischia. Ceratopsia with

secondarily straight ceratobranchial.

Osteological correlates and muscular reconstruction

Some ornithischians show distinctive osteological correlates on surface: (1) dorsal crest, (2) ventromedial ridge, and (3) dorsal groove in distal portion of ceratobranchial, and (4) ventrolateral ridge (Fig. 7, 8). Dorsal crest is an attachment scar for m.

geniohyoideus principalis that protracts hyoid apparatus dorsally toward mandible. The

dorsal crest is present in ceratobranchials of a majority of ornithopods, such as,

Theiophytalia, *Protohadros*, *Plesiohadros*, *Edmontosaurus*, *Kamuysaurus*, and

Corythosaurus (Fig. 7) and *Stegosaurus* (USNM4935). Ventromedial ridge forms

medial groove above it, and attached by m. hyoglossus which moves tongue itself.

Ventromedial ridge is present in ceratobranchials of some ornithopods, such as,

Plesiohadros, *Edmontosaurus*, and *Corythosaurus* (Fig. 7) and some ankylosaurs, such

as, *Pinacosaurus* (IGM100/3186) and *Euoplocephalus* (AMNH FARB5405).

Development of ventromedial ridge is limited to derived clade compared to dorsal crest.

Dorsal groove in distal portion of ceratobranchial is attachment scar of m.

branchiohyoideus which rises basihyal upward. This feature is seen in *Plesiohadros*, and

Edmontosaurus. Ventrolateral ridge is present in ceratopsids, such as, *Styracosaurus*,

Centrosaurus, and *Pachyrhinosaurus* (Fig. 8). This surficial feature is an attachment site for m. geniohyoideus lateralis that protracts hyoid apparatus anteriorly toward mandibular symphysis.



Figure 7. Osteological correlates of ceratobranchials of ornithopods (*Plesiohadros*, *Protohadros*, and *Edmontosaurus*), turtle (*Podocnemis expansa*) and birds (*Sagittarius pserpentarius* and *Leptoptilos*). dc, dorsal crest; mc, medial crest; vmr, ventromedial ridge; mg, medial groove; ar, arytenoid; cr, cricoid; bh, basihyal; cb1, ceratobranchial 1;

cb2, ceratobranchial 2; and eb, epibranchial. Scale bar = 5 cm.

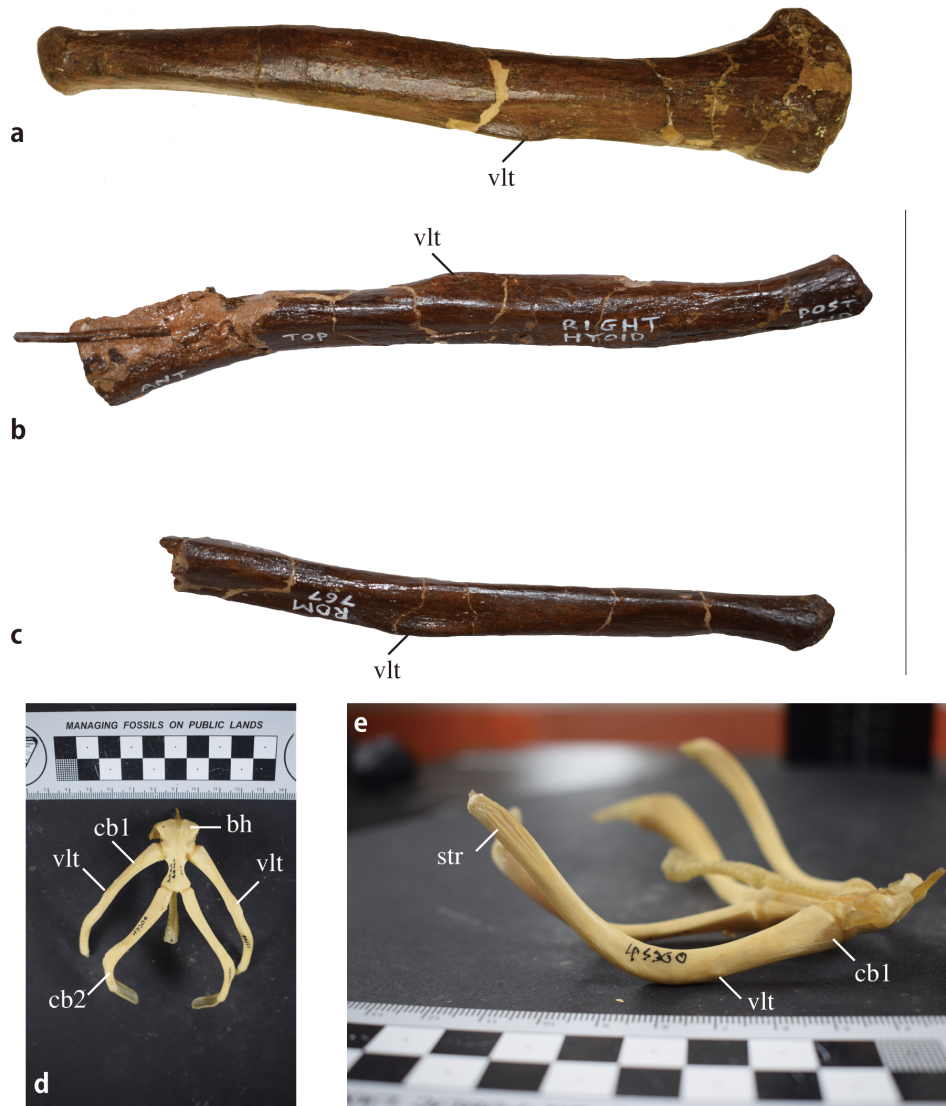


Figure 8. Osteological correlates for *m. geniohyoideus* on ceratobranchials of ceratopsians (*Styracosaurus* CMN344 (a), *Centrosaurus* ROM767 (b, c)), and turtle (*Chelydra serpentina* (d, e)). vlt, ventrolateral crest; mg, medial groove; str, striation; bh, basihyal; cb1, ceratobranchial 1; cb2, ceratobranchial 2; and eb, epibranchial. Scale bar = 10 cm.

Discussion

Form/ function relationships

Since *m. branchiomandibularis* attaches to dorsal surface of distal portion of ceratobranchial and medial side of mandible, curved ceratobranchial is suited for dorso-ventral motion of hyoid apparatus. Dorsal deflection of ceratobranchials are present in ornithopods and ankylosaurs, therefore, these ornithischians could have moved hyoid apparatus, especially basihyal, dorsoventrally. Furthermore, hadrosauroids exhibit three osteological correlates, including dorsal crest, such as, ventromedial ridge, and dorsal groove in distal portion of ceratobranchial, while ceratopsians shows ventrolateral ridge. Ankylosaurs shows ventromedial ridge and *Stegosaurus* displays dorsal crest, but thyreophorans have small sample size of ceratobranchial and their evolutionary trajectory still remains unknown. Hadrosaurids develop dorsal crest of ceratobranchial. Around dorsal crest, the proximal portion is widening and there is a groove medial to the crest, which is homologous to dorsal shelf in crocodylians and some sauropods and groove in some birds. This indicates that this morphology is large attachment site for *m. geniohyoideus*. Both ventrolateral ridge of ceratopsids and dorsal

crest of hadrosauroids are inserted by different branches of the same muscle, m. geniohyoideus. M. geniohyoideus protracts hyoid apparatus anteriorly toward mandibular symphysis. These ridges of the two groups suggest that both ceratopsids and hadrosauroids have been capable of moving their hyoid apparatus forward.

Evolution of ceratobranchial in ornithischian dinosaurs

In hadrosaurids and neoceratopsians, the hyoid modifications have been retained prior to their convergent acquisition of dental tissue complexity (retention of hard mantle dentine and vasodentine, Erickson et al., 2012, 2015) and dental battery that holds more than three teeth in each alveolus tightly packed with adjacent teeth. This suggests that the adaptation on food intake have advanced the masticatory sophistication in neornithischian dinosaurs. Acquisition of predentary advanced the hyoid modifications in each clade of ornithischians, suggesting modified hyoid have complemented functional rostrum or had no function in food intake in early evolution of each clade, in contrast to sauropodiforms (chapter 4). However, dorsal crest, ventromedial ridge, dorsal deflection of ceratobranchials in ornithomimid indicate their step-wise acquisition

of functional tongue in their food intake and mastication. Interestingly, ceratopsians show straight, short, relatively simple ceratobranchial in both bipedal and quadrupedal taxa, indicating that ceratopsians have less utilized their tongue in feeding. In Triassic, sauropodiforms have already radiated and retained their basic bodyplan for herbivory, while early ornithischians still have been small and less diverse (Brusatte et al., 2010; Langer et al., 2010; Irmis et al., 2010). Therefore, the early ornithischians may have developed other ecological traits for different niche from sauropodiforms as herbivore and lingual motion might not have been significant in their feeding strategy. After ornithischian diversification, although sample size is limited in thyreophorans, straight ceratobranchials are present in narrowed-rostrum ornithischians (*Stegosaurus* & ceratopsians) and ceratobranchials are curved in broad-rostrum ornithischians (ornithopods and ankylosaurs). Ceratobranchial curvature reflects lingual motion and likely depends on their feeding strategy as well as rostral morphology (Mallon & Anderson, 2014). This study proposed lingual motion have facilitated different feeding strategy and niche partitioning in each clade as well as other ecomorphologies in ornithischians.

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VI. FUNCTIONAL MORPHOLOGY OF HYOLARYNGEAL APPARATUS OF
PINACOSAURUS (DINOSAURIA) AND ITS NOVEL INSIGHT TO
HYOLARYNGEAL APPARATUS IN ARCHOSAURIA

ABSTRACT

Tongue and voice box (hyolaryngeal apparatus) are unique for tetrapods, and playing functional roles in feeding, respiration, and vocalization. However, its evolution still remains largely unknown because it was regarded as cartilage and hardly preserved in fossils except neognath birds. Here we study ankylosaur dinosaur fossils and show the first fossil larynx of non-avian reptiles and new paleobiological insights in extinct non-avian dinosaurs. The larynx of *Pinacosaurus* is composed of cricoid and arytenoid, lacking procricoid, structurally similar to reptiles, suggesting that the ancestor of Dinosauria had non-avian laryngeal components. Additionally, the *in situ* hyolaryngeal apparatus of *Pinacosaurus* indicates that the stem archosaurs lack paraglossal, ceratobranchial 2, and epibranchial like crocodylians, while the stem dinosaurs separate larynx from basihyal like birds. Furthermore, *Pinacosaurus* uniquely displays a firm

cricoid-arytenoid joint, a prominent arytenoid process attached by a large dilator muscle to open glottis, and an enlarged larynx as in vocal reptiles and birds, suggesting its vocalization. Significantly, this oldest laryngeal fossil bridges the missing link between crocs and birds, and sheds light on evolution of the larynx and vocalization toward birds.

INTRODUCTION

Hyolaryngeal apparatus, composed of hyoid and larynx, is a unique feature of tetrapods associated with feeding, respiration, and vocalization and has been playing key roles in the tetrapod evolution (Reilly & Lauder, 1990; Iwasaki 2002; Fitch & Suthers, 2016). The anatomy and function of the hyolaryngeal apparatus have been widely studied in modern amphibians (Carroll 2007), squamates (Schwenk 2000; Schwenk & Rubega, 2005), turtles (Schumacher 1973), crocodylians (Schumacher 1973; Reese 1945; Riede et al., 2015), birds (McLelland 1989; Homberger 2017), and mammals (Frey et al., 2016). Among extinct tetrapods, hyoids are occasionally preserved in fossil specimens, and the evolution of the hyoids has been previously

discussed (Hill et al., 2015). Larynx is an important module for acoustic communications but its evolution is unknown. No larynx has been reported in extinct non-avian tetrapods because it is cartilaginous in all tetrapods except neognath birds.

Among modern archosaurs, the hyolaryngeal apparatuses of crocodylians and birds differ anatomically and functionally from each other (refs, Schmacher 1973). Larynx produces sound in crocodylians (Schmacher 1973) and resonates sound, produced by syrinx, in neornithine birds (McLelland 1989a; Clarke et al., 2016; Kingsley et al., 2018). Preserved hyoids in non-avian dinosaurs are only ceratobranchials except the abelisaurid *Carnotaurus* (basihyal and ceratobranchial 1) and some ankylosaurs (basihyal, and ceratohyal, and ceratobranchial 1 in *Saichania chulsanensis* and paraglossal, ceratobranchial 1, ceratobranchial 2, and epibranchial in *Pinacosaurus grangeri* (Bonaparte et al., 1990; Maryanska 1977; Hill et al., 2015). Herein, we re-examine the apparatus in these ankylosaurs because of its preservation to argue the identification of the hyolaryngeal elements and reveal its function in *Pinacosaurus* and the hyolaryngeal evolution in Archosauria.

MATERIAL AND METHOD

Ankylosaur dinosaur *Pinacosaurus* (IGM100/3186) is examined as hyolaryngeal apparatus of fossil archosaurs. This specimen was discovered from Ukhaa Tolgod, Mongolia and its geological age is middle Campanian of the Late Cretaceous (Hill et al., 2015). The specimen is better prepared after the previous publication in 2015. Computed Tomography scanning is conducted to study its morphology.

For comparison, extant species of reptiles and birds (45 specimens of turtles, 11 of lizards, 4 of crocodylians, and 50 of birds) are examined and widths of cricoid and mandible are measured. I also studied the palaeognath bird skeletons, such as extant *Nothura* (AMNH10804), *Nothoprocta* (AMNH 6498, 6502) and extinct *Dinornis* (AMNH7301), and fossil neognath *Presbyornis* sp (USNM PAL299846).

RESULT

Pinacosaurus grangeri (IGM100/3186) is the best preserved hyolaryngeal apparatus in ankylosaurs. Here we revise the identification of the elements described in Hill et al. (2015): the paraglossal is reidentified as the cricoid, ceratobranchial 1 as the arytenoid,

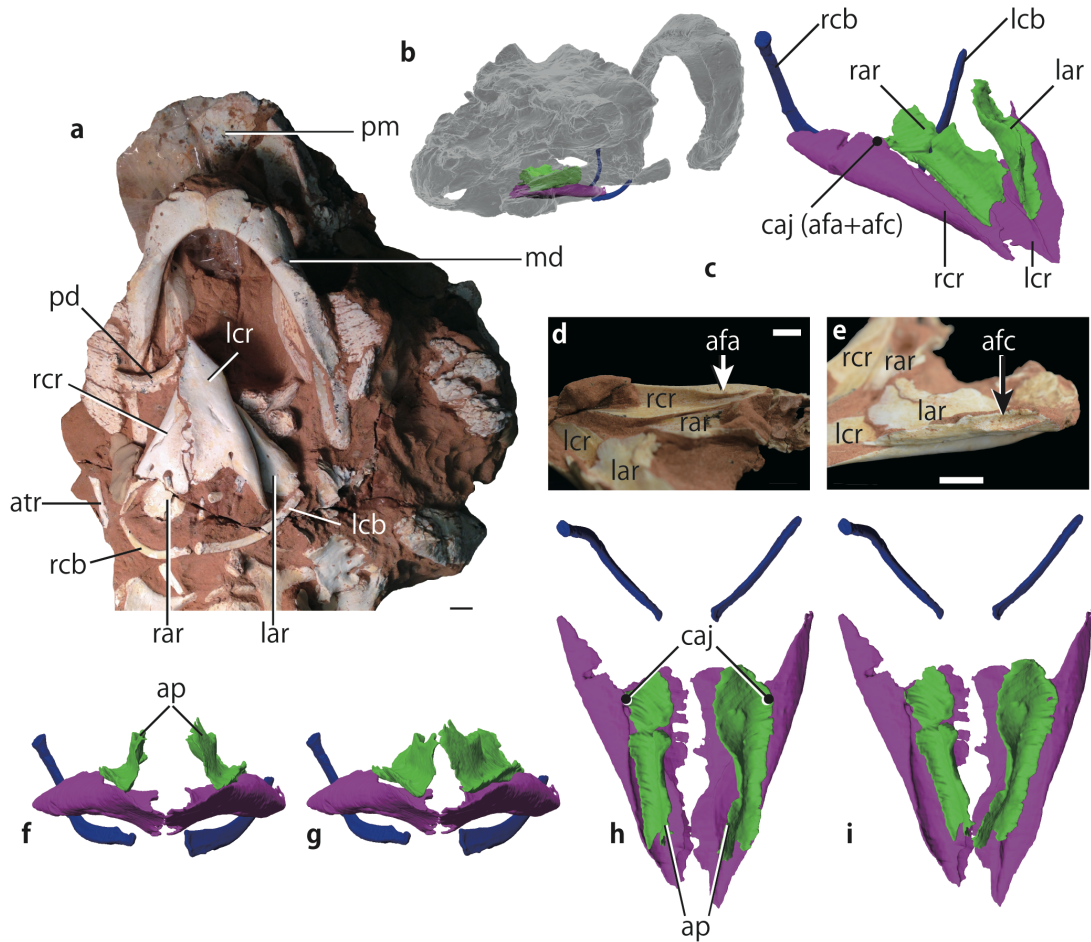


Figure 1. *in situ* hyolaryngeal apparatus and skull of *Pinacosaurus* in ventral view (a) and 3D reconstruction of skull mandible, and hyolaryngeal apparatus (b), and hyolaryngeal apparatus in left oblique view (c). Crico-arytenoid joint of right cricoid in medial view (d), and that of left arytenoid in dorsolateral view (e). Arytenoid motion in glottal opening (f) and closing (g) in anterior views, and opening (h) and closing (i) in dorsal views. afa, articular facet for arytenoid; afc, articular facet for cricoid; ap, arytenoid process; atr, atlas rib; caj, crico-arytenoid joint; lcb, left ceratobranchial; lcr,

left cricoid; md, mandible; pm, premaxilla; pd, preedntary; rar, right arytenoid; rcb,

right ceratobranchial; rcr, right cricoid. Scale bars, 1 cm.

ceratobranchial 2 as ceratobranchial 1, and epibranchial as an atlas rib. IGM100/3186 preserves three in situ paired symmetrical hyolaryngeal elements (cricoid, arytenoid, and ceratobranchial 1) (Fig. 1a, c). The cricoid and arytenoid are articulated and lie anterior to the ceratobranchial 1. The basihyal is not present, probably because it was unossified. Paired atlas ribs are preserved, where one is located lateral to the jaw joint and another is posterior to the cricoid.

Both cricoids (Fig. 1f-i) are complete but remain unfused along the midline, while those in the ankylosaurid *Saichania* are fused into a single element (Maryanska, 1977). This probably has to do with the immaturity of IGM100/3186 (Hill et al., 2015). The cricoids are the largest bones of the hyolaryngeal elements. They are at least 64.7 mm wide which is about three fourths the width of the mandible. The cricoid is pointed anteriorly and widely expanded posteriorly, with a concave posterior margin, forming an arrow-headed shape in dorsal view. The cricoid body forms the floor of the element and is thin along the midline and thickens laterally. The lateral edge of the cricoid body curls dorsally, forming the cricoid wing. A dorsomedially projecting thin lamina extends anteroposteriorly from the anterior apex of the cricoid body and ends medial to

the cricoid wing. At the intersection of the cricoid lamina and wing, a shallow groove (approximately 2 cm long) forms an articular facet for the arytenoid (Fig. 1d). The dorsal surface above the groove has a rugose surface, indicative of joint cartilage for the arytenoid. This rugose articular surface of the firm crico-arytenoid joint might support active motion of arytenoid by contraction of the glottis by dilator muscle. Only in birds does the arytenoid exhibit a distinct joint surface proximally, instead of a connective tissue bridge as in other reptiles (Extended Data Fig. 2a, 3d). A minute foramen lies near the posterior edge of the cricoid body on each side (Fig. 1a, Extended Data Fig. 1d), similar to two posterior notches in the cricoid of *Alligator mississippiensis* (Schumacher 1973) and the angular foramen on the cricoid in several birds (Extended Data Fig. 2c, 3b) and chicken embryos (Mori 1957).

The arytenoid lies dorsal to the cricoid (Fig. 1c, f-i). It is anteroposteriorly long and bears short dorsolateral and long dorsomedial wings, that form a J-shape in cross-section (Fig. 1). The dorsomedial wing is thin, and its anterior third projects dorsally to form the arytenoid process as in modern turtles (Siebenrock, 1898) and birds (McLelland 1989; Soley et al., 2015). The arytenoid process is an attachment site for m.

m. dilator laryngis which opens the glottis (entrance of trachea). In birds it originates from the caudolateral ends of cricoid (McLelland 1989; Homberger 2017), while, in crocodylians it originates from the posterolateral margin of basihyal and cricoid (Schumacer 1973; Riede et al., 2015). The arytenoid process of *Pinacosaurus* is not as prominent as that of *Saichania* (Maryanska 1977). This is probably due to its early ontogenetic stage. In birds the arytenoid process ossifies late in ontogeny (McLelland 1989). The dorsolateral wing is less developed than the dorsomedial wing. Furthermore, the lateral surface of the dorsolateral wing bears a ridge with a rugose surface that articulates with a corresponding rugose surface lying at the constriction of the above mentioned cricoid groove (Fig. 1e). This forms the ridge-and-groove articulation between the cricoid and arytenoid. This unique morphology of articular facet is not found in other reptiles and birds.

The paired ceratobranchials have proximal ends that lie medially along the midpoint axis of the body, while their distal ends splay laterally. This symmetrical arrangement of the ceratobranchials along the midline and the dorsal position of the arytenoid to the cricoid indicate that the hyolaryngeal apparatus is preserved in almost life position

although they are slightly displaced posteriorly. Ceratobranchial 1 is long, slender, and slightly curves ventrally. It is 36 mm long, about the half length of mandible, and about 70 % of cricoid length. Its proximal end is circular in cross-section and has a flat surface. Lateral side of the proximal portion of the shaft is concave. The distal end is elliptical in cross-section and slightly expanded. Another pair of hourglass-shaped bones, preserved lateral to the ceratobranchials 1, is atlas ribs, identical to those of the holotypic specimen of *Pinacosaurus* (AMNH6523, Gilmore 1933) and *Saichania* (Maryanska 1977).

DISCUSSION

New interpretation of hyolaryngeal apparatus of *Pinacosaurus* (Dinosauria)

In the past study, Maryanska (1977) considered that *Saichania* preserved a basihyal with entoglossal process, a ceratohyal, and ceratobranchials, referring to *Sphenodon* and *Lacerta*. Following this study, a juvenile specimen of *Pinacosaurus* was reported as preserving four hyoid bones: paraglossal, ceratobranchial 1, 2, and epibranchial (Hill et al., 2015), but this identification contradicts to the results of this

study that proposes one hyoid bone and two laryngeal bones: ceratobranchial, cricoid, and arytenoid.

The identification of the bones made by Hill et al. (2015) worth reconsidering in the following seven characters: presence of paraglossal, absence of paraglossal-basihyal joint, medial groove in lateral margin of paraglossal, inossification of basihyal, plate-like configuration of ceratobranchial 1, presence of ceratobranchial 2, and presence of epibranchial. First, presence of paraglossal in dinosaur is ambiguous in principle of extant phylogenetic bracket (Witmer 1995) because paraglossal is present in birds, while, absent in crocodylians and the other reptiles. Furthermore, despite of such a large paraglossal, there is no paraglossal-basihyal joint that is seen in some neognath birds (Yoshida unpublished data). Moreover, medial groove of lateral margin was not interpreted previously in terms of homology and function, and is absent in paraglossal of neognath birds. Second, morphology of the ceratobranchial 1 is generally rod shape as in the other dinosaurs. Presence of ceratobranchial 2 is unlikely because both extant archosaurs, crocodylians and birds, have no ceratobranchial 2. Rather, the proposed ceratobranchial 2 is similar in morphology to ceratobranchial 1 of other ornithischians

in its rod shape (Fig. 3). Finally, epibranchial is also absent in crocodylians and paleognath birds, indicating its lack in non-avian dinosaurs.

Instead, this study newly proposes an alternative identification that some of those elements of *Pinacosaurus* are ossified laryngeal elements. The cricoid body, arytenoid, ceratobranchial, and atlas rib was interpreted as paraglossal, ceratobranchial 1, ceratobranchial 2, and epibranchial, respectively. This identification is consistent with *in situ* condition of the *Pinacosaurus* fossil. The laryngeal elements are composed of cricoid and arytenoid and both of them are cartilaginous in Crocodylia (Riede et al., 2015), but ossified in Neognathae (McLelland 1989). The new interpretation of this study also has some controversial points: ossification of larynx, and its large size. Ossification of larynx occurs only in neognath birds among archosaurs, which suggests peculiarity of *Pinacosaurus*. Cause of its ossification is unclear developmentally or evolutionarily, however, morphological analogy should be concerned. Second, its large size is also noteworthy compared to modern birds. However, turtle hyoid is large. Ontogenetic proportion must be considered too. Therefore, the identification of this study is more accountable and simpler than the past identification of Hill et al. (2015).

Moreover, other ankylosaurs, such as *Saichania* (Maryanska 1977) and *Edmontonia* (AMNH FARB5381, Hill et al., 2015), show the similar bones, indicating its ankylosaurid synapomorphy. The preservation of the cricoid in the juvenile *Pinacosaurus* is consistent with the fact that avian cricoid become ossified in early developmental process (Nickel et al., 1977).

Fossil record and evolution of larynx

Fossilized larynx has never been discovered in non-avian archosaurs and even rarely preserved as fossil birds. The oldest record of larynx in the fossil record was the anseriform *Presbyornis* sp from the Early Eocene Green River Formation in Wyoming, showing only its ventral surface of cricoid (Olson & Feduccia, 1980). Some of the hyolaryngeal elements of *Pinacosaurus* and *Saichania*, which were originally identified as hyoids (paraglossal and ceratobranchial 1) (Maryanska 1977; Hill et al., 2015), are actually the larynx (cricoid and arytenoid), suggesting that this is the first report of ossified larynx in non-avian tetrapods, and laryngeal ossification was dated back to the Mesozoic dinosaurs.

The evolutionary trends of hyolaryngeal apparatus in Archosauria illustrate progressive acquisitions of characters (Fig. 2). Ceratobranchial 2 is commonly present in non-archosaurian reptiles, and lost in Archosauria (Li et al., 2018). The hyolaryngeal apparatus of crocodylians is composed of four elements (arytenoid, cricoid, basihyal, and ceratobranchial 1), where all are cartilaginous except ceratobranchial 1. *Pinacosaurus*, a non-theropod dinosaur, retained the same bone composition of hyolaryngeal apparatus and cartilaginous basihyal as crocodylians but obtained shared characters with birds in the arrangement and morphology of larynx, such as the ossification of larynx, no contact between larynx and the basihyal, the arytenoid process of the arytenoid, a single articular joint between the cricoid and arytenoid, and a pointed tip of the cricoid. The acquisition of avian laryngeal characters in *Pinacosaurus* suggests that the separation of larynx from hyoid and modifications of laryngeal elements might have established independent modularity of larynx in Dinosauria. The basihyal of the theropod *Carnotaurus* and birds is ossified. The other laryngeal elements (arytenoid and cricoid) are not preserved in *Carnotaurus*, which may suggest that it lost its ossification reversely or simply because of preservation. The hyolaryngeal apparatus of birds

retained two additional elements (paraglossal and procricoid) and the epibranchial is present in neognath birds.

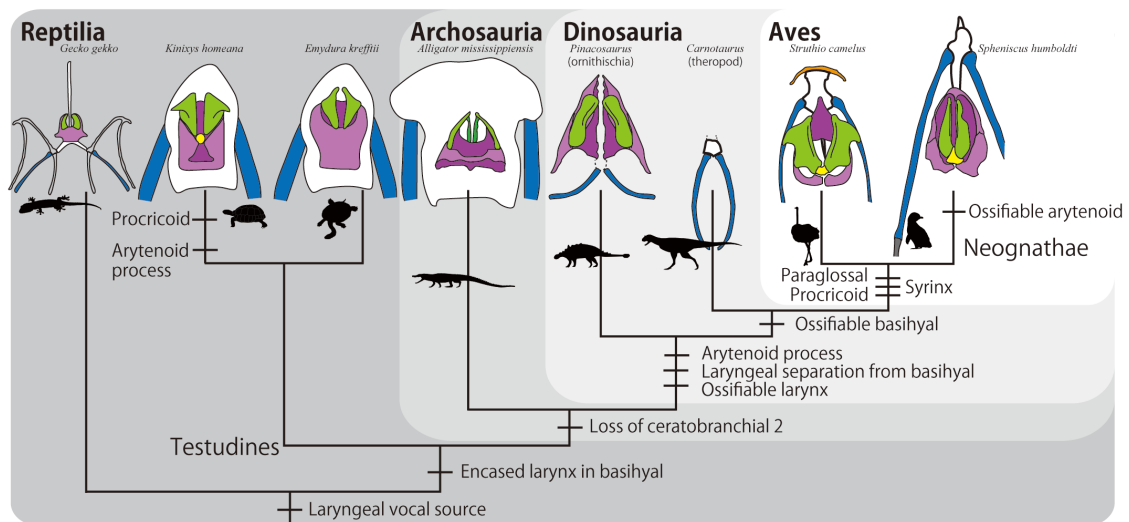


Figure 2. Phylogenetic framework of hyolaryngeal apparatus in Archosauria.

Function of larynx of *Pinacosaurus*

Larynx of reptilians, including birds, is an entrance of tracheal passage and three functions have been suggested (a barrier to foreign materials entering trachea (airway protection), opening of glottis for respiration (respiratory modulation), and generation and modulation of sound) (White 1975; Kirchner 1993). Hypertrophied larynx is associated with loud and explosive distress call to predators, being exemplified with gekkotans (Russell et al., 2014). Vocal turtles (Testudinidae, Trionychidae, Emydidae, and Bataguridae, Gans & Maderson 1973; Galeotti et al., 2005) possess larger larynx than non-vocal turtles (Fig. 4). Birds are a unique group among reptiles because this group utilizes the larynx to resonate sound, generated by syrinx, for extensive acoustic communication. Birds show larger larynx than other non-avian reptiles and the larynx of *Pinacosaurus* is placed even larger than birds, suggesting that it may have actively vocalized for communication (Fig. 4).

The arytenoid process and firm crico-arytenoid joint in *Pinacosaurus* enable arytenoid rotate to open and close glottis. Its working muscle is m. dilator laryngis which originates from caudolateral ends of cricoid and inserts in anterior portion of

arytenoid in birds (McLelland 1989; Homberger 2017), while, in crocodylians, from posterolateral margin of basihyal and cricoid into arytenoid process (Schumacer 1973; Riede et al., 2015). Besides, the articular surface of crico-arytenoid joint is rugose, where cartilage likely covered as well as general articular surface in bones (Fig. 1), and its firm crico-arytenoid articulation might support active motion of glottis. Only in birds, arytenoid exhibits distinct joint surface on its proximal end, not simply bridged via connective tissue like other reptiles. These two traits indicate that *Pinacosaurus* may actively open and close glottis, controlling air pressure difference across glottis. Therefore, these three morphological features (enlarged larynx, arytenoid process, and crico-arytenoid joint) suggest that the larynx of *Pinacosaurus* functions in vocalization for social communication (e.g. courtship, parental call, defense against predator, and territorial call).

Furthermore, among the three traits, firm crico-arytenoid joint of the *Pinacosaurus* enables great mobility of arytenoid, which infers the larynx of *Pinacosaurus* was sound modulator and presence of other sound-source organ as in birds. Birds resonate sounds by open-mouth and/or closed-mouth vocalizations. Linear

regression analyses demonstrate that the slope of closed-mouth vocalization is slightly steeper than that of open-mouth vocalization, and *Pinacosaurus* is included within the 99% confidence of the regression line of birds employing closed-mouth vocalization, while excluded from the one of birds with open-mouth vocalization (Fig. 4). Because closed-mouth vocalization is convergently seen in crocodylians, ostrich, emu, doves, and pectoral sandpipers, it is suggested that it is unlikely ancestral condition in the stem birds in previous study (Riede et al., 2016); however, closed-mouth vocalization in *Pinacosaurus* and crocodylians may support that it is common in non-avian dinosaurs, and an ancestral condition for the stem birds. Closed-mouth vocalization usually accompanies with inflation of cavities and skins in an oropharyngeal-esophageal region, and ankylosaurs similarly have seem to employ such an inflation of that cavity and nasal emission of sound like modern crocodylians although their gular pouch might be limitedly stretchable due to their gular ossicles covering the region.

Ankylosaurs possessed complex and elongate nasal cavity (Witmer & Ridgely, 2008), which is considered as vocal or thermal regulatory function. When ankylosaurs close a mouth and emit sound from nostrils, such elongate nasal cavity possibly

contributes to generating lower vocal-tract frequencies. Similarly, in lambeosaurines, their elongate cranial crest increases vocal tract length and could produce low resonance frequency (Weishampel 1981). Longer distance from vocal source to acoustic output increases amplitude and produces lower fundamental frequency as acoustic resonance (ref). In fact, some of modern birds (e.g. anseriforms, gruiforms) possess looped trachea that lengthen vocal tract from syrinx to larynx to exaggerate apparent body size (Fitch 1999).

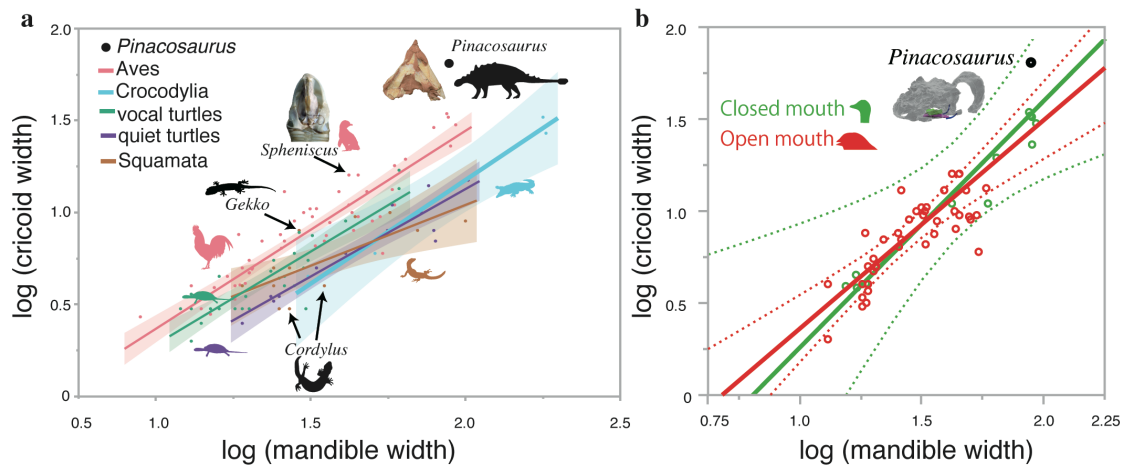


Figure 3. Relative size of larynx (cricoid width) to mandible width in reptiles and birds

(a) and only birds (b). Linear regression line showing the 95% confidence intervals of

Ordinary Least Squares in A and 99% in B.

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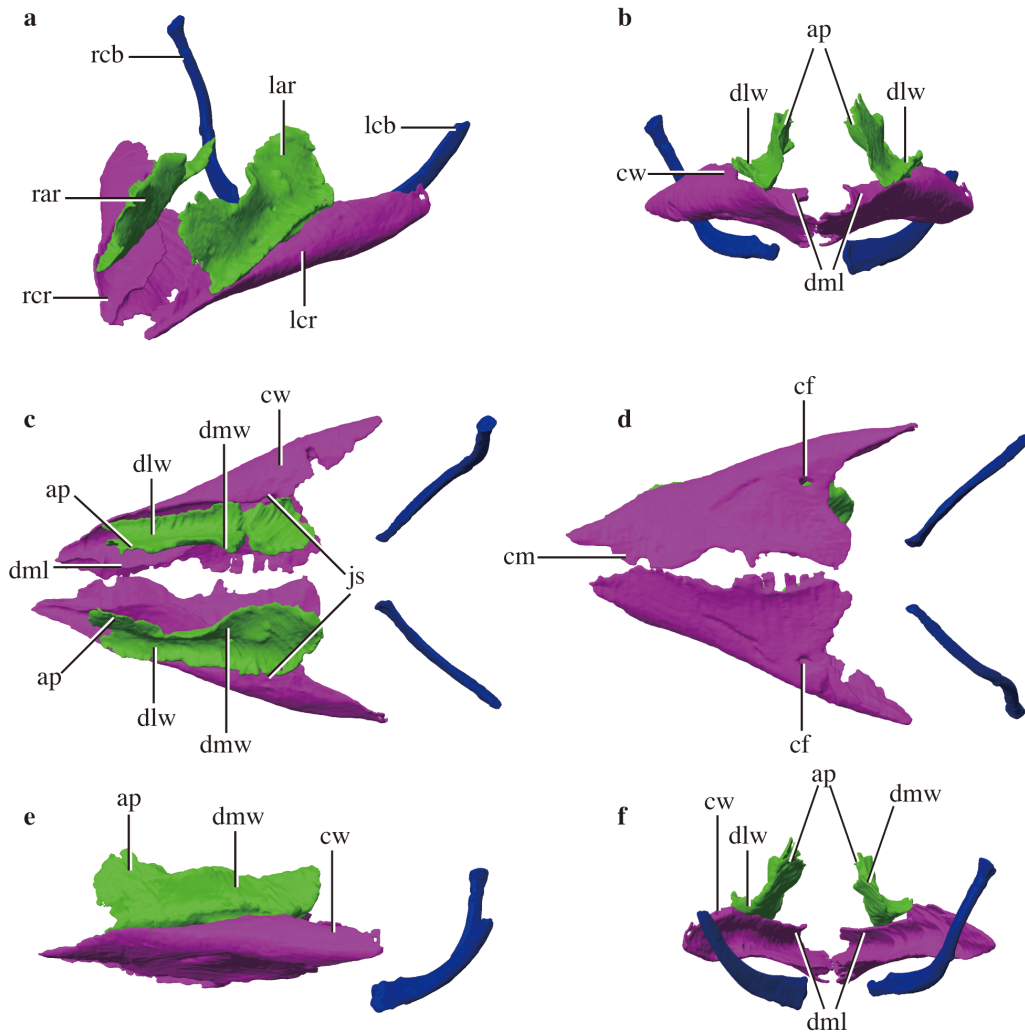
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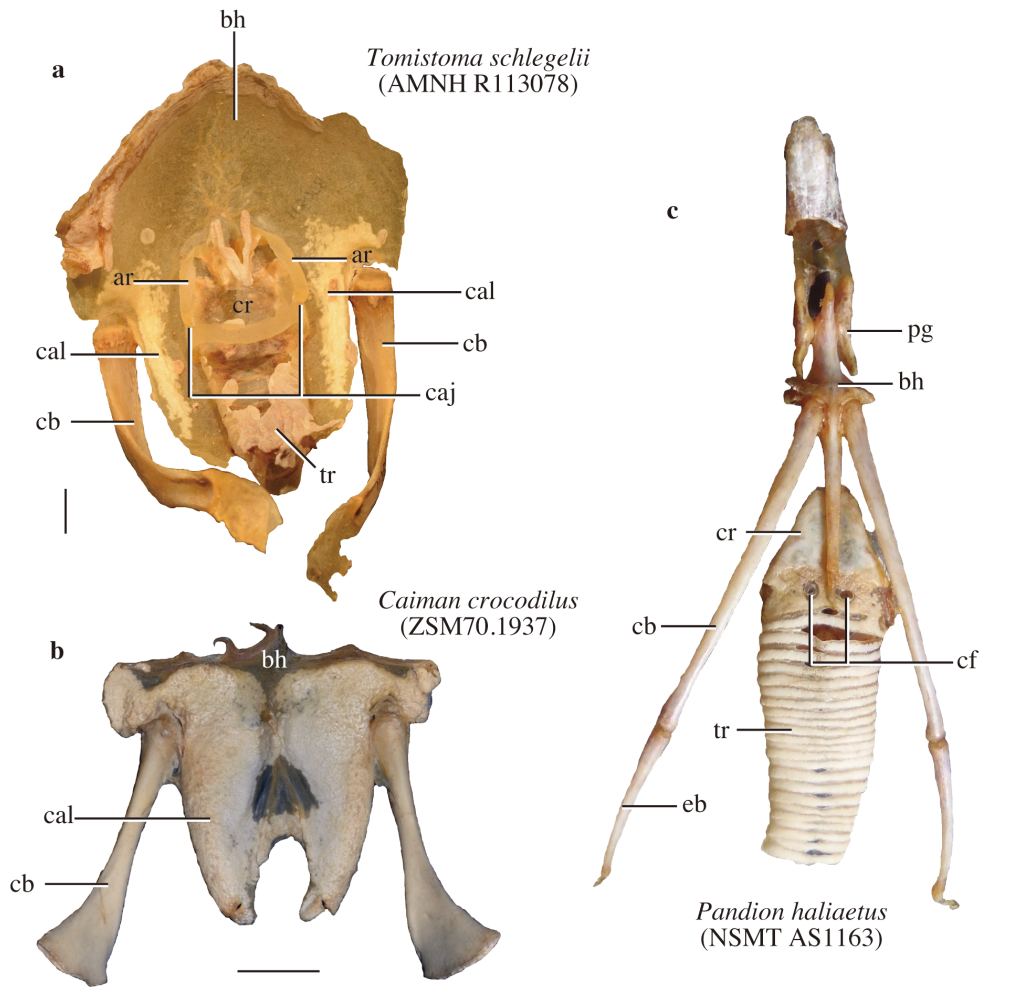
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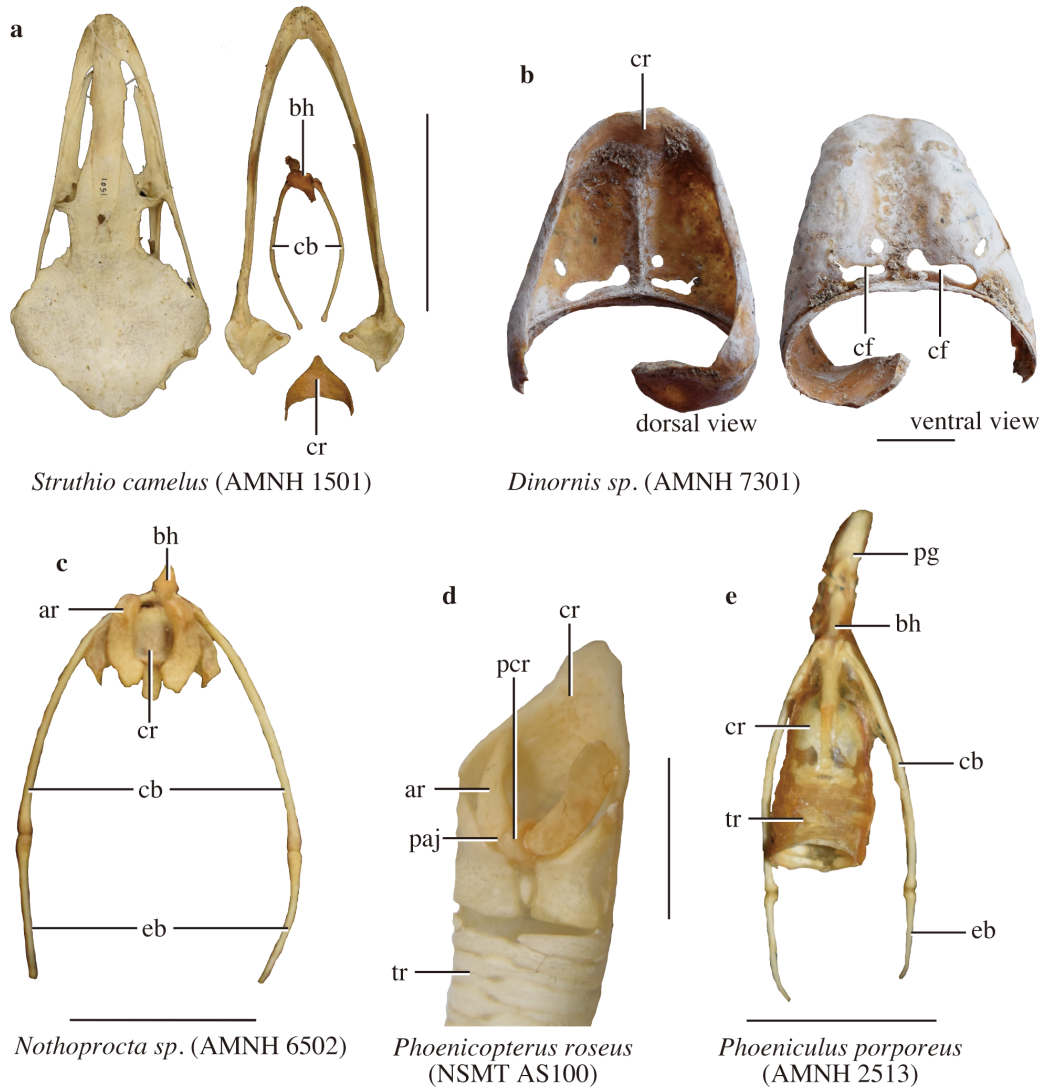
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Extended Figure 1. 3D reconstructions of hyolaryngeal apparatus of *Pinacosaurus grangeri* (IGM100/3186). a, in oblique view. b, anterior view. c, dorsal view. d, ventral view. e, left lateral view. f, posterior view. ar, arytenoid; bh, basihyal; cb, ceratobranchial; cr, cricoid; eb, epibranchial: pcr, procricoid; ap, arytenoid process; cf, cricoid foramen; cm, coracoid midline; cw, cricoid wing; dlw, dorsolateral wing; dmw, dorsomedial wing; dml, dorsomedial lamina; and js, joint surface.

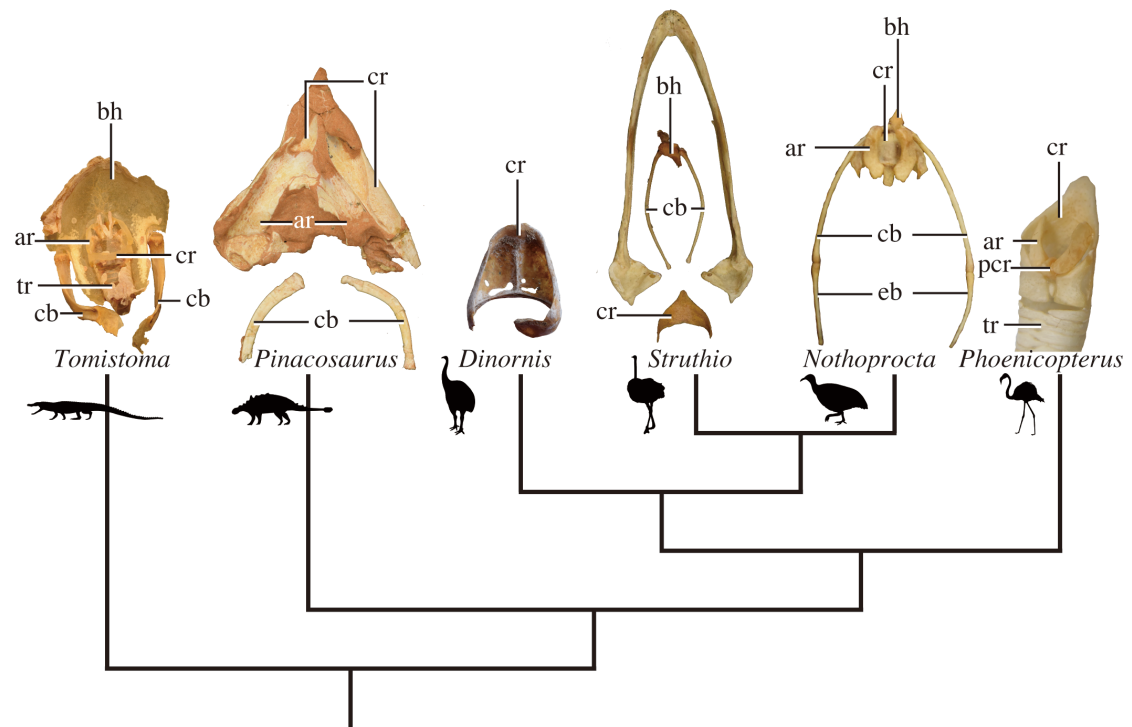


Extended Figure 2. Archosaur skeletons with hyolaryngeal apparatus. *Tomistoma schlegelii* (AMNH R113078) (a). *Caiman crocodilus* (ZSM70.1937) (b). *Pandion haliaetus* (NSMT ASA1163) (c). Scale bar = 1 cm. ar, arytenoid; bh, basihyal; caj, cricoarytenoid joint; cb, ceratobranchial; cr, cricoid; eb, epibranchial; pcr, procricoid; pg, paraglossal; and tr, tracheal ring.

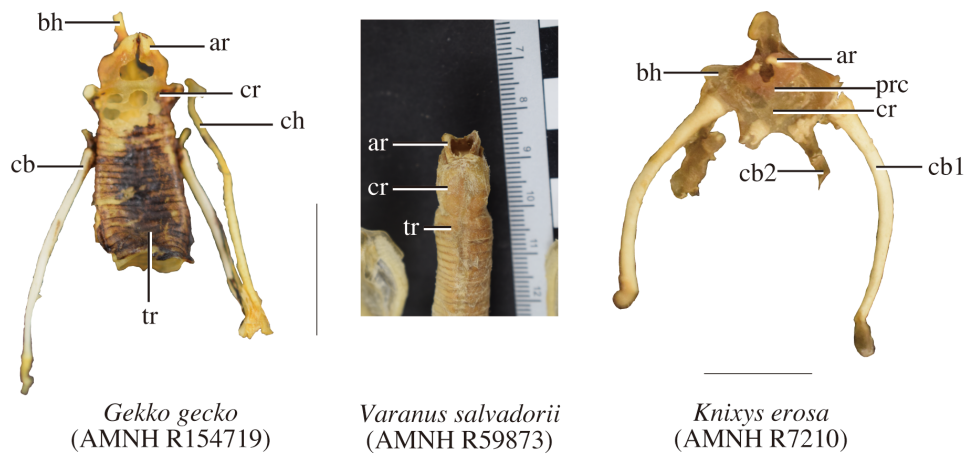


Extended Figure 3. Avian skeletons with hyolaryngeal apparatus. *Struthio camelus* (AMNH1501) (a). *Dinornis* sp. (AMNH7301) (b), *Nothoprocta* sp. (AMNH6502) (c), *Phoenixipterus roseus* (NSMT AS100), (d), and *Phoenixipterus porpureus* (AMNH2513) (e). Scale bar = 10 cm in (a), 1cm in (b), (c), (d), and (e). ar, arytenoid; bh, basihyal; cb, ceratobranchial; cr, cricoid; eb, epibranchial; pcr, procricoid; pg, paraglossal; paj,

procricoid-arytenoid joint; and tr, tracheal ring.



Extended Data Figure 4. Archosaur skeletons with hyolaryngeal apparatus in a phylogenetic framework. Not to scale. ar, arytenoid; bh, basihyal; cb, ceratobranchial; cr, cricoid; eb, epibranchial; pcr, procricoid; and tr, tracheal ring.



Extended Data Figure 5. Non-archosaur reptilian skeletons with hyolaryngeal apparatus.

Gekko gecko (AMNH R154719) (a). *Varanus salvadorii* (AMNH R59873) (b). *Knixys erosa* (AMNH R7210) showing partially-ossified arytenoids (c). Scale bar = 1 cm. ar, arytenoid; bh, basihyal; caj, cricoarytenoid joint; cb, ceratobranchial; cr, cricoid; ch, ceratohyal; eb, epibranchial; pcr, procricoid; and tr, tracheal ring.

VII. CONCLUSION

This thesis largely reveals new perspectives of tongue and larynx (hyolaryngeal apparatus) of archosaurs, using anatomy, network analysis, morphometrics, functional morphology, and evolutionary models. The chapter I summarizes the previous studies, and clarifies the problems to be solved. In the chapter II, the author conducts dissection of modern reptiles and birds, and network analysis of the obtained data. The results reveal the modular evolutions on the hyolaryngeal apparatus in reptiles and birds and ceratobranchial becomes important for Archosauria in terms of network centrality. In the chapters III to VI, a lot of fossil specimens were examined to know the evolution. In the chapter III, the author describes a new specimen of Goniopholididae, and discovered the first ceratobranchial of the group. Morphometrics and dissection of modern crocodylians demonstrate that ceratobranchial has evolved to be dorsal deflected and shortened for specialized respiration in aquatic environment in Neosuchia, including Goniopholididae and modern crocodylians. This study reveals that modern crocodylian respiratory system had already appeared in the early evolution of Neosuchia prior to postcranial modifications in the evolution toward

modern crocodylians. Broad rostrum of the new species also broadens ecological diversity of Goniopholididae as evidence for their success in the freshwater environment of the Late Jurassic. In the chapters IV and V, the author provides detailed descriptions of ceratobranchials of herbivorous dinosaurs, sauropods, ornithopods, ceratopsians, ankylosaurs (e.g. *Psittacosaurus*, *Styracosaurus*, *Plesiohadros*, and *Giraffatitan*) and quantitative comparisons in the course of herbivory in dinosaur evolution. The results demonstrate that ceratobranchial have been curved in neornithischians and sauropodiforms, and shortened and straight in ceratopsians. Furthermore, these herbivorous dinosaurs show distinctive osteological correlates for different hyolingual muscles among them. Therefore, the herbivorous dinosaurs have changed their hyoids in their early evolution and likely employed different lingual motions. In chapter VI, ankylosaur *Pinacosaurus* from the Upper Cretaceous Djadokhta Formation, Mongolia, show the best preserved hyolaryngeal apparatus among non-avian dinosaurs. In comparison with reptiles and birds, this is the first report of larynx and its vocalizing function in non-avian dinosaurs. Significantly, this oldest laryngeal fossil also first bridges the missing link between crocodylians and birds, and

sheds light on the evolution of the larynx and vocalization in Archosauria. In sum, hyolaryngeal apparatus of Archosauria has been significant in respiration, feeding, and vocalization in their evolution.

TABLES

[illegible]

Alligator mississippiensis	tongue	skull	mandible	basihyal	ceratobranchial	epibranchial	cricoid	arytenoid	trachea	coracoid	cervical vertebra	episternum	m. hyoglossus	m. geniohyoideus	m. branchiohyoideus dorsalis	m. branchiohyoideus ventralis	m. omohyoideus	m. episternobranchialis	m. episternobranchiotendineus	m. cricoarytenoideus	m. constrictor laryngius	m. intermandibularis	m. genioglossus	m. constrictor colli	m. constrictor profundus
tongue													1										1		
skull			1								1														
mandible		1												1	1				1			1	1	1	
basihyal					1											1		1		1					
ceratobranchial				1		1							1	1	1	1	1								
epibranchial					1										1		1								
cricoid								1	1											1	1				
arytenoid							1													1	1				
trachea							1																		
coracoid												1					1								
cervical vertebra		1																							1
episternum										1								1	1						
m. hyoglossus	1				1																				
m. geniohyoideus			1		1																				
m. branchiohyoideus dorsalis			1		1	1										1									
m. branchiohyoideus ventralis				1	1										1										
m. omohyoideus					1	1				1															
m. episternobranchialis				1								1													
m. episternobranchiotendineus			1									1													
m. cricoarytenoideus				1			1	1																	
m. constrictor laryngius							1																		
m. intermandibularis			1																						
m. genioglossus	1		1																						
m. constrictor colli			1																						
m. constrictor profundus											1														

Crocodylus siamensis

	tongue	skull	mandible	basihyal	ceratobranchial	epibranchial	cricoid	arytenoid	trachea	coracoid	cervical vertebra	episternum	m. hyoglossus	m. geniohyoideus	m. branchiohyoideus dorsalis	m. branchiohyoideus ventralis	m. omohyoideus	m. episternobranchialis	m. episternobranchiotendineus	m. arytenoideus	m. constrictor laryngius	m. intermandibularis	m. genioglossus	m. constrictor colli	m. constrictor profundus
Crocodylus siamensis	tongue												1										1		
	skull		1								1														
	mandible		1											1	1				1			1	1	1	
	basihyal				1											1		1							
	ceratobranchial			1		1							1	1	1	1	1	1							
	epibranchial				1										1		1								
	cricoid							1	1												1				
	arytenoid							1												1					
	trachea							1																	
	coracoid											1					1								
	cervical vertebra		1																						1
	episternum									1								1	1						
	m. hyoglossus	1			1																				
	m. geniohyoideus			1	1																				
	m. branchiohyoideus dorsalis			1	1	1										1									
	m. branchiohyoideus ventralis				1	1										1									
	m. omohyoideus				1	1				1															
	m. episternobranchialis				1	1						1													
	m. episternobranchiotendineus			1								1													
	m. arytenoideus							1																	
	m. constrictor laryngius							1																	
	m. intermandibularis			1																					
	m. genioglossus	1		1																					
	m. constrictor colli			1																					
	m. constrictor profundus										1														

Struthio camelus		tongue	skull	mandible	paraglossal	basihyal	ceratobranchial	epibranchial	urohyal	cricoid body	cricoid wing	arytenoid	procricoid	trachea	cervical vertebra	m. ceratoglossus	m. branchiomandibularis	m. geinoceratohyoideus	m. hyomandibularis	m. serpihyoideus	m. genioglossus	m. constrictor colli cervicalis	m. constrictor colli intermandibularis	m. cricohyoideus	m. ceratocricicoideus	m. basiarytenoideus	m. ceratohyoideus	m. constrictor glottidis	m. dilator glottidis	m. intermandibularis
	tongue			1											1					1										
	skull			1											1							1								
	mandible		1														1	1	1	1										1
	paraglossal	1				1										1					1									
	basihyal				1		1		1			1													1					
	ceratobranchial					1		1								1		1	1						1		1			
	epibranchial						1										1									1				
	urohyal					1																								
	cricoid body										1				1					1				1	1			1		
	cricoid wing									1		1		1										1	1				1	
	arytenoid					1						1	1													1		1		
	procricoid												1															1	1	
	trachea									1	1																			
	cervical vertebra		1																			1								
	m. ceratoglossus	1			1		1																							
	m. branchiomandibularis			1				1																						
	m. geinoceratohyoideus			1			1																							
	m. hyomandibularis			1			1																							
	m. serpihyoideus			1						1																				
	m. genioglossus	1			1																									
	m. constrictor colli cervicalis														1															
m. constrictor colli intermandibularis			1																											
	m. cricohyoideus					1				1																				
	m. ceratocricicoideus						1			1																				
	m. basiarytenoideus											1																		
	m. ceratohyoideus						1																							
	m. constrictor glottidis									1	1	1																		
	m. dilator glottidis										1	1																		
	m. intermandibularis			1																										

(Boga–Tomlinson 2000)

(Boga-Tomlinson 2000)

Gallus gallus

Gallus gallus	tongue	skull	mandible	paraglossal	basihyal	ceratobranchial	epibranchial	urohyal	cricoid body	cricoid wing	arytenoid	procricoid	trachea	m. ceratoglossus	m. branchiomandibularis a	m. branchiomandibularis c	m. hyoglossus rostralis	m. hyoglossus obliquus	m. stylohyoideus	m. serpihyoideus	m. interceratoideus	m. cricohyoideus	m. arytenoideus	m. constrictor laryngius	m. intermandibularis
tongue				1																					
skull			1																						
mandible		1													1	1			1	1				1	
paraglossal	1				1									1			1	1	1						
basihyal				1		1		1											1			1			
ceratobranchial					1		1							1							1				
epibranchial						1									1	1									
urohyal					1																				
cricoid body										1			1									1		1	
cricoid wing									1			1	1										1	1	
arytenoid												1											1		
procricoid										1	1														
trachea									1	1															
m. ceratoglossus				1		1																			
m. branchiomandibularis a			1				1									1									
m. branchiomandibularis c			1				1								1										
m. hyoglossus rostralis				1														1							
m. hyoglossus obliquus				1													1								
m. stylohyoideus			1	1	1																				
m. serpihyoideus			1																						
m. interceratoideus						1																			
m. cricohyoideus					1				1																
m. arytenoideus										1	1														
m. constrictor laryngius									1	1															
m. intermandibularis			1																						

tomberger & Meyers, 1989)

(Tomberger & Meyers, 1989)

Anatomical network analysis of hyolaryngeal apparatus in Archosauria Tables.

Table. Parameters of musculoskeletal network of five modern archosaurs

	N	K	D	C	L	H	Q
	Number of nodes	Number of connections	Density	Clustering Complexity	Average shortest path length	Heterogeneity	
<i>Chelydra</i>	43	64	0.071	0.203	3.262	0.934	0.459
<i>Alligator</i>	25	31	0.103	0.133	2.745	0.639	0.48
<i>Crocodylus</i>	25	32	0.107	0.167	2.7	0.668	0.476
<i>Struthio</i>	29	41	0.101	0.243	3.203	0.606	0.542
<i>Gallus</i>	25	33	0.11	0.36	3.53	0.588	0.559

PHYLOGENETIC DATASETS OF CROCODYLIFORMES

486 characters and 104 taxa

CHARACTERS

1 'Skull height, in posterior view (Clark 1994, ch3mod; Andrade & Bertini 2008a, ch02): 0. skull higher than wide, or subequal 1. skull evidently wider than high ',

2 'Skull geometry, relative position of tooth row, quadrate articular facet and occipital condyle (Wu & Sues 1996, 24mod; Sereno et al. 2003, ch46mod; Pol 2003, ch104mod; Turner & Buckley 2008, ch105mod): 0. tooth row and quadrate condyle aligned, both at a lower level than the occipital condyle 1. tooth row at a lower level than the quadrate condyle, which is aligned to the occipital condyle 2. tooth row quadrate and occipital condyle all aligned in the same plane 3. tooth row and occipital condyle aligned, but quadrate condyle at a slightly lower level 4. tooth row and quadrate condyle unaligned and quadrate at a lower level, but both below the occipital condyle 5. tooth row and quadrate condyle unaligned and tooth row at a lower level, but both below the occipital condyle ',

3 'Skull geometry, relative position of tooth row and occipital condyle (Wu & Sues 1996, 24mod; Sereno et al. 2003, ch46mod; Pol 2003, ch104mod; Turner & Buckley 2008, ch105mod): 0. unaligned, tooth row at a lower level than occipital condyle 1. tooth row and occipital condyle aligned in the same plane',

4 'Skull geometry, relative position of quadrate and occipital condyles (Wu & Sues 1996, 24mod; Sereno et al. 2003, ch46mod; Pol 2003, ch104mod; Turner & Buckley 2008, ch105mod): n0. unaligned, quadrate condyle at a lower level than the occipital condyle 1. quadrate and occipital condyles aligned in the same plane',

5 'Rostrum, length relative to the total skull length (Wu & Sues 1996, ch4mod; Ortega et al. 2000, ch3+4mod): 0. brevirostrine, rostrum length no more than 55% of the total length 1. mesorostrine, rostrum length shorter than 67% of the total length 2. sublongirostrine, rostrum length longer than 66% of the total length, but not longer than 70% 3. longirostrine, rostrum length longer than 70% of the total length ',

6 'ORD Rostrum, relation between height and width (Clark 1994, ch3mod): State (1) does not imply the rostrum will be tubular, although a tubular rostrum is most likely (1) in proportion. 0. wider than high, platyrostral 1. height and width subequal 2. higher than wide, oreinrostral',

- 7 'ORD Rostrum, relation with the skull at maturity, in dorsal view (Clark 1994, ch2):0. rostrum well defined, broadening abruptly at orbits 1. rostrum poorly defined, smoothly broadening and fitting the skull at orbits 2. rostrum poorly defined, as broad as skull or slightly wider, smoothly fitting the skull at orbits ',
- 8 'Rostrum, relation with the skull at maturity, in lateral view (Andrade et al., 2011): 0. rostrum smoothly fits the skull, skull roof progressing towards the tip of the snout at about the same level 1. rostrum smoothly decreases in height from skull, at least towards the mid-rostrum 2. rostrum and skull with a poor fit ',
- 9 'Rostrum, dorsal projection (Andrade et al., 2011):State (1) is not the hump-like boss seen in *Crocodylus acutus* (Brochu 1999; ch101). Instead, the whole rostrum bulges dorsally/anterodorsally. 0. absent, rostrum straight or low 1. present and evident, rostrum bulges dorsally, with nasals assuming an arched profile in lateral view',
- 10 'Ornamentation, bony surface sculpted with an anastomosed arrange of wrinkles and ridges, composing a vermiform-dendritic pattern (Ortega et al. 2000, ch01mod): Wrinkle is equivalent to groove sensu Ortega et al. 2000), but not sensu Buffrenil 1982; here, use of groove follows Buffrenil (1982), as elongated pits. 0. absent 1. present',
- 11 'Ornamentation, bony surface sculpted with elliptic to subpolygonal pits and grooves,composing a pitted pattern (Ortega et al. 2000, ch01mod):Groove sensu Buffrenil (1982) = elliptic pit. 0. absent 1. present ',
- 12 'Ornamentation, proportion between pits and grooves relative to the ornamented area, at late ontogeny (Andrade et al., 2011): 0. ornamentation dominated by pits, with grooves almost entirely absent 1. pits and grooves well represented on the skull, with grooves usually present (e.g., maxillo-jugal suture, frontal, dentary) late in ontogeny 2. ornamentation dominated by grooves',
- 13 ' Ornamentation, presence of pitted pattern on the postorbital bar, if skull sculpted (Clark 1994, ch25rev):n 0. absent 1. present',
- 14 'Ornamentation, presence of pitted pattern on the jugal (Andrade et al., 2011):0. absent 1. present ', 15 'Ornamentation, distribution of pitted pattern on the jugal surface (Andrade et al., 2011): 0. evident ornamentation only occurs at the anterior ramus 1. evident ornamentation occurs on the anterior and posterior rami',
- 16 'Ornamentation, presence of pitted pattern on the quadratojugal (Pol 1999a, ch161; Pol & Apesteguia 2005, ch144; Turner & Buckley 2008, ch145): 0. absent 1. present, restricted to the distal end',

- 17 'Ornamentation (mandible), presence of strong pitted pattern on surangular-articular (Andrade et al., 2011):0. absent 1. present',
- 18 'Ornamentation (mandible), presence of strong pitted pattern on angular (Andrade et al., 2011): 0. absent 1. present ',
- 19 'Ornamentation (dermal armour), type of sculpture (Ortega et al. 2000, ch111): 0. vermiform-dendritic pattern 1. pitted pattern',
- 20 'Sculpturing, palatal surface of maxilla (Ortega et al. 2000, ch02):0. absent, palatal surface smooth. 1. present, palatal surface ornamented with ridges',
- 21 'Sculpturing, presence on the palatal surface of pterygoid (Clark 1994, ch40):State (1) is present in Protosuchidae. 0. absent, surface smooth 1. present ',
- 22 'Neurovascular foramina, presence of an expanded network of openings on the dorsal surface of the rostrum and ventral-lateral surfaces of the mandible (Andrade et al., 2011):0. absent, neurovascular openings limited to a single line, near the ventral margin of the rostrum and dorsal margin of dentary 1. present at least at the premaxillae, maxillae and dentaries ',
- 23 'Neurovascular foramina (premaxilla), overall distance to the alveolar margin and teeth (Andrade & Bertini 2008, ch17part):Note that coding changes substantially from the original (Andrade & Bertini 2008, ch17), and that complementary characters on neurovascular foramina are present. 0. ventralmost foramina reach area next to the alveolar margin, close to teeth 1. ventralmost foramina clearly apart from the alveolar margin, distant to the teeth ',
- 24 'Neurovascular foramina (anterior maxilla), overall distance to the alveolar margin and teeth (Andrade & Bertini 2008, ch17part):State (0) is putative apomorphy of derived eusuchians, but is also present in other mesoeucrocodylian clades. (1) is a common condition in Crocodylomorpha, occurring even in basal eusuchians. 0. ventralmost foramina reach area next to the alveolar margin, close to teeth 1. ventralmost foramina clearly apart from the alveolar margin, distant to the teeth',
- 25 'Neurovascular foramina (mid maxilla) forming a strongly arched line at mid-rostrum, at maturity (Andrade et al., 2011):State (1) is putative apomorphy of Araripesuchus 0. absent, line of foramina follows the overall outline of the margin 1. present, ample area of smooth margin ventral to the arched line of foramina',
- 26 'Neurovascular foramina (posterior maxilla), distribution on the alveolar margin (based on Andrade & Bertini 2008, ch17):State (1) is putative apomorphy of

goniophilidids. 0. ventralmost foramina not high on the maxillary margin, either close or next to the alveoli 1. ventralmost foramina high on the maxilla (up to twice the distance from other foramina), very distant to the alveoli',

27 'Neurovascular foramina (dentary), distribution of neurovascular foramina relative to the alveolar margin, in non-tubular snouted forms (Andrade et al., 2011):n0. foramina form a simple straight to ventrally-arched line1. foramina form a sinusoid line, following the dorsal fluttings, when fluttings are presentn',

28 'Foramen at premaxillo-maxillary suture in lateral view (Pol 1999, ch149; Ortega et al. 2000, ch13rev; Turner & Buckley 2008, ch135; Sereno & Larsson, ch84mod): 0. absent 1. present ',

29 'Perinarial crests, presence and morphology (Andrade et al., 2011):State (1) is present within Goniopholididae. 0. absent, surface even or bearing a perinarial fossa 1. present as well defined and distinct ridges, cornering the lateral to posterior borders of the naris ',

30 'Lachrymal crest anterior to orbit, presence (Young & Andrade 2009):Lachrymal refers to the lachrymal fossa, immediately anterior to the orbit, not the lachrymal bone. State (1) is a putative apomorphy of Metriorhynchidae. 0. absent 1. present',

31 'ORD Naris, orientation in the sagittal plane (Clark 1994, ch6mod; Sereno et al. 2003, ch2+ch7): Assignment of dyrosaurids and most goniopholidids to state (2) is not consensual, but these forms contrast with the morphology seen in Pelagosaurus, Sarcosuchus and Sebecus, and therefore should not be coded as (1). In some goniopholidids, the dorsal orientation can be somewhat obscured by the presence of perinarial crests. However, the narial vestibulum is dorsally oriented, widely deviating from the typical antero-dorsal. 0. not dorsalized, either anterior or lateral, but nasal cavity not visible in dorsal view 1. antero-dorsal 2. dorsal',

32 'Naris, shape of narial opening in anterodorsally or dorsally oriented naris (not considering the internarial bar, when present) (Andrade et al., 2011): State (1) based on Salisbury et al. (1999), for Goniopholis simus. 0. subcircular, approximately as long as wide 1. heart-shaped 2. keyhole-shaped, subcircular anteriorly, but elongated and subquadratic posteriorlyn3. highly ellipticn4. wider than longn',

33 'Naris, distance from the anteriormost edge of premaxillae (based on Clark 1994, ch5mod; Ortega et al. 2000, ch17mod):Please note differences from the original codings, particularly Clark (1994). In the current dataset, (1) is putative apomorphy of crown

Eusuchia, and is paralleled in Cricosaurus. 0. narial opening is close to the anterior tip of the snout, regardless of the presence of contact between anterior rami of premaxillae, or the orientation of naris 1. narial opening is distant to the anterior tip of the snout, with anterior rami of premaxillae meeting broadly anterior to naris ',

34 'Naris, presence of an anterior narial notch (Andrade et al., 2011): 0. absent; 1. present',

35 'Naris, presence of lateral narial notch (Pol 1999a, ch135; Turner & Buckley 2008, ch123): 0. absent 1. present',

36 'Naris, composition of dorsal/posterior border (Pol 1999a, ch136mod; Pol 2003, ch124; Turner & Buckley 2008, ch124mod): 0. formed mostly by the nasals 1. formed mostly by premaxilla, or nasal excluded from dorsal/posterior border',

37 'Naris, presence and morphology of the internarial bar, in late ontogeny (Clark 1994, ch66mod; Sereno et al. 2003, ch7mod): 0. absent, external nares confluent 1. present, not arched dorsally/anterodorsally and with nasal contribution 2. present, evidently arched dorsally and with nasal contribution 3. present, arched dorsally and with no nasal contribution ',

38 'Naris, projection of the internarial bar relative to the main body of premaxilla and narial opening, in late ontogeny (Andrade et al., 2011): 0. does not project anterior to the main body of premaxilla 1. strongly projected anteriorly from narial opening, anterior to main body of premaxilla',

39 'Naris, presence of dorsal projection of anterior rami of premaxillae, and proportional participation in the internarial bar (Clark 1994, ch4rev): 0. premaxillae does not project, or projection is incipient and poorly defined, feebly contributing to internarial bar 1. premaxillae project from the medial contact of anterior rami, composing at least the base of the internarial bar, or an evident bar-like projection if bar is absent ',

40 'Perinarial fossa, presence and extent (Sereno et al. 2003, ch13mod; Turner & Buckley 2008, ch226; Sereno & Larsson 2009, ch82mod): 0. absent or incipient 1. present, small, shallow and mostly limited to the ventral part of the naris 2. present, extremely well-developed and deep, widely extending lateral to the naris',

41 'Postnarial fossa, presence (Andrade et al., 2011): State (1) is putative apomorphy of derived goniopholidids, but still poorly sampled in Neosuchia. 0. absent 1. present',

42 'Intranarial fossa, presence at the lateral walls, inside narial cavity, at the vestibulum (Andrade et al., 2011): State (1) is putative apomorphy of Metriorhynchidae. The

internarial fossa is an additional chamber that creates an internal border of the external naris; must not be mistaken with the naso-oral fossa, or with the perinarial fossa. 0. absent 1. present ',

43 'Antorbital cavity, presence (Clark 1994, ch67mod):0. absent 1. present',

44 'Antorbital cavity, presence of internal antorbital fenestra (Clark 1994, ch67mod):n0. absent; 1. present, connecting with internal sinus',

45 'Antorbital cavity, relation between external and internal antorbital fenestrae (Andrade et al., 2011): 0. external and internal fenestrae subequal or not distinguishable1. external fenestra larger than internal fenestra, but no more than twice its area2. external fenestra much larger than internal fenestra, or external fenestra present and internal fenestra closed',

46 'Antorbital cavity, shape (Gasparini et al. 2006, ch246): 0. subcircular to subpolygonal1. strongly elliptic, length at least twice its height, and obliquely orientated at approximately 30 degrees with respect to the longitudinal axis',

47 'Antorbital cavity, size (area) of external antorbital fenestra, relative to the orbit (Clark 1994, ch67mod): 0. small, less than 50% the orbit area, or antorbital cavity absent; 1. large, almost as large as the orbit',

48 'Antorbital cavity, size (length) of internal antorbital fenestra relative to the orbit (Clark 1994, ch67mod):n0. small, internal fenestra is less than 25% of the length of the orbit, or internal fenestra is absent; 1. medium, internal fenestra is approximately 25-50% of the length of the orbit2. large, internal fenestra is more than 50% of the length of the orbit3. very large, internal fenestra approximately the same size as the orbit',

49 'Antorbital cavity, nasal participation in the internal fenestra (Ortega et al. 2000, ch70rev):n0. absent, nasals excluded from the internal fenestra by a maxillo-lachrymal contact1. present, nasals broadly reach the internal fenestra (or reach deep into the fossa, if the fenestra is closed)',

50 'Antorbital cavity, jugal participation in the external fenestra (Wu & Sues 1996, ch14rev; Ortega et al. 2000, ch71rev):nShould be scored alongside the characters regarding the antorbital fenestra, not jugal, to facilitate cross-checking of inapplicable states due to the absence of the antorbital fenestra.n0. absent, jugal excluded from the external fenestra by a maxillary-lachrymal contact1. present, jugal takes part in the external fenestra',

- 51 'Antorbital cavity, position relative to the rostrum (Andrade et al., 2011):State (1) is putative apomorphy of *Thalattosuchia*.n0. closer to the orbit than to the alveolar margin 1. closer to the alveolar margin than to the orbitn',
- 52 'Antorbital cavity, position relative to the orbit (Andrade et al., 2011):State (1) is putative apomorphy of *Neosuchia*.n0. close to the orbit, with lachrymal narrow between orbit and antorbital cavityn1. distant to the orbit, with lachrymal wide between orbit and antorbital cavityn',
- 53 'Lachrymal fossa, presence (Andrade et al., 2011):0. absent, bony surface completely plain or convex 1. present as a small and shallow depression at the anteriormost corner of the orbit, but with most bony surface plain or convex 2. present and fully developed, with most bony surface anterior to orbit concave ',
- 54 'Rostrum, orientation of external surface of premaxillae and maxillae (Pol 1999: ch153mod; Turner & Buckley 2008, ch139mod):0. premaxillae and maxillae face laterally 1. rostrum with ventral region facing laterally to ventrolaterally, and dorsal region facing dorsolaterally',
- 55 'Rostrum, morphology of the external surface of premaxilla and maxilla (Andrade et al., 2011):0. rostrum with a continuous surface, either convex or plain 1. rostrum with distinct ventral and dorsal surfaces, plain and separated by a somewhat distinct anteroposterior ridge or edge',
- 56 'Rostrum, presence of constriction at the premaxillae-maxillae suture, in dorsal view, either forming a notch, a shallow concavity or a narrow slit (Andrade et al., 2011): 0. absent; 1. present',
- 57 'Rostrum, type of constriction at the premaxilla-maxilla suture (Clark 1994, ch9mod):n 0. narrow slitn1. wide, poorly-defined concavity, or not constricted at alln2. well-definednotch',
- 58 'Rostrum, morphology of notch at the premaxillae-maxillae suture (Andrade et al., 2011):0. notch absent, or poorly encasing the tooth (< 50% of crown perimeter), usually only part of the lingual surface of the crown 1. notch closely encasing tooth (c. 50%-60%), at least the lingual surface of the crown 2. notch strongly encase tooth in a scabbard-like notch (c. 70%), including most of lingual/labial surfaces of the crown ',
- 59 'Rostrum, presence of a posterodorsal process of premaxilla, at contact with maxilla and nasal (Pol, 1999a, ch138; Turner & Buckley 2008, ch125):n0. absent; 1. present, extending posteriorly, wedging between maxilla and nasalsn',

60 'Rostrum, morphology of contact at premaxillae-maxillae suture, in dorsal/lateral views (Andrade et al., 2011):Based on Gasparini et al. (1991, ch3) and description of Hamadasuchus (Larsson & Sues, 2007). The anterior process may be wedge-shaped, or not. 0. simple, suture not interdigitating 1. complex, with an anteriorly directed process from maxilla fitting the premaxilla ',

61 'Rostrum, presence of wedge-like process of maxilla to the premaxilla, at premaxilla-maxilla suture (Gasparini et al. 1991, ch3; Turner & Buckley 2008, ch213):State (1) is a putative apomorphy of Peirosauridae, but note that Hamadasuchus also have an anteriorly directed process, only not wedge-shaped, and the same suture is unknown in Sebecus, although the suture was reconstructed by Colbert (1946) as lacking such process.n0. absent 1. present, wedge-like, anteriorly directed and fitting the premaxilla',

62 'Premaxillae anterior to naris, morphology (Clark 1995, ch5mod): State (0) is putative apomorphy of Notosuchidae + Sphagesauridae; (1) of Araripesuchus +Libycosuchus. 0. anterior rami of premaxillae do not meet medially, anterior/ventral to naris, with both premaxillae in contact only through palatine rami 1. anterior rami of premaxillae meet anterior to naris, through a very narrow band, but not projecting vertically 2. anterior rami of premaxillae broadly meet anterior to naris, forming a vertical wall, which may be straight or slightly convex ',

63 'Premaxilla, type of contact with maxilla (Clark 1994, ch8): State (1) is a putative apomorphy of Crocodyliformes. 0. premaxilla loosely overlies maxilla on face 1. premaxilla and maxilla suture together along butt joint ',

64 'Premaxillae, lateral projection relative to maxillae (Andrade et al., 2011): 0. absent, premaxillae subequal or narrower than maxillae at anterior to mid rostrum 1. present, premaxillae clearly wider than maxillae at anterior to mid rostrum',

65 'Premaxillae, general profile in dorsal view (Andrade et al., 2011): State (1) is putative apomorphy of Metriorhynchidae; (2) of Sphagesauridae; (4) of derived goniopholidids. 0. round to triangle-shaped, premaxillae smoothly fitting the rostrum 1. lanceolate, premaxillae smoothly fitting the rostrum 2. subquadratic, premaxillae smoothly fitting the rostrum 3. paddle-shaped, expanded laterally 4. axe-shaped, expanded laterally ',

66 'Premaxillae, presence of a subelliptic naso-oral fossa (=incisive foramen, fossa premaxillaris) at medial contact of ventral rami (Brochu 1999, ch124part): 0. absent, premaxillae fully in contact medially along the palaten1. present as a discrete fossa or

foramen, less than half the greatest width of premaxillaen2. large, more than half the greatest width of premaxillaen',

67 'Premaxillae, position of the naso-oral fossa in the palatine rami, relative to the alveolar margin (Brochu 1997, 1999, ch153mod; Turner & Buckley 2008, ch270mod):?0. completely situated far from premaxillary tooththrow, at the level of the second or third alveolus, or posterior 1. abuts premaxillary tooththrow 2. projects between first premaxillary teeth ', 68 '68. Premaxillae, contribution of maxillae to the naso-oral fossa at medial contact of ventral rami (Clark 1994, ch7rev; Brochu 1999, ch124part):n0. absent, premaxillae contact medially, posterior to the naso-oral foramenn1. present, maxillae take part at least on the posterior border of the foramen',

69 'Premaxillae, shape of naso-oral fossa (Andrade et al., 2011): 0. oblong, leaf-like 1. teardrop-shaped to slit-like 2. complex, triangular, arrow-headed or fleur-de-liz 3. diamond-shaped 4. elliptic and elongated 5. subcircular ',

70 '70. Premaxillae, shape of naso-oral fenestra (Andrade et al., 2011): 0. both anterior and posterior ends tapering to an acute end 1. tapering anteriorly only, with round or complex distal end 2. anterior and posterior ends rounded, not tapering ',

71 'Premaxilla, presence of foramen in the perinarial depression (Gasparini et al. 2006, ch237; Turner & Buckley 2008, ch237): 0. absent 1. present',

72 ' ORD Nasals, length (Clark 1994, ch13+14): 0. poorly elongated, anteriorly limited by the maxillae only 1. elongated, contacting the maxillae and premaxillae, but not reaching the naris 2. evidently elongated, taking part in the naris',

73 ' ORD Nasals, morphology in dorsal view (Andrade & Bertini 2008a, ch21): State (2) is present in Simosuchus. 0. triangular, lateral margins strongly confluent anteriorly 1. rectangular or subrectangular, lateral marginsmostlyparallel,orlateral margins poorly confluent anteriorly 2. triangular, lateral margins diverging anteriorly ',

74 ' Nasals, general structure (Andrade et al., 2011): 0. flattened 1. dome-like ',

75 ' Nasals, dorsal surface close to the posterior end (Andrade et al., 2011): State (2) is based on Peng & Shu (2005), and shared by Hsisosuchus and Calsoyasuchus. 0. continuous, lacking a medial groove or trench 1. slightly concave, forming a shallow and poorly defined depression, anteroposteriorly oriented 2. deeply trenched, with a steep longitudinal depression at midline',

76 ' Nasals, morphology of lateral border, posterior to external nares, in dorsal view (Pol 1999, ch140mod; Pol & Apesteguia 2005, ch127mod):0. laterally concave 1.

straight or convex',

77 ' Nasals, fusion at maturity (Gasparini et al. 2006, ch257; Sereno & Larsson 2009, ch10): State (1) is putative apomorphy of Dyrosauridae, but is also present in Mahajangasuchidae.n0. absent, nasals unfusedn1. present, nasals at least partially fusedn',

78 ' Maxilla, participation in the orbit (Andrade 2005, ch16; Andrade & Bertini 2008, ch15) :0. absent, excluded from the orbit by lachrymal-jugal contactn1. present, maxilla takes part in the orbit',

79 ' Maxilla, morphology of ventral margin (Wu & Sues 1996, ch29mod; Martinelli 2003, ch24mod; Turner & Buckley 2008, ch107mod): Note the different coding from previous works. (1) appears as the most common condition in Mesoeucrocodylia. Condition (1) implies that the smooth surface must extend for at least most of the maxillary ventral margin. 0. not distinct from the remaining surface of maxilla, slightly convex 1. maxillae with a distinct ventral surface alongside the alveolar margin, smooth and mostly plane',

80 ' Maxilla, projection of ventral margin in lateral view (Ortega et al. 2000, ch21mod): 0. ventral maxillary margin is straightn1. ventral maxillary margin festooned, being convex and concave at locations,nassuming a sinusoidal profilen2. ventral maxillary margin is overall convex, from contact with premaxilla to contactnwith jugaln',

81 'Maxilla, projection of ventral margin in dorsal view (based on Ortega et al. 2000, ch130; Pol & Apesteguia, 2005, ch171): 0. maxilla does not project laterally at all, and is narrow throughout 1. maxilla expands laterally in locations (coincident with festooning waves, when present), with maxilla sinusoidal in dorsal view 2. maxilla is wide throughout, with no flutting prominent in dorsal view',

82 ' Maxilla, number of waves, when festooning present (based on Clark 1994, ch79; Ortega et al. 2000, ch21):n0. a single clearly identifiable wave is present, at the anterior section of the maxilla, with ventral maxillary margin poorly sinusoidaln1. two major waves clearly identifiable, separated by an evident concave area, with ventral maxillary margin strongly sinusoidal and a corresponding dorsally directed wave on the dorsal edge of the dentaryn',

83 ' Maxilla, lateral exposure of occlusal pit for the 11th dentary tooth, at maturity (Andrade et al., 2011): 0. not exposed laterally, dentitions may overbite or interlock, but lateral wall of occlusal pit is closed 1. laterally open, with occusal surface exposed as a

shallow notch,

84 ' Maxilla, position of largest alveolus (Ortega et al. 2000, ch156mod): 0. largest alveolus is the third or anteriorn1. largest alveolus is the fourth or posterior',

85 ' Maxilla, presence of multiple cecal recesses at the surface within narial canal (based on Witmer 1995; Brochu 1997, ch148):State (1) is putative apomorphy of *Crocodylus* + *Mecistops*.n0. absent, surface imperforaten1. present',

86 ' Maxilla, presence of lateral fossa/fossae next to the alveolar margin (Andrade et al., 2011):nCharacters tests the putative homology between maxillary fossae found in goniopholidids, hsisosuchids and *Rugosuchus*.n0. absent, maxillary bony surface convex or flatn1. present',

87 ' Maxilla, presence of multiple fossae along most of its lateral face (Wu et al. 2001b): 0. absent; 1. present',

88 . Maxilla, presence of a shallow fossa at maxilla-jugal contact (Andrade et al., 2011) :n0. absent; 1. present',

89 . Maxilla, presence of a maxillary depression, next to the maxilla-jugal contact (Wu et al. 1997, ch127; Sereno et al. 2003, ch14; Lauprasert et al. 2007, ch97mod): 0. absent; 1. present',

90 . Maxilla, morphology of anterior border of maxillary depressions (Andrade et al., 2011):n0. shallow, anterior edge of depression usually poorly defined, or maxillary depression is absent; 1. deep, anterior border always well-defined relative to dermal surface of maxilla',

91 '91. Maxilla, extent of contact with nasal (Andrade et al., 2011):n0. small sutural contactn1. extensive contact',

92 . Maxilla, presence of an evident posteromedial process between lachrymal and nasal (Brochu 1999, ch93): 0. absent, maxillary posteromedial process no more than feeblen1. present, maxilla sends an evident posteromedial process within lachrymal',

93 . Maxilla, presence of broad contact with prefrontal (based on Clark 1994, ch11; and in Ortega et al. 2000, ch165part): 0. maxilla and prefrontal do not contact at all, or with a feeble contactn1. present and evident, maxilla extensively contacts prefrontal',

94 . Lachrymal, relative proportions at maturity (Andrade et al., 2011): 0. subquadratic, or shorter than widen1. longer than wide',

95 '95. Lachrymal, proportional length (Andrade et al., 2011):n0. short to poorly elongated, AP/ML index closer to 2, or smallern1. proportionally long, AP/ML index

closer to 3, or higher',

96 . Lachrymal, exposure in dorsal aspect (Andrade et al., 2011): 0. absent, lachrymal is vertically oriented and only exposed in lateral aspectn1. present, either vertical or horizontal',

97. Lachrymal, presence of a posteroventral process (Andrade et al., 2011):n0. absent, lachrymal does not progress below orbit, or barely projects through a broad and short wedgen1. present, progress below orbit as an acute processn2. present, progress below orbit as a truncated processn',

98 . Lachrymal, extent of contact with nasal (based on Clark 1994, ch11+12; as in Ortega et al. 2000, ch165rev): 0. nasal and lachrymal do not contact at all, or with a feeble contactn1. present and evident, lachrymal extensively contacts nasal',

99 . Prefrontal-lachrymal crest dorsal to orbit, presence and morphology (Brochu 1999; ch144mod): See also Poe (1977) and Norell (1988). 0. absent, or incipient and laterally directed, as a simple edge 1. present and evident, projecting dorsally and short, only slightly progressing anterior to the orbit 2. present and evident, projecting dorsally and long, broadly progressing on the rostrum as very prominent divergent crests',

100 . Transverse rostral crest, presence (Andrade et al., 2011): 0. absent; 1. present',

101 . Transverse frontal crest anteromedial to the orbits, presence (Andrade et al., 2011): 0. absent, dorsal skull surface plain or bearing a sagittal crestn1. present, crescent-shaped (facing anteriorly), and transecting the skull from orbit tonorbitn',

102 . Frontal sagittal crest, presence (Clark 1994, ch22mod, part):n0. absent1. present',

103 '103. Parietal sagittal crest, presence (Clark 1994, ch22part):nMust not be mistaken for a narrow parietal between the supratemporal fossae.n0. absent; 1. present',

104 '104. Crests margining the border of the supratemporal fossae, dorsally projected (Andrade et al., 2011): State (1) is also described as "margins uprolled" (see Mook, 1964). 0. absent, or present only in part of the perimeter 1. present around the full perimeter ',

105 '105. Supratemporal fenestra, presence of a shallow fossa at its anteromedial corner (Brochu 1999, ch92rev; Turner & Buckley 2008, ch265rev):0. absent, anteromedial corner of supratemporal fenestra smooth 1. present',

106 '106. Supratemporal fenestra, size proportional to the orbit at maturity (Clark 1994, ch68mod; Sereno et al. 2003, ch4mod; Andrade & Bertini 2008, ch38mod):Size refers to fenestra only, not fossa; based on major axis of the fenestra and antero- posterior axis

of orbit 0. clearly smaller than the orbit 1. fenestra subequal to the orbit 2. supratemporal fenestra larger than orbit',

107 '107. Supratemporal fossa, size proportional to the orbit at maturity (based on Clark 1994, ch68; Brochu 1999, ch87; Ortega et al. 2000, ch70): 0. clearly smaller than the orbit, or fossa closed by skull table elements 1. fossa subequal to the orbit 2. supratemporal fossa larger than orbit ',

108 '108. Supratemporal fossa, relation with surrounding dermal bones of skull roof (Norell 1988, ch9mod; Brochu 1999, ch87mod): 0. dermal bones of skull roof do not overhang rim at maturity, or slightly overhang rim at part of the external fenestra 1. dermal bones of skull roof consistently overhang rim of supratemporal fenestra around the entire edge, near maturity 2. dermal bones of skull roof overhang rim of supratemporal fenestra near maturity, closing or nearly closing the fenestra during ontogeny',

109 . Supratemporal fossa, presence of a main axis (Andrade & Bertini 2008a, ch36): 0. main axis indistinct, or poorly distinct 1. main axis evident and much longer than secondary axis ',

110 '110. Supratemporal fossae, orientation of the main axis at late ontogeny (Andrade & Bertini 2008a, ch37): 0. both axis diverge anteriorlyn1. both axis paralleln2. both axis converge anteriorlyn',

111 . Supratemporal fossae, overall shape (Andrade et al., 2011): 0. elliptic 1. square-shaped to subrectangular 2. triangle-shaped, axis converging medially 3. circular 4. triangle-shaped, axis converging anteromedially ',

112 . Supratemporal fossae, angle between posterolateral process of the frontal and the intertemporal bar (Wilkinson et al. 2008, ch26mod; Young & Andrade 2009, ch26mod): See diagrammatic explanation for this character in Wilkinson et al. (2008: p.1311, Fig. 4). 0. angle of c. 90 degrees, with anteromedial corner of the supratemporal fossae mostly rounded 1. angle of c. 50 degrees, with anteromedial corner of the supratemporal fossae acute, wedge-like',

113 '113. Supratemporal fossae, shape of medial borders (Andrade et al., 2011): n0. convex, so the intertemporal bar has a double-concave profile1. borders straight, paralleln2. straight, either convergent or divergent',

114 '114. Supratemporal fossa, presence of foramina on the medial parietal wall (Norell 1988, ch51, Brochu 1999, ch104): n0. absent, wall imperforaten1. present, wall bearing

foramina',

115 '115. Skull roof at orbits, general morphology of periorbital elements (frontal, postorbital, palpebral) (Andrade et al., 2011): 0. overall level with each other and with the remaining skull table 1. lateral processes of frontal arched laterodorsally, with palpebral and postorbital curved dorsally',

116 '116. Skull roof, alignment of parietal, frontal and nasals in a steep angle (Andrade et al., 2011): 0. absent; 1. present',

117 '117. Supratemporal skull roof (posterior to orbit), general proportions (Andrade et al., 2011): For the purposes of scoring this character, skull roof limits are set as follows: postorbitals (anterior, lateral); parietal/supraoccipital (posterior). Always considered dorsal margin only, not anterior/lateral/posterior. 0. about as long as wide 1. clearly longer than wide (at least 1.5x) ',

118 '118. Supratemporal skull roof, dorsal surface (Clark 1994, ch24): 0. surface complex 1. flat skull table present, formed by flattened and levelled surfaces of frontal, postorbital, squamosal and parietal ',

119 . Supratemporal skull roof, dorsal curvature and elongation of squamosal prongs, at maturity (Brochu 1999, ch140): 0. with broad curvature and short squamosal prongs 1. with nearly horizontal sides and significant squamosal prongs',

120 . Supratemporal skull roof, morphology of frontoparietal suture (Brochu 1999, ch86): 0. concave anteriorly, `V` or `U-shaped` 1. transverse to the skull, either straight or complex 2. concave posteriorly, `V` or `U-shaped` ',

121 '121. Supratemporal skull roof, position of frontoparietal suture at medial line of skull, relative to the orbit (Andrade et al., 2011): 0. frontoparietal suture is evidently posterior to orbits 1. frontoparietal suture is at a very anterior position, almost medial to posteriormost border of the orbits, always as a straight line transecting most of the skull roof, and frontal-postorbital contact is extremely reduced',

122 '122. Supratemporal skull roof, position of frontoparietal suture at medial line of skull, relative to the postorbital bars (reformulated from Clark 1994, ch23mod; Brochu 1999, ch81; Buckley & Brochu 1999, ch81): 0. distal margin of frontal is medial to the (dorsal end of) postorbital bars, or slightly anterior 1. distal margin of frontal is posterior to the postorbital bars, but not reaching the mid skull roof 2. distal margin of frontal is posterior to the postorbital bars, frankly reaching into the intertemporal bar and mid skull roof',

123 '123. Supratemporal skull roof, morphology of the postorbital (=anterolateral) corner of skull roof, in dorsal view (Clark 1994, ch29mod): 0. distinct anterior (or anterolateral) and lateral edges, separated by a round to acute anterolateral corner, or a projecting process 1. anterior and lateral edges, separated by a distinct anterolaterally facing edge 2. anterior to lateral edges continuous, curved, without an anterolaterally projecting edge, corner or process '

124 '124. Supratemporal skull roof (parietal and squamosals), posterior extension of its posterior margin over the occipital surface (Andrade et al., 2011):n0. absent or feeble1. present and evident',

125 '125. Prefrontal, lateral projection (Gasparini et al. 2006, ch247): 0. small to medium, not overhanging the orbit 1. extremely enlarged, overhanging the orbit',

126 '126. Prefrontals, extension of posterior end (Andrade et al., 2011): 0. short, limited to the anteromedial border of the orbit, with frontal reaching the medial to posteromedial border of the orbit 1. long, composing the anteromedial and medial borders of the orbit, with frontal reaching orbit medially and posteromedially 2. very long, reaching the posteromedial borders of the orbit, with frontal reaching orbit posteromedially only ',

127 '127. Prefrontal pillar, presence of contact between prefrontal descending process and palatine ascending process (Clark 1994, ch15part; Andrade & Bertini 2008, ch27):n0. absent; 1. presentn',

128 '128. Prefrontal pillar, structure at contact between prefrontal and palatine processes (Clark 1994, ch15part; Andrade & Bertini 2008, ch27):n0. small contact arean1. robust contact suture',

129 . Prefrontal pillar, morphology of descending process of prefrontal (Ortega et al. 2000, ch30part; Turner & Buckley 2008, ch182part):n0. descending process transversely expanded, with the lateromedial lamina well developed and anteroposterior lamina small or absent; 1. descending process longitudinally expanded, with the anteroposterior lamina well developed and lateromedial lamina small or absent',

130 . Prefrontal pillar, morphology of ascending process of palatine, when pillar complete (Ortega et al. 2000, ch30part; Turner & Buckley 2008, ch182part):n0. ascending process transversely expandedn1. ascending process columnar, or anteroposteriorly elongatedn',

131 . Prefrontal pillar, morphology of medial process (Brochu 199, ch136):n0.

expanded dorsoventrally 1. expanded anteroposteriorly',

132 . Frontals, fusion of main body at maturity (Clark 1994, ch21mod): 0. not fused, and a medial suture fully persists in late ontogeny, with frontals paired 1. frontals are completely fused into a single element, or at least the main body is completely fused',

133 . Frontal, width relative to the total skull width, at maturity (Andrade et al., 2011): 0. narrow, c. 1/5th of skull width, or narrower 1. wide, c. 1/3rd of skull width, or more',

134 . Frontal, proportional width of main body (between orbits) relative to width of the supratemporal skull roof, at maturity (Andrade et al., 2011): 0. narrow, usually 20-30% of the width of the skull roof 1. wide, usually 40-50% of the width of skull roof',

135 . Frontal, general geometry (Brochu 1997, ch103mod; Pol et al. submitted, ch103): In state (1), orbit borders may be upturned without constituting a crest; crests may be present in species with a flat frontal (e.g., *Goniopholis simus*). 0. essentially flat, lateral margins flush with skull surface 1. concave, medial borders of the orbit upturned, forming ridged orbital margins',

136 . Frontal, morphology of anterior process (Andrade et al., 2011): 0. wide throughout 1. wide posteriorly and tapering anteriorly, wedge-like to triangle-shaped 2. narrow throughout, as a distinct projection',

137 . Frontal, morphology of anteriormost border of anterior process (Andrade et al., 2011): 0. truncated 1. wedge-like, either broad or acute',

138 . Frontal, medial surface (Andrade et al., 2011): State (1) is putative apomorphy of *Goniopholis*, but may be present in other goniopholidids. 0. frontal is continuous, from anterior margin to posterior end 1. frontal is divided into two plain surfaces, being the anterior at a slightly more ventral level than the posterior',

139 . Frontal, presence of a tuberosus intumescent projection on the medial line, between the orbits (Andrade et al., 2011): Based on description by Andrade & Hornung (submitted). State (1) is present in *Goniopholis*. 0. absent 1. present, well defined',

140 '140. Frontal, extension of anterior margin at late ontogeny (Andrade et al., 2011): 0. short, does not progress anterior to the orbits 1. long, progress anterior to the orbits',

141 . Frontal, participation in the primary medial border of orbit, at dorsal skull roof (Andrade et al., 2011): Based on Salisbury et al. (1999), Schwarz (2002), and Andrade & Hornung (submitted). 0. extensive participation in the orbit 1. excluded from the orbit by prefrontal-postorbital contact, or participation is very restricted',

- 142 . Frontal (anterior process), position relative to tip of prefrontal (Serenio et al. 2001, ch27; Turner & Buckley 2008, ch238): 0. ends evidently posterior to tip of prefrontals 1. reach or barely surpass the anteriormost tip of prefrontals ',
- 143 . Frontal, presence of wedge-like processes projecting posterolaterally from the distal margin (Andrade et al., 2011) :0. absent 1. present, wedging between postorbital and parietal, and frankly projecting towards or inside the supratemporal fossaen',
- 144 . Parietals, fusion in adults (Ortega et al. 2000, ch28):n0. absent, parietals are paired elementsn1. present, parietal is a single elementn',
- 145 . ORD Parietal, morphology of the medial surface at maturity (Clark 1994, ch33mod): 0. broad throughout, with a wide sculpted region separating fossae 1. narrow, but with a flattened surface separating fossae, which may be sculpted or not 2. narrow, forming a sagittal crest ',
- 146 . Parietal, dorsal projection of the medial surface, relative to the skull roof (Andrade et al., 2011):n0. does not project dorsallyn1. projects dorsallyn',
- 147 . Postparietal (=dermosupraoccipital), presence as a distinct element (Clark 1994; ch34rev):n0. absent or fused with parietaln1. presentn',
- 148 . Upper temporal bars, orientation in dorsal view (Ortega et al. 2000, ch157mod): Upper (=postorbital-squamosal) temporal bar. 0. temporal bars mostly parallel, giving the skull roof a rectangular outline in dorsal view 1. temporal bars oblique and anteriorly convergent, giving the skull roof a trapezoidal outline in dorsal view',
- 149 '149. Upper temporal bars, outline of lateral margins in dorsal view (Andrade et al., 2011): 0. margin mostly straight or slightly convex 1. margin strongly sinusoidal ',
- 150 . Upper temporal bar, position relative to intertemporal bar (Andrade et al., 2011):n0. upper temporal bar is leveled with intertemporal barn1. upper temporal bar is ventrally displaced relative to the intertemporal bar, coincidentnwith the horizontal plane, and rotated, with dorsal surface exposed laterally andnventral surface mediallyn2. upper temporal bar is diagonally displaced relative to the intertemporal bar (posteriornend more ventrally displaced than anterior end), but not rotatedn',
- 151 . Upper temporal bar, relative participation of postorbital (Ortega et al. 2000, ch33mod): State (1) is putative apomorphy of Thalattosuchia 0. small, postorbital represents c. 30% of the bar 1. extensive, postorbital represents c. 50% (or more) of the bar ',
- 152 . ORD Postorbital, presence and elongation of a robust anterolateral process

projecting from its dorsal surface and postorbital bar (Clark 1994, ch28mod; Turner & Buckley 2007, ch28mod): 0. absent or poorly developed 1. present and short, but evident 2. present and very long, reaching the lateral corner of the orbit',

153 . Postorbital, relation of anterolateral process and its lamina (when present) to the orbit and anterior jugal ramus (Andrade et al., 2011): State (1) present in pholidosaur and dyrosaur-like taxa either where the anterolateral process of postorbital is long or simply well developed. 0. orbit not shielded laterally by a postorbital process and its lamina 1. postorbital process almost reaching or reaching the dorsal edge of the anterior jugal ramus, with process and lamina shielding the posterolateral-lateral sections of the orbit ',

154 . Squamosals, presence of horn-like flanges projecting dorsolaterally from the lateral edge (Andrade et al., 2011): Based on Brochu (2007) and Turner & Buckley (2008). 0. absent, lateral surface of squamosal level with frontal or at a lower plane 1. absent, but edges buttressed and evidently enlarged 2. present',

155 . Squamosal, presence of an extra lobe, unsculpted, at the posterodorsal corner (Clark 1994, ch35; Lauprasert et al. 2007, ch32): State (1) is putative apomorphy of Atoposauridae 0. absent, posterodorsal border of squamosal squared off 1. present, unsculpted lobe projecting posterolaterally',

156 . Squamosal, orientation of the posterior face at the occipital surface, at maturity (Andrade & Bertini 2008a, ch77): 0. mostly vertical, facing posteriorly 1. inclined, facing posterodorsally',

157 . ORD Orbits, orientation in dorsal view (not considering palpebrals) (Andrade et al., 2011): Must not consider palpebrals to determine orientation 0. orbits fully lateral 1. orbits face dorsolaterally 2. orbits with a strong dorsal component ',

158 . Orbits, orientation in lateral view (Andrade et al., 2011): Must not consider palpebrals to determine orientation 0. orbits are lateral-dorsal, with a small anterior component, frontal horizontal or poorly inclined 1. orbits have a strong anterior component, frontal steep and facing anterodorsally ',

159 . Orbits, presence of sclerotic ring (Andrade et al., 2011): 0. absent 1. present',

160 . Orbit, composition of anterior (lachrymal) border (Andrade et al., 2011): n0. lachrymal, but with extensive participation of jugal 1. lachrymal only, neither prefrontal nor jugal reach the lachrymal area 2. lachrymal, but with extensive participation of prefrontal',

161 . Orbit, morphology of medial (primary) border (Andrade et al., 2011): Based on description by Andrade & Hornung (submitted). 0. medial and distal borders at a broad angle (>90 degrees), primary orbit is circular to polygonal 1. medial and distal borders at an acute angle (<90 degrees) and forming a posteromedial corner, with primary orbit triangular ',

162 . Laterotemporal fenestra, size proportional to orbit in late ontogeny (Andrade et al., 2011):Based on Clark et al. (2004). 0. small to absent, no more than 20% the area of the orbit 1. large, area is usually no less than 50% of the area of the orbit ',

163 . Laterotemporal fenestra, proportions (Andrade et al., 2011): Based on Benton & Clark (1988) 0. longer than high or subequal, usually half the height of the orbit 1. higher than long, and usually as high as the orbit ',

164 . Laterotemporal fenestra, shape (Andrade et al., 2011):nBased on Benton & Clark (1988)n0. elliptic to subpolygonaln1. clearly triangular '

165. Laterotemporal fenestra, orientation (Ortega et al. 2000, ch46):n0. faces laterallyn1. faces laterodorsallyn',

166 . Laterotemporal fenestra, position of jugal-quadratojugal suture relative to the posteroventral corner (Norell 1989, ch10mod; Brochu 1999, ch75mod; Ortega et al. 2000, ch39mod): 0. jugal-quadratojugal suture lies at ventral edge of the fenestra, with quadratojugal taking part in the lower temporal bar 1. jugal-quadratojugal suture lies at posterior angle of the fenestra, with quadratojugal barely reaching the distal end of the lower temporal bar 2. jugal-quadratojugal suture at posterodorsal edge of the fenestra, with quadratojugal excluded from the lower temporal bar ',

167 . Laterotemporal fenestra (spina quadratojugalis), presence of a quadratojugal spine in the distal border of the fenestra (Brochu 1999, ch114; Ortega et al. 2000, ch46):n0. absent; 1. presentn',

168 . Laterotemporal fenestra (spina quadratojugalis), position of spine on the quadratojugal border, when present (Brochu 1999, ch114mod):n0. low. near distal corner of infratemporal fenestran1. high, between distal and upper corners of infratemporal fenestran',

169 . Laterotemporal fenestra (spina quadratojugalis), orientation of spine, when present (Brochu 1999, ch114mod):n0. anteriorly-anterodorsally orientedn1. dorsally-anterodorsally orientedn',

170 . Laterotemporal fenestra (spina quadratojugalis), elongation of quadratojugal spine,

when present and fully preserved (Brochu 1999, ch114mod):n0. shortn1. longn',

171 . Jugal, participation in the ventral border of the orbit (Mueller-Towe 2006, ch139rev):n0. reduced participation, or excluded from the orbit by a lachrymal-postorbital contact, ventral to the orbitn1. jugal forms large part or all of the ventral margin of the orbit',

172 . Jugal, cross-section of anterior ramus, beneath orbit (Andrade & Bertini 2008a, ch47): 0. subcircular to subpolygonal, ramus rod-like 1. elliptic to laminar, lateral surface of ramus evidently flattened',

173 . Jugal, cross-section of posterior ramus, beneath laterotemporal fenestra (Clark, 1994, ch18rev): State (1) is putative apomorphy of Sphagesauridae. 0. subcircular to subpolygonal, ramus rod-like 1. elliptic, lateral surface of ramus evidently flattened, blade-like',

174 . Jugal, height of anterior ramus relative to the height of posterior ramus (Clark 1994, ch17mod):n0. anterior ramus approximately as broad as posterior ramusn1. anterior ramus approximately twice as broad as posterior ramus',

175 . Jugal (anterior ramus), height below orbit at maturity (Andrade et al., 2011): 0. low, jugal only forms a narrow band of bone 1. high, broadly separates orbit from ventral plane of cranium',

176 . Jugal, alignment of anterior and posterior processes (Turner & Buchley 2008, ch286): State (1) is putative apomorphy of Kaposuchus + Mahajangasuchus. 0. inline dorsoventrally 1. anterior and posterior processes at a sharp angle to one another, with both processes sloping ventrally to form a strongly arched jugal ',

177 . Jugal, presence of fossa at ventrolateral surface near ectopterygoid contact (Sereno & Larsson 2009, ch46): Reworded from the original. When fossa is present, lateral jugal surface smoothly progress towards contact with ectopterygoid. The jugal ventral fossa is a putative apomorphy of Mahajangasuchus and Kaposuchus. 0. absent, jugal-ectopterygoid contact is inset from lateral surface of jugal, or at ventral surface of jugal 1. present as a smooth but evident depression, below orbit ',

178 . Jugal (anterior ramus), projection of ventral margin at maturity (Andrade et al., 2011): 0. absent, ventral margin of anterior jugal ramus level with the ventral margin of posterior ramus 1. present and poor, jugal gradually flares ventrally at a low angle, and ventral projection is modest 2. present and deep, jugal flares anteriorly at a steep angle, and ventral projection is conspicuous ',

- 179 . Jugal (anterior ramus), presence of a ridge at dorsal edge, and relation with postorbital bar (Ortega et al. 2000, ch34mod; Turner & Buckley 2008, ch167mod): 0. ridge absent, postorbital bar becomes flush with dorsal surface of jugal 1. ridge present, separating postorbital bar from lateral surface of jugal, but neither conspicuous, nor projecting dorsally 2. ridge present and conspicuous, projecting dorsally and separating postorbital bar from lateral surface of jugal ',
- 180 . Jugal (anterior ramus), presence and number of neurovascular foramina (Andrade 2005, ch43mod; Andrade & Bertini 2008a, ch43mod): 0. single enlarged foramen anteriorly directed 1. absentn2. multiple (2-5) small foramina, usually ventrally orientedn',
- 181 . Jugal (anterior ramus), participation in the rostrum (Pol 1999, ch134; Turner & Buckley 2008, ch122): 0. ramus short, does not progress anterior to the anteriormost border of the orbit, and does not take part in the rostrum 1. at least moderately elongated, clearly surpassing the anteriormost border of the orbit ',
- 182 . Jugal (anterior ramus), length (Andrade et al., 2011): 0. short to moderately elongated, but does not reach beneath the antorbital fenestra, poorly contributing to rostrum 1. long, progress below antorbital fenestra and extensively takes part in the rostrum ',
- 183 . Jugal, morphology of anterior end at maturity (Andrade et al., 2011):0. rounded or wedging dorsally/medially 1. truncated 2. wedging ventrally/distally',
- 184 . Jugal fit to maxilla (Andrade et al., 2011): 0. ventral border of jugal continuous with ventral border of maxilla, with outline in lateral view straight or smoothly curved 1. ventral borders of jugal and maxilla not leveled and with a poor fit, as the maxilla is at a lower level relative to the jugal ',
- 185 . Jugal, presence of a blade-like prong, laterally projecting from midbody (Novas et al. 2009):n0. absent; 1. presentn',
- 186 . Palpebrals, presence and number (Clark 1994, ch65mod; Turner & Buckley 2008, ch65): 0. absent, or (anterior) palpebral is deeply fused with prefrontal 1. one large (anterior) palpebral present 2. two large palpebrals (anterior and posterior) present',
- 187 . Palpebrals, overall structure and size (based on Clark 1994, ch65mod): 0. palpebrals are small and gracile 1. palpebrals are robust and large 2. palpebrals are robust, but small ',
- 188 . Palpebral (anterior), shape (Andrade et al., 2011): 0. elongated, scickle-like 1.

elongated, delta-like 2. rectangular ',

189 . Palpebral (anterior), attachment to the skull (Pol & Norell, 2004b, ch181; Turner & Buckley, ch214):0. reduced contact, palpebral sutured to skull only closer to its anterior edge, or not sutured at all 1. long contact, palpebrals well sutured to the skull by at least anterior and medial edges 2. extensive contact, palpebral fully sutured to the skull by anterior, medial and posterior edges (including lateral end of posterior edge) ',

190 . Palpebrals, contact between anterior and posterior elements, when both are present (Andrade et al., 2011):0. no sutural contactn1. small, posterior palpebral only contacts the anterior palpebral by the lateralmost endnof posterior edgen2. extensive, posterior palpebral contacts the anterior palpebral by most or all thenposterior edge',

191 . Postorbital bar, general structure at maturity (Norell 1989, ch3; Brochu 1999, ch70rev; Andrade & Bertini 2008a, ch53): 0. slender, gracile 1. massive and robust ',

192 . Postorbital bar, cross-section (Benton & Clark 1988; Norell & Clark 1990. ch3; Clark0. subcircular, bar cylindricaln1. elliptical, bar transversely flattenedn',

193 . Postorbital bar, relation to dermis (Andrade & Bertini 2008a, ch49):n0. subdermic, distinct, originating mesially from the jugal ramusn1. dermic, gradually narrowingn',

194 . Postorbital bar, inclination in lateral view (Andrade & Bertini 2008, ch54):0. vertical 1. inclined, with dorsal end distal to the ventral end',

195 . Postorbital bar, inclination in anterior view (Andrade et al., 2011): 0. vertical 1. inclined, with dorsal end medial to the ventral end',

196 . Postorbital bar, presence and number of projections (Norell 1989, ch2mod; Brochu 1999, ch134rev): 0. no projection 1. single projection, generally not prominent 2. two prominent projections ',

197 . Postorbital bar, contribution from ectopterygoid (Clark 1994; ch26mod; Sereno et al. 2003, ch22; Andrade & Bertini 2008a, ch51):n0. absent, bar does not receive contribution from ectopterygoidn1. present, bar receives contribution from ectopterygoid',

198 . Postorbital bar, presence of ectopterygoid-postorbital contact (Clark 1994; ch26m; Pol 2003, ch144; Ortega et al. 2000, ch36; Andrade & Bertini 2008a, ch52):n0. absent; 1. presentn',

199 . Postorbital bar, composition of lateral surface (Gasparini et al. 2006, ch244):State (1) is putative apomorphy of Thalattosuchia 0. lateral surface formed by postorbital and jugal 1. lateral surface formed by postorbital only, with jugal only exposed at the medial

face of the bar ',

200 . Postorbital bar, morphology of postorbital-jugal contact (Clark 1994, ch16mod; Ortega et al. 2000, ch37mod): 0. postorbital anterior to jugal 1. postorbital medial to jugal, or slightly posterior to 2. postorbital lateral to jugal ',

201 . Postorbital bar (postorbital), relation with dorsal part of the postorbital (Norell & Clark 1990, ch3; Clark 1994, ch30; Salisbury et al. 2006, ch175): 0. bar broadens dorsally, continuous with dorsal part of postorbital 1. dorsal part of the postorbital bar constricted, with clear limits from the main body of the postorbital ',

202 . Postorbital bar (postorbital), presence of a vascular opening at the lateral edge of the bar, close to the dorsal surface of the postorbital (Clark 1994, ch27): Note that scoring of state (0) can be highly influenced by preservation. 0. absent 1. present ',

203 . Quadratojugal, morphology of dorsal process at posterodorsal angle of laterotemporal fenestra (Clark 1994, ch19mod; Turner & Buckley 2008, ch19): 0. narrow relative to main body, contacting only a small part of postorbital 1. dorsal end expanded as a broad sheet, extensively contacting the postorbital ',

204 . Quadratojugal, extension of anterodorsal ramus (Buscalioni et al. 1992, ch6; Brochu 1999, ch80): 0. quadratojugal reaches dorsal angle of infratemporal fenestra 1. quadratojugal does not extend to dorsal angle of infratemporal fenestra, and quadrate participates in laterotemporal fenestra ',

205 . Maxillo-palatine fenestrae (Andrade & Bertini 2008a, ch85): Maxillo-palatinae fenestrae are here considered as homologous to the primary choanae of goniopholidids. 0. absent 1. present, subcircular 2. present, anteroposteriorly elongated ',

206 . ORD Suborbital fenestrae, presence and size (Andrade et al., 2011): 0. absent 1. present, much smaller than orbits 2. present, subequal or larger than orbits ',

207 . Suborbital fenestrae, shape of anterior border (Andrade & Bertini 2008, ch86): Original scoring for *Malawisuchus* and *Candidodon* was (1), but possibly due to taphonomic deformation, and both taxa should be scored as (?) until detailed description is provided for each taxon. Nonetheless, state (1) is present in *Thalattosuchia*. 0. rounded, smooth 1. in sharp angle, forming a notch, fissure-like ',

208 . ORD Anterochoanal fossae (Andrade et al., 2011): (1-2) present in *Eusuchia*, as putative apomorphy of crocodyloids 0. absent, bony surface flat 1. present as shallow fossa 2. present as deep fossae ',

209 . Parachoanal fossae, presence (Andrade & Bertini 2008, ch103): 0. absent; 1.

presentn',

210 . Palate, palatine rami of premaxillae (Andrade et al., 2011): A putative intermediate state can be inferred, where the rami exist as medial laminae, but are not in contact; in this case, the character would be considered as ordered. 0. absent 1. present, in contact at the medial line and forming the anteriormost section of the secondary bony palate ',

211 . Palate, presence of contact between ventral rami of the maxillae (Clark 1994, ch10): A putative intermediate state can be inferred, where the rami exist as medial laminae, but are not in contact; in this case, the character would be considered as ordered. 0. absent, ventral rami are poorly developed and do not meet at medial line, with secondary palate not formed 1. present, ventral rami meet each other at medial line, or meet vomer, and secondary bony palate formed ',

212 . ORD Palate, presence of palatal shelves of palatines, and their relation with the narial passage (Clark 1994, ch37part): Note that in (2) the palatal laminae may not be in contact (e.g., *Eutretauranosuchus*) 0. palatal shelves of palatine absent, narial passage only bounded dorsally, by the pterygoid 1. narial passage at least partially bounded by palatal shelves of the palatine, laterally, creating the choanal groove 2. narial passage at least mostly bounded by palatal shelves of the palatine, laterally and ventrally, forming the nasopharyngeal duct ',

213 . Palate, relation between palatal shelves of the palatine (Clark 1994, ch37part): Note that, in (1) the anterior projection of the choanal septum may caudally separate the palatal shelves of the palatine, which is here not considered as a reversion, but as another character. 0. palatal shelves of palatine absent or not fully in contact at medial line 1. palatal shelves of palatine fully developed, bounding the narial passage ventrally and in contact at medial line, creating fully formed nasopharyngeal duct, with secondary palate complete',

214 . Palate, participation of maxilla in the suborbital fenestra (Novas et al. 2009, ch231): 0. takes part in the suborbital fenestra 1. fully excluded from the suborbital fenestra by a palatine-ectopterygoid contact, anterior to suborbital fenestra',

215 . Palate, composition of anteromedial border of suborbital fenestrae (Andrade & Bertini 2008a, ch88part): 0. entirely composed of palatines, which expand laterally and reach the anteriormost border of the fenestra 1. palatal ramus of maxilla takes part in the anteromedial border of the fenestra',

- 216 . Palate, presence of maxillary process to palatine, next to the anterior border of antorbital fenestra (Andrade & Bertini 2008a, ch88part):0. absent; 1. present, palatines composing a three-radiated blade anteriorly',
- 217 . Palate, direction of the sutural contact of premaxilla-maxilla, at the palate (Ortega et al. 2000, ch9mod):0. curved posteriorly, premaxillary palate projects over maxillary palate1. straight, poorly arched or complex 2. curved anteriorly, maxillary palate projects over premaxillary palate',
- 218 . Palate, presence of maxilla-pterygoid contact medial to suborbital fenestra, in ventral view (Sereno & Larsson, 2009):State (1) is putative autapomorphy of Kaprosuchus. 0. absent, palatines take part in the suborbital fenestra 1. present, excluding palatines from suborbital fenestra ',
- 219 . Palate, relative position of the distalmost suture of palatine, at the border suborbital fenestra (Brochu 1999, ch85; Salisbury et al. 2006, ch85):0. suture is at distal end of suborbital fenestra, or lateral to it, but very close1. suture is located medial to posterior angle of suborbital fenestra, and far from it',
- 220 . Palate canals, presence (Andrade et al., 2011):0. absent 1. present',
- 221 . Vomer, ventral exposure on palate (Norell 1988, ch22; Brochu 1999, ch125; Ortega et al. 2000, ch59):0. not exposed on palate, hidden by palatal branch of maxillaen1. exposed on palate between premaxillae and maxillaen',
- 222 . Palatines, progression of the palatine process through the palate (if palatines meet in the midline of palate):n0. short, anterior border medial to the anteriormost margin of the suborbital fenestrae, or barely anterior to themn1. long, anterior border of palatines clearly surpassing the anteriormost border of the suborbital fenestraen',
- 223 . Palatines, proportional length of anterior process, projecting at maxillary palate (Andrade et al., 2011):0. anterior process of palatines short, with length subequal to widthn1. evidently longer than widthen',
- 224 . Palatines, overall morphology of palatine process (Andrade et al., 2011): 0. wide, fan-like 1. wide posteriorly and tapering anteriorly, wedging between palatine rami of maxilla 2. lateral margins parallel or flaring anteriorly',
- 225 . Palatines, morphology of anterior face of palatine process near medial line (Andrade et al., 2011): 0. rounded or pointed anteriorly, either U-shaped or V-shaped 1. truncated, maxillo-palatine suture transversally oriented relative to the skull 2. invaginated by at least a broad and short maxillary wedge, maxillo-palatine suture

M-shaped',

226 . Palatines, presence of a long medial process of the maxilla, posteriorly directed and dividing the anterior face of palatine process (Andrade et al., 2011):0. absent, anterior face of palatine process U-shaped, V-shaped or broad M-shapedn1. present, anterior face of palatine process clearly bifid, narrow M-shaped',

227 . Palatines, heart-shaped anterior face of palatine process (Brochu 1999, ch108mod):0. absent, maxillo-palatine suture U-shaped, V-shaped, or M-shapedn1. present, anterior palatine process invaginated close to the medial line by maxilla,nwith maxillo-palatine suture assuming a heart-shaped profilen',

228 . Palatine bar, presence (Martinelli 2003, ch36mod; Turner & Buckley 2008, ch232mod):0. absent; 1. present, gracilen2. present as distinctively robust bars',

229 . Nasopharyngeal duct, width at its narrowest section relative to the skull width:n0. narrow in proportion to skull width, no more than 25%n1. wide in proportion to skull width, no less than 30%',

230 . Nasopharyngeal duct, presence of a deep sulcation on the ventral surface, where the medial contact of palatine occurs (Andrade et al., 2011):n0. absent; 1. present',

231 . Nasopharyngeal duct, cross-section (Andrade et al., 2011):n0. width is subequal to height, or greatern1. evidently higher than wide',

232 . Anterochoanal sagittal crest, presence (Andrade et al., 2011):0. absent, bony surface is smooth to concaven1. present, pterygoid surface at medial line projects ventrally anterior to the internal naris, forming a discrete and short acute crestn2. present, bony surface of palatines projects ventrally at medial line, anterior to the internal naris, forming a discrete and short acute crestn',

233 . Choanae, size (area) relative to skull (Clark 1994, ch42mod):n0. very smalln1. ample',

234 . Choanae and perichoanal fossa, width relative to the width of the nasopharyngeal duct (Andrade et al., 2011):nBased on Clark (1994), ch44; Sereno et al. (2003), ch31; Andrade & Bertini (2008a), ch101n0. narrow, width evidently smaller than the narrowest section of the nasopharyngeal ductn1. subequal, wider than the narrowest section of the nasopharyngeal duct, but not wider than the widest sectionn2. proportionally wide, clearly wider than the widest section of the nasopharyngeal duct',

235 . ORD Choanae, position of anterior border of the internal naris relative to nasopharyngeal duct and suborbital fenestra (Clark 1994, ch44mod, part; Pol & Norell

2004ab, ch44mod, part): 0. anterior border situated anterior to the suborbital fenestra 1. anterior border situated at mid-nasopharyngeal duct 2. anterior border close to the posterior end of the nasopharyngeal duct, or posterior to it',

236 . Choanae, position of anterior border of the internal naris relative to pterygoid surface at medial line (Clark 1994, ch44mod, part; Pol & Norell 2004ab, ch44mod, part): Note that anterior pterygoid processes should not be considered (e.g., *Kaprosuchus*). 0. close to anterior end of pterygoid, or anterior to it 1. at mid/posterior pterygoid surface',

237 . Choanae, position of posterior border relative to pterygoid ventral surface (Andrade et al., 2011): Based on Clark (1994, ch44); Pol & Norell (2004ab, ch44). Putative transition between extreme states (2-0) prevents use of this character as an ordered series. 0. posterior border situated near the anterior edge of the pterygoids, or anterior to pterygoids 1. posterior border situated approximately at mid-terygoid 2. posterior border at posterior pterygoid surface',

238 . Choanae, shape of anterior border in palatal view (Andrade et al., 2011): 0. rounded, straight, or invaginated 1. choanal opening wedges between bony lamina as an acute V-shape, internal nares assuming a lanceolate profile ',

239 . Choanae, shape in palatal view (Andrade 2005, ch87mod; Andrade & Bertini 2008, ch91mod): 0. subcircular, elliptic or lanceolate 1. triangle-like 2. rectangular 3. V-shaped or reversed triangle 4. butterfly-shaped n',

240 . Choanae, general morphology (Andrade et al., 2011): 0. choanae wider than long 1. length and width subequal 2. choanae longer than wide',

241 . Choanae, orientation (Andrade & Bertini 2008a, ch93): Note corrected data from original analysis 0. ventrally oriented 1. posteroventrally oriented',

242 . Choanae, participation of pterygoid in the choanal border (Clark 1994, ch43mod; Brochu 1999, ch71mod; Jouve et al. 2005; ch4mod; Turner & Buckley 2008, ch43mod): 0. pterygoid only bounds the posterior border of the choanae 1. pterygoid forms at least the posterior and lateral choanal borders 2. anterolateral rami of pterygoid embrace most of the choanae, but do not meet medially, at the anterior choanal border (either by the presence of palatine or ventral exposure and expansion of interchoanal septum) 3. anterolateral rami of pterygoid completely embrace the choanae, meeting medially at its anterior border (eusuchian choanae) n',

243 . Choanae, presence of extensive contact between converging perichoanal pterygoid

laminae, anterior to choanae (Andrade et al., 2011): 0. absent, anterior pterygoid laminae narrow anterior to choanae, or not in contact at all 1. present, anterior pterygoid laminae widely meet anterior to choanae ',

244 . Interchoanal septum, exposure at internal naris (Clark 1994, ch69mod; Brochu 1999, ch152mod; Ortega et al. 2000, ch137rev): 0. nasopharyngeal septum absent or recessed, not dividing the internal narial openingn1. present, nasopharyngeal septum of pterygoid fully dividing the choanal opening, ornevidently projecting from ventral surface of pterygoid, if choanal groove is not enclosed by palatinesn',

245 . Interchoanal (nasopharyngeal) septum, exposure at the ventral surface of the nasopharyngeal duct, anterior to the choanae (Andrade et al., 2011):Based on Clark (1994), ch43; Turner & Buckley (2008), ch43(mod) 0. absent, or nasopharyngeal septum receded and not exposed ventrally at all 1. present, interchoanal septum projects anteriorly between palatines, and expands ventrally, creating a wide surface at the anterior choanal border',

246 . Interchoanal septum, presence of an acute groove on its ventral surface (Turner, 2004, ch126; Turner & Buckley 2008, ch271): 0. absent, ventral surface smooth to slightly depressedn1. present and evident, well marked',

247 . Interchoanal septum, shape (Pol & Apesteguia 2005, ch186mod; Turner & Buckley 2008, ch191mod): 0. narrow vertical bony sheetn1. narrow vertical bony sheet, expanded ventrally, T-shaped in cross-sectionn2. narrow vertical bony sheet, inflated ventrally and forming a robust bar, semicircularn in cross-section',

248 . Interchoanal septum, morphology of ventralmost surface, as septum approaches choanal opening (Pol & Apesteguia 2005, ch220mod; Turner & Buckley et al. 2008, ch225): 0. parallel sided 1. tapers anteriorly 2. expanding both anteriorly and posteriorly, hourglass-shaped 3. tapers both anteriorly and posteriorly ',

249 . Perichoanal ridge, presence at anterolateral edge of internal naris, late in ontogeny (based on Brochu 1999, ch73mod): 0. absent, all anterolateral edge of choanae flush with remaining bony surface 1. present as a well defined wall, bounding at least the anterolateral border of the internal naris ',

250 . Perichoanal ridge, presence at posterolateral edge of choana, late in ontogeny (Andrade et al., 2011):n0. absent, all posterolateral edge of choanae flush with remaining bony surfacen1. present as a well defined wall, bounding at least the posterolateral border of theninternal narisn',

- 251 . Perichoanal ridge, presence of a continuous wall around the internal naris, early in ontogeny (Brochu 1999, ch73mod): 0. absent or incomplete, at least part of the choanal margin flush with bony surfacen1. present, continuous',
- 252 . Ectopterygoid, relation with maxilla and toothrow (Brochu 1997, ch91m; Turner & Buckley 2008, ch264m): 0. ectopterygoid abuts maxillary toothrow at medial wall of distal alveolin1. ectopterygoid broadly separated from last teeth in the toothrow by palatal ramus of maxilla, or barely contacting maxillan',
- 253 . Ectopterygoid, presence of broad contact with palatine ramus of maxilla (Andrade et al., 2011): 0. absent, ectopterygoid does not contact maxilla, or barely contacts its caudal end,nmedial to jugaln1. presentn',
- 254 . Ectopterygoid, morphology of medial process (Ortega et al. 2000, ch146; Turner & Buckley 2008, ch180):n0. single 1. forkedn',
- 255 . Ectopterygoid, development of the medial ramus (Andrade 2005, ch93; Zaher et al. 2006, ch196mod; Andrade & Bertini 2008a, ch98):n0. small, do not take part in the internal narisn1. well-developed, taking part in the internal naris',
- 256 . Ectopterygoid, morphology of the distal ramus (Andrade et al., 2011): 0. laminar, extending as a flattened sheet over the pterygoid wingn1. robust, extending as a rod over most of the pterygoid wing, with subcircular cross- section through most of its lengthn',
- 257 . Ectopterygoid, length of posterior ramus, at maturity (Norell 1988, ch32mod; Brochu 1999, ch149; Turner & Buckley 2008, ch269):n0. reaches posterior tip of lateral pterygoid flangen1. pinched off anterior to posterior tip of lateral pterygoid flange',
- 258 . Pterygoids, fusion posterior to choanae (Clark 1994, ch41):State (1) is putative apomorphy of Mesoeucrocodylian0. not fusedn1. fusedn',
- 259 . Pterygoid, participation in the suborbital fenestra (Martinelli 2003, ch35mod; Andrade & Bertini 2008c, ch89mod):n0. pterygoid takes part in the suborbital fenestran1. pterygoid excluded from the suborbital fenestra by a palatine-ectopterygoid contact',
- 260 . Pterygoid, presence of depression on primary pterygoidean palate posterior to choanae (Ortega et al. 2000, ch139rev; Turner & Buckley 2008, ch42):State (1) is present in several derived notosuchians. 0. absent or moderate in size, being narrower than palatine bar 1. wider than palatine bar ',
- 261 . ORD Pterygoid ventral rami (wings), size (Andrade & Bertini 2008a,

ch94mod):n0. very small or vestigialn1. well-developedn2. extremelly well-developed',
 262 . Pterygoid ventral rami (wings), ventral surface at distal end (Andrade et al., 2011):Based on the discussions and descriptions by Ortega (2000, 2004), Sereno et al. (2003), Peng & Shu (2005), and Turner & Buckley (2008). Bar transverse to the skull (=palatine bar sensu Ortega 2004) is also present in Iberosuchus (1). 0. plain surface 1. evident transverse ridge on ventral surface, forming a vertically oriented post- choanal wall, or a buttressed bar',
 263 . Pterygoid ventral rami (wings), structure (Andrade & Bertini 2008c, ch96):n0. laminarn1. robustn',
 264 . Pterygoid ventral rami (wings), orientation in lateral view (Andrade & Bertini 2008a, ch95):n0. poorly to mildly inclined, no more than 45 degreesn1. strongly verticalized, 50 degrees or more relative to the horizontal plane',
 265 . Pterygoid ventral rami (wings), extension of posterior border of ventral wings, in ventral view:n0. relatively anterior, not covering the anteromedial end of quadratesn1. relatively posterior, covering the anteromedial end of quadrate',
 266 . Supraoccipital, presence and development of tuberos prominences (Clark 1994, ch64; Jouve et al. 2005; ch3):0. absent 1. present, modest but evident 2. present and extremely developed ',
 267 . Supraoccipital, morphology of posterior wall (Andrade et al., 2011): 0. essentially flat, or projecting distally 1. strongly concave',
 268 . Exoccipitals, overall morphology (Norell 1988, ch20mod; Clark 1994, ch57mod; Brochu 1999, ch151):0. terminate dorsal to basioccipital tubera 1. send robust process ventrally and participate in basioccipital tubera 2. send slender process ventrally to basioccipital tubera ',
 269 . Exoccipitals, presence of a large ventrolateral part ventral to paroccipital process (Clark 1994, ch60):Note different codings in derived notosuchians 0. absent 1. present',
 270 . Exoccipitals, presence of medial contact between both elements (Clark 1994, ch62; Ortega et al. 2000, ch63):nCan also be defined as the participation of supraoccipital in the foramen magnum.n0. do not meet in midlinen1. meet on the midline, dorsal to the basioccipital, excluding the supraoccipital from thenforamen magnumn',
 271 . Exoccipitals, presence of a pronounced transverse ridge dorsal to foramen magnum (based on Peng & Shu 2005):State (1) is putative apomorphy of

- Hsisosuchidaen0. absent or incipientn1. present',
- 272 . Exoccipitals, participation in the occipital condyle (based on Peng & Shu 2005; as in Jouve et al. 2005, ch5):n0. absent or incipient, neither reaching the articular surface nor meeting mediallyn1. present and evident, reaching the articular surface and meeting mediallyn',
- 273 . Exoccipital, presence of descending flange ventral to subcapsular process (Clark 1994, ch58):State (1) is putative apomorphy of protosuchids, but also present at least in *Araripesuchus tsangatsangana*.n0. absent; 1. present, laterally concave',
- 274 . Exoccipital, extent of contact with the quadrate (Clark, 1994: ch48mod):n0. absent or narrow n1. broad contact present, stabilizing the quadraten',
- 275 . Exoccipital, presence of ventrolateral contact with the ventromedial part of quadrate (Clark 1994, ch51mod): 0. absent, quadrate does not contact exoccipitaln1. present, exoccipital and quadrate enclosing carotid artery and forming passage for cranial nerves IX-XI',
- 276 . Exoccipital, presence of individualised passage (metopic foramen) for cranial nerve IX (Clark 1994, ch59; Ortega et al. 2000, ch64):n0. absent, cranial nerves IX-XI pass through a common large foramenn1. metopic foramen present, medial to cranial passage for nerves X-XI',
- 277 . Exoccipitals, presence of an evident boss on lateral edge of paroccipital process (Brochu 1999, ch141part, rev; Turner & Buckley 2008, ch268part, rev; Sereno & Larsson 2009, ch166part): 0. absent, exoccipital with small or no boss on paroccipital process 1. present, paroccipital process with a proportionally robust, thickened lateral/ventrolateral edge ',
- 278 . Exoccipitals, elongation of lateral end (=paraoccipital process) relative to the skull roof (Brochu 1999, ch141part, rev; Turner & Buckley 2008, ch268part, rev; Sereno & Larsson 2009, ch166part): 0. relatively short, does not progress lateral to the skull roofn1. relatively long, clearly progress lateral to the skull roof',
- 279 . Exoccipital, projection of the lower margin of paraoccipital process (Andrade et al., 2011): State (0) is putative apomorphy of Mesoeucrocodylia, but with reversion in *Dyrosauridae* 0. absent or feeble, ventral border usually level with foramen magnum 1. present and evident, lower margin reaching ventrally at least as far as the same level as the occipital condyle',
- 280 . Exoccipital, morphology of ventral border of paraoccipital process (Andrade et al.,

2011):State (1) is putative apomorphy of Dyrosauridae 0. either projects as a wide blade, or projection is feeble/absent 1. projects ventrally as a narrow bar, rod-like ',

281 . Crista interfenestralis between fenestrae pseudorotunda and ovalis, orientation (Clarkn1994, ch61):n0. nearly verticaln1. horizontaln',

282 . Mastoid antrum, extension into supraoccipital (Clark 1994, ch63): 0. absent, does not extend into supraoccipital 1. present, extends through transverse canal in supraoccipital to connect middle ear regions',

283 . Lateral carotid foramen, position relative to basisphenoid (lateral exposure), at maturity (Brochu 1999, ch128): 0. opens lateral to basisphenoid lateral exposure 1. opens dorsal to basisphenoid lateral exposure ',

284 . Anterior foramen for palatine ramus of cranial nerve VII, position relative to basisphenoid rostrum (Brochu 1999, ch164):0. ventrolateral to basisphenoid rostrum 1. ventral to basisphenoid rostrum ',

285 . Laterosphenoid, orientation of capitate process (Brochu 1999, ch130; Salisbury et al. 2006):n0. capitate process oriented laterally towards midlinen1. capitate process oriented anteroposteriorly towards midlinen',

286 . ORD Basisphenoid, ventral exposure in adults and young individuals, but not immature or hatchlings (Clark 1994, ch55rev+56rev; Ortega et al. 2000, ch68mod): 0. extremely reduced surface, exposed as a transversal slit, almost obliterated ventrally by the basioccipital and the pterygoidsn1. well-exposed, although basisphenoid surface clearly smaller than basioccipital surfacen2. ample surface exposed ventrally, basisphenoid at least as long as the basioccipital, or longer',

287 . Basioccipital, cross-section of occipital condyle (Andrade et al., 2011):State (1) is putative apomorphy of Dyrosauridaen0. subcircular, condyle not compressedn1. stronglyelliptic,condyledorsoventrallyflattened',

288 . Basioccipital, presence of basal tubera (Clark 1994, ch57; Lauprasert et al. 2007, ch46):n0. absent; 1. tubera present, large and pendulous',

289 . Basipterygoid process, development (Clark 1994, ch54rev):0. small or absent 1. prominent, forming a movable joint with pterygoid, and with basisphenoid joint suturally closed ',

290 . Eustachian tubes, relation to basioccipital and basisphenoid (Clark 1994, ch52):State (0) occurs also in Dibothrosuchus and Postosuchusn0. not enclosed between basioccipital and basisphenoid 1. entirely enclosed between the basioccipital and

basisphenoid',

291 . ORD Quadrate, orientation of main body in lateral view (Ortega et al. 2000, ch44mod): 0. poorly inclined, subverticaln1. slightly inclined posteriorly, approximately 45 degreesn2. strongly inclined, with quadrate almost horizontal',

292 . ORD Quadrate, orientation in dorsal view (Andrade et al., 2011):0. does not project laterally to the skull, with the lateral surface of the quadrate covered by the squamosal 1. slightly projected laterally to the skull, with most of the laterodistal end of the quadrate covered by the squamosals 2. strongly projected laterally to the skull, exposing most of the distal end of the quadrate ',

293 . Quadrate, orientation of distal end and condylar head (Pol 1999, ch166mod; Ortega et al. 2000, ch44mod; Turner & Buckley 2008, ch149mod): 0. directed posteroventrally 1. directed mostly ventrally, or anteroventrallyn',

294 . Quadrate, presence of preotic siphonial foramen on medial surface, close to tympanum (based on Clark 1994, ch45part):0. absent 1. present',

295 . Quadrate, presence of fenestrae on the dorsolateral-posteromedial surfaces (Clark 1994, ch45part; Ortega et al. 2000, ch51rev; Sereno et al. 2003, ch35):n0. fenestrae absent or limited to one opening (preotic siphonial foramen)n1. two or more fenestrae additional to siphonial foramen (if siphonial foramen present)n',

296 . Quadrate, structure (Andrade et al., 2011):Based on description of Notosuchus by Bonaparte (1991), but see also Andrade & Bertini (2008a).0. non-pneumatic 1. highly pneumatic ',

297 . Quadrate, morphology of posterior edge (Clark 1994, ch46):n0. broad medial to tympanum, gently concaven1. posterior edge narrow dorsal to exoccipital contact, strongly concave',

298 . Quadrate, articulation of primary head (Clark 1994, ch47):n0. prootic, squamosal, and exoccipitaln1. prootic and laterosphenoid',

299 . Quadrate, position of foramen aerum, next to the articular condyle (Brochu 1999, ch121mod):n0. foramen aerum single, on mediodorsal angle of the quadrate, close to the condylen1. foramen aerum single, on dorsal surface of the quadrate, close to the condylen2. foramen aerum double, being the medial foramen on the mediodorsal angle of the quadrate and distant to the condyle, and the lateral foramen on the dorsal surface and close to the condylen',

300 . Quadrate condyle, size of medial hemicondyle relative to lateral hemicondyle, and

presence of intercondylar groove (Ortega et al. 2000, ch53; Andrade & Bertini 2008a, ch68; Turner & Buckley 2008, ch170): 0. medial hemicondyle smaller or subequal to lateral one, poorly curved, and with intercondylar groove incipient at best 1. medial hemicondyle evidently larger than the lateral one, round and projecting ventrally, with intercondylar groove evident',

301 . Quadrate condyle, expansion of medial hemicondyle (Brochu 1999, ch112mod, part): 0. absent; 1. present, medial hemicondyle is expanded.',

302 . External auditory meatus, general morphology (Andrade et al., 2011): State (1) is putative apomorphy of crown eusuchians. 0. subpolygonal to elliptic 1. triangle-shaped, with apex directed dorsally ',

303 . External auditory meatus, size (Andrade et al., 2011): 0. very small, poorly visible (even in lateral view) 1. medium to large, conspicuous',

304 . External auditory meatus, position of squamosal-quadrate suture at distal edge (Brochu 1999, ch132): 0. squamosal-quadrate suture extends dorsally along posterior margin of external auditory meatus, directed anterodorsally 1. squamosal-quadrate suture extends only to posteroventral corner of external auditory meatus, directed anteroventrally or horizontal',

305 . Otic aperture, morphology of distal margin (Brochu 1999, ch102mod; Salisbury et al. 2006, ch102mod; Delfino et al. 2008, ch102mod): 0. posterior margin not defined and gradually merging into the exoccipital, or smooth and continuous with the paraoccipital process, but never invaginated 1. distal margin inset or invaginate',

306 . Cranioquadrate canal, presence and position (Clark 1994, ch49mod): 0. absent 1. at least partially enclosed by quadrate, exoccipital and squamosal, with distal end near lateral edge of skull 2. at least partially enclosed by quadrate, exoccipital and squamosal, with distal end located ventral to paraoccipital process',

307 . Cranioquadrate canal, general structure (Andrade et al., 2011): 0. canal laterally open or not formed, and cranioquadrate passage absent 1. passage fully formed, with canal enclosed at least distally by the exoccipital and squamosal, regardless of the participation of the quadrate 2. passage fully formed, with canal laterally enclosed by quadrate and squamosal, and exoccipital only bounding the canal medially 3. passage fully formed, with canal laterally enclosed by quadrate and exoccipital, regardless of the participation of the squamosal ',

308 . Cranioquadrate canal, lateral contact between quadrate and exoccipital (Andrade

et al., 2011):n0. narrow or absent; 1. broadn',

309 . Cranioquadrate passage, exposure in occipital view (Buscalioni & Sanz 1990; Ortega et al. 2000; ch160mod; Buscalioni et al. 2001, ch166rev; Delfino et al. 2005, ch166rev):n0. exposed on occipital surface 1. shielded posteriorly by the ventral border of paraoccipital process, with passage not exposed in occipital view',

310 .Oral symphyseal fossa, presence (Andrade et al., 2011):0. absent 1. present as a small depressed area, anteroposteriorly elongated, located at the medial line of symphysis, in the oral cavity ',

311 . Posteroventral symphyseal fossa, presence of a single depressed area at the posterior end of symphysis, in ventral view (Andrade et al., 2011): 0. absent or feeble1. evident, deep, longer than wide',

312 . External mandibular fenestra, presence (Clark 1994, ch75mod; Ortega et al. 2000, ch80rev): 0. absent 1. present as a diminutive passage 2. present as an evident fenestra ',

313 . External mandibular fenestra, size relative to the orbit (Andrade et al., 2011):0. extremely reduced or absent, less than 50% of the length of the orbit, with surangular and angular sutured along most of (or all) their length 1. small, approximately with the same length of the orbit 2. large, evidently longer than the orbit ',

314 . External mandibular fenestra, orientation of main axis (Andrade et al., 2011):n0. horizontal1. main axis inclined, directed anteroventrally-posterodorsally',

315 . External mandibular fenestra, shape (Andrade et al., 2011): 0. subcircular to poorly elliptic 1. highly elliptic, anteroposterior axis much longer than dorso-ventral axis, three times or more, but both ends rounded 2. slit-like, proportionally very long and both ends acute 3. broad teardrop-like 4. narrow teardrop-like 5. triangle ',

316 . External mandibular fenestra, morphology of anterior margin (Andrade et al., 2011): 0. curved, with a broad arched margin anteriorly 1. anterodorsal and anteroventral margins poorly arched, meeting at an acute angle anteriorly, anterior end is wedge-like',

317 . Mandible, presence of evident festooning at anterior mandible (Andrade et al., 2011):n0. absent, margin straight, in lateral view1. present, projecting dorsally at the premaxilla-maxilla suturen',

318 . Mandible, presence of evident festooning at mid mandible (after Ortega et al. 2000, ch21rev): 0. absent, margin straight in lateral view, or moderately concave 1. present and incipient, with dorsal edge of dentary weakly sinusoidal in lateral view 2.

present and evident, with dorsal edge of dentary strongly sinusoidal in lateral view ',

319 . Mandible, overall morphology in dorsal view: State (1) is putative apomorphy of Alligatoridae/Alligatoroidea, but occurs in Mahajangasuchus, Anatosuchus and Comahuesuchus. 0. mandible is narrow, hemimandibles are confluent, with left and right alveolar margins running alongside each other 1. mandible is broad, hemimandibles are mostly parallel, but alveolar margins meet medially at first alveolus forming a wide arched line, giving the mandible a broad-U shape',

320 . Mandible, orientation of hemimandibles at their medial contact (Andrade et al., 2011): 0. evidently acute angle, hemimandibles meet at c. 45 degrees of each other, or less 1. broad angle, hemimandibles meet at c. 70 degrees of each other, or more',

321 . Mandible, morphology of distal rami in dorsal/ventral views (Andrade et al., 2011): 0. distal rami mostly straight or poorly curved 1. distal rami strongly curved medially at mid-mandible, giving the mandible a broad-Y shape',

322 . ORD Mandible, ventral border at angular, in lateral view (Andrade et al., 2011): 0. angular straight and mostly horizontal, or poorly curved, from the anterior to the posterior end 1. angular evidently (but gently) curved 2. angular abruptly curved, always below glenoid fossa, with mid-posterior sections of angular sub-vertical, facing posteriorly ',

323 . Mandible, morphology of ventral margin, in lateral view (Andrade et al., 2011): 0. mandible is curved ventrally, with maximum curvature at anterior section of angular, below the mandibular fenestra (when present), or not curved at all 1. mandible is curved posteroventrally, with maximum curvature at posterior section of angular, below (or almost below) the mandibular glenoid fossa, usually posterior to mandibular fenestra (when present) n',

324 . Mandible, dorsal border at dentary-surangular contact, in lateral view (Clark 1994, ch74; Sereno et al. 2003, ch41): 0. mostly straight 1. gently arched dorsally 2. strongly arched dorsally',

325 . Mandible, presence of an evident coronoid process, projecting dorsally or anterodorsally (Andrade & Bertini 2008a; ch112): 0. absent; 1. present n',

326 . Mandible, relation between surangular and articular (Brochu 1999, ch60): 0. truncated, sulcus present between surangular and articular 1. continuous, articular flush against surangular',

327 . Mandible, position of caudal end of surangular-angular suture relative to articular

(Brochu 1999, ch67):n0. lingually meets articular at ventral tipn1. meets articular dorsal to ventral tip',

328 . Mandible, morphology of angular-surangular suture and relation with external mandibular fenestra, at late ontogeny (Norell 1988, ch40; Brochu 1999, ch47): 0. angular-surangular suture mostly horizontal, contacting fenestra at posterior anglen(when fenestra is present)n1. angular-surangular suture curves ventrally at anterior end, passing broadly alongnventral margin of fenestra (when fenestra is present)',

329 . Mandible, presence of a splenial crest (Andrade et al., 2011):0. absent 1. present as a long, laminar and horizontal blade, next to the alveolar margin, projecting medially ',

330 . Mandible, presence of a conspicuous and robust surangular crest on the lateral surface of the mandible, next to the glenoid fossa (Turner & Buckley 2008, ch287):n0. absent; 1. presentn',

331 . Symphysis, orientation relative to the horizontal plane (Andrade et al., 2011):Based on discussion by Ortega et al. (2000). 0. horizontal or slightly inclined 1. inclined dorsally

332 . Symphysis, length relative to width (Andrade et al., 2011):0. short, length and width subequal or shorter than wide, and mandible "U" or "V- shaped" 1. proportionally long, longer than wide, and mandible "V" or "Y-shaped" 2. extremely long, length at least five times its width, and mandible "Y-shaped" ',

333 . Symphysis, morphology of anterior end (Andrade et al., 2011): 0. symphysis tapers anteriorly, with no constriction at mid-posterior sections 1. symphysis clearly constricted at fifth-sixth alveoli 2. symphysis flares anteriorly, with anterior region bearing teeth 1-4 at anterior margin and posterior region narrower (but constriction poorly defined) 3. symphysis flares anteriorly, with anterior region bearing teeth 1-2 at anterior margin and posterior region narrower (but constriction poorly defined) ',

334 . Symphysis, morphology of dorsal surface (Pol & Apesteguia 2005, ch184; Turner & Buckley 2008, ch189): 0. flat or slightly concaven1. strongly concave and narrow, trough shaped',

335 . Symphysis, presence of posterior splenial peg (Pol & Apesteguia 2005, ch181):0. absent 1. present ',

336 . ORD Symphysis, shape of anterior end in dorsal view (Andrade et al., 2011):0.

anterior end expanded, fan-like 1. anterior end expanded, rounded to sub-quadratic 2. not expanded',

337 . Dentary, presence of an occlusal pit or strong concavity for the reception of an enlarged maxillary caniniform (Buckley & Brochu 1999, ch105mod; Turner & Buckley, ch158mod): 0. absent 1. present, occlusal concavity lateral to the 5th-7th alveolin2. present, occlusal concavity lateral to the 8th-9th alveolin',

338 . Dentary, morphology of distal end (Clark 1994, ch70mod): 0. dentary tappers posterodorsally into a single ramus, usually acute, extending only dorsal to the mandibular fenestra1. dentary extends dorsally to the mandibular fenestra, and almost vertically ventral to the anterior margin of the fenestra (posteroventral ramus incipient)n2. dentary distal end bifurcated, usually extending both dorsally and ventrally to the mandibular fenestra (if fenestra present and not reduced), with posteroventral ramus evidently present and well developedn',

339 . Dentary, morphology of dorsal ramus at distal end, next (dorsal) to mandibular fenestra (Andrade et al., 2011): 0. dentary ramus dorsal to fenestra follows dorsal edge of fenestra 1. dentary ramus dorsal to fenestra projects posteroventrally as a laminar blade, partially shielding the fenestra laterally and creating a secondary, straight to slightly convex anterodorsal border.',

340 . Dentary distal end, extension relative to the distal margin of the orbit (Andrade et al., 2011):n0. relatively short, do not reach posterior to the orbitn1. relatively long, reaches posterior to the orbitn',

341 . Splenials, general structure (Ortega et al. 1996, ch7; Buckley & Brochu 1999, ch110; Turner & Buckley 2008, ch161):n0. thin posterior to symphysisn1. robust dorsally, posterior to symphysis',

342 . Splenials, involvement in symphysis, in ventral view (Clark 1994, ch77mod; Brochu 1999, ch43mod; Ortega et al. 2000, ch88mod):0. absent, splenials do not take part in the symphysis 1. present, splenials are visible at the distal end of symphysis, in ventral view',

343 . Splenials, extent of involvement in symphysis (Clark 1994, ch77mod; Turner & Buckley 2008, ch77mod):n0. marginal, or none at alln1. modest but evident, with length of splenials at symphysis approximately the same as the width of the symphysisn2. extensive participation, length of splenials at symphysis much longer than width of symphysis',

- 344 . Splenials, morphology at their contact in the symphysis, in ventral view (Pol & Apesteguia 2005, ch180; Turner & Buckley 2008, ch185):n0. V-shapedn1. U-shaped',
- 345 . Splenial, participation in the medial wall of the posterior mandibular alveoli (Andrade et al., 2011):nIn (1), if splenial is removed, the alveoli get exposed medially.n0. does not take part, splenial may reach the alveolar margin, but alveoli are delimited solely by the dentaryn1. participates in the distalmost alveoli, supporting teeth',
- 346 . Surangular, extension of the anterior lateral ramus (Andrade et al., 2011):n0. short, does not extend beyond the orbitn1. long, extends at least to the same relative position as the anterior border of the orbit,nor reaches beyond the orbitn',
- 347 . Surangular, proportional development of lateral and medial rami, at anterior end (Andrade & Bertini 2008a, 2008b, ch113mod; Turner & Buckley, 2008, ch289):n0. medial ramus absent or incipient, with lateral ramus well developed 1. medial ramus well developed, subequal ro lateral ramus, and dentary-surangular suture evidently complex
348. Surangular, morphology of lateral anterior process (Ortega et al., 2000; ch96): 0. single 1. forked, with a dorsal and a ventral process evident ',
- 349 . Surangular, relative length of the anterior processes of the lateral anterior ramus (Brochu 1999, ch48mod):n0. unequal, dorsal process much longer, or ventral process absent; 1. subequal to equaln2. unequal, ventral process longer',
- 350 . Surangular, presence of extension to the retroarticular process (Norell 1988, ch42mod; Brochu 1999, ch51rev):n0. absent, pinched off anterior to tip of retroarticular process, or surangular excluded from processn1. present, extends to posterior end of retroarticular processn',
- 351 . Coronoid, relation with foramen intermandibularis medius (Norell 1988, ch12; Brochu 1999, ch46):n0. limited, coronoid only bounds posterior half of the foramenn1. extensive, completely surrounds foramenn2. extensive, obliterates foramen',
- 352 . Coronoid, morphology of dorsal edge (Brochu 1999, ch54):n0. slopes strongly anteriorlyn1. almost horizontal',
- 353 . Angular, presence of insertion area for M pterygoideus posterior onto its lateral surface (Clark 1994, ch76):n0. absent, M pterygoideus posterior limited to the posterior/ventral surfaces of angularn1. present and evidentn',
- 354 . Prearticular, presence (Clark 1994, ch72rev; Sereno et al. 2003, ch39):0. absent 1.

present',

355 . Mandibular glenoid fossa, length relative to width (Wu & Sues 1996, ch23mod; Ortega et al. 2000, ch105; Turner & Buckley 2008, ch104): 0. short, length smaller than width, matching the dimensions of the quadrate condyle 1. length at least equal to width, or longer, and evidently longer than the quadrate condyle',

356 . Mandibular glenoid fossa, development of posterior margin (Pol & Apesteguia 2005, ch181mod):0. posterior margin smoothly progressing to the retroarticular process, with glenoid fossa poorly defined 1. posterior margin delimited by a corner, and the glenoid fossa clearly delimited 2. posterior margin well developed, evidently high ',

357 . Mandibular glenoid fossa, participation of surangular in the articulation (Buckley & Brochu 1999, ch 102; Ortega et al. 2000, ch99mod; Turner & Buckley 2008, ch156): 0. does not take part, or barely takes part on the lateral wall of the fossa 1. broadly participates in the glenoid fossa, forming approximately one third of its surface, with quadratojugal also broadly contributing to the quadrate condyle ',

358 . Retroarticular process, development (Clark 1994, ch71part):For practical purposes, a retroarticular process is here considered as (1) when its orientation can be established. 0. absent or poorly developed 1. present and evidently projecting posterior to glenoid fossa ',

359 . ORD Retroarticular process, length of the attachment surface for the adductor muscles relative to its width (Jouve et al. 2005, ch1mod):n0. short, subequaln1. moderately elongated, evidently longer than widthn2. extremely elongate, more than twice its widthn',

360 . ORD Retroarticular process, orientation in lateral view (Norell & Clark 1990, ch7mod; Clark 1994, ch71part; Brochu 1999, ch50):0. posteroventrally oriented 1. posteriorly oriented 2. posterodorsally oriented ',

361 . Retroarticular process, position of distalmost tip relative to the mandibular glenoid fossa (Andrade et al., 2011):0. tip at the same level or below 1. tip clearly in a more dorsal plane than the glenoid fossa ',

362 . Retroarticular process, morphology and orientation in dorsal/posterior view (based on Clark 1994, ch71part):n0. surface poorly concave and facing dorsally, or at least lateral surface facing dorsally- laterodorsally and medial surface facing mediodorsally (if surface divided)n1. surface strongly concave, facing dorsomediallyn',

363 . Retroarticular process, morphology of the surface for the attachment of adductor

muscles (Andrade et al., 2011):n0. triangleshapedn1. ellipsoid, rectangular or spoon shapedn2. shovel shaped',

364 . Retroarticular process, presence of a longitudinal anteroposteriorly oriented crest or ridge dividing the attachment surface for the adductor muscles:nMedial surface facing dorsally to mediodorsally, and a lateral facing dorsally to laterodorsally.n0. absent; 1. present, dividing the surface into medial and lateral portions.',

365 . Retroarticular process, position of the posteromedial wing (Jouve et al. 2005; ch2; Jouve et al. 2006, ch179):n0. posteromedial wing dorsally situated, or at mid height on the retroarticular processn1. posteromedial wing ventrally situated on the retroarticular processn',

366 . Retroarticular process, position and orientation of the foramen aerum (Norell 1988, ch16mod; Brochu 1999, ch49):n0. foramen aerum medially oriented, opening at the medial margin of retroarticularnprocess laminan1. foramen aerum dorsally oriented, lateral from the medial margin of retroarticularnprocess',

367 . Dentition, relation between tooth rows on both sides of the skull (Novas et al. 2009):0. forming one continuous set of teeth, both in the cranium and mandible 1. forming two distinct sets, tooth rows at posterior set convergent rostrally and almost in touch each other, at mid-palate and mandible ',

368 . Posterior maxillary teeth, transverse section (Buckley et al. 2000, ch116mod; Ortega et al. 2000, ch104mod; as in Andrade & Bertini 2008, ch135):n0. evident lateral compression affecting both edges of the crown, making both edgesnevident regardless of the presence/absence of carinae/keeln1. transverse section circular to subcircular, without significant lateral compressionn2. transverse section "teardrop-like" (=triangular), with asymmetric lateral compressionnoccuring on the distal margin onlyn',

369 . Mid to posterior mandibular teeth, transverse section (Buckley et al. 2000, ch116mod; Ortega et al. 2000, ch104mod; as in Andrade & Bertini 2008, ch146):n0. evident lateral compression affecting the entire crown, making evident both mesialnand distal edges, regardless of the presence/absence of carinae/keeln1. transverse section circular to subcircular, without significant lateral compressionn2. transverse section "teardrop-like" (=triangular), with asymmetric lateral compressionnoccuring on the mesial margin only',

370 . Dentition, presence of facettted teeth (Young & Andrade 2009, ch130):0. absent 1.

present, most crowns with at least the labial surface with three facets',

371 . Dentition, presence of laminar teeth (Andrade et al., 2011):
For practical purposes, "laminar tooth" is here considered as tooth with cross-section highly elliptical at the base of crown, with mesial-distal axis approximately twice the labial-lingual axis, or greater.
0. absent; 1. present, laminar teeth dominate dentition',

372 . Dentition, presence of spatulated teeth (Buckley et al. 2000, ch116mod): 0. absent; 1. present',

373 . Anterior to mid dentition, general crown robustness (Andrade et al., 2011):
"Inflated" crowns pertain to the crunch guild, while very blunt bulbous crowns pertain to the crush guild (see Massare, 1987). 0. teeth slender, sharpening apically 1. teeth robust, "inflated", or bulbous apically ',

374 . Mid to posterior dentition, presence of pebbled ornamentation on tooth crown surface (Andrade et al., 2011): 0. absent; 1. present, enamel ornamented with a pebbled pattern',

375 . Mid to posterior dentition, presence and morphology of ridged ornamentation on enamel surface of teeth (Andrade & Bertini 2008a, ch123mod):
0. enamel ornamentation absent or incipient 1. present, composed of basi-apical well-defined ridges, conspicuous and set apart to each other, never anastomosed 2. present, composed of numerous basi-apical well-defined ridges, conspicuous and set close to each other, rarely anastomosed, with anastomosis stronger apically 3. present, composed of numerous basi-apical low ridges, feeble and set close to each other, poorly anastomosed, with anastomosis stronger apically 4. present, composed of numerous basi-apical low ridges, feeble and set close to each other, anastomosed into a fabric of ridges distributed through most of the crown',

376 . Mid to posterior dentition, presence of accessory ridges on labial-lingual surfaces of crown (Andrade et al., 2011): 0. absent; 1. present, basi-apical, evident and well-spaced, formed by enamel and dentine',

377 . Mid to posterior dentition, number of cusps per tooth (Gomani 1997, ch46mod; Buckley et al. 2000, ch113mod; Pol 2003, ch162mod; Turner & Buckley 2008, ch188mod):
0. each crown has single apical cusp, regardless of presence of accessory cusps in cingulum
1. each crown has one main cusp aligned with smaller cusps, arranged in a single row
2. several cusps, unequal in size, arranged in more than one row
3. multiple small cusps, subequal in size, along edges of occlusal surface',

378 . Carinae, presence of keel at the edge of tooth crown (Andrade et al., 2011):n0. absent; 1. present',

379 . Carinae (mid-posterior dentition), presence and morphology of denticles at crown edges (Buckley et al. 2000, ch104mod; Sereno et al. 2003, ch53mod; Andrade & Bertini 2008a, ch132rev): 0. homogenous carina, serrated with cuneiform to ripple-like true denticles (ziphodont)n1. true denticles absent, crowns either with a smooth edge (non-ziphodont), or anhomogenous carina where crenulations may appear as a result of superficialnornamentation (false-ziphodont)n2. heterogeneous carina, composed by tubercle-like true denticles (ziphomorph)n',

380 . Carinae (maxillae), distribution of denticles at crown edges (Andrade & Bertini 2008a, ch132mod): 0. mesial and distal crown edges with the same morphology, either with or without true denticlesn1. mesial carina absent and distal carina present',

381 . Carinae (mid-posterior mandible), distribution of denticles at crown edges (Andrade & Bertini 2008a, ch132mod):State (1) is putative apomorphy of Sphagesaurus, but unknown in Armadillosuchus.n0. mesial and distal crown edges with the same morphology, either with or without truendenticlesn1. mesial carina present and distal carina absent, with mid-posterior teeth occluding asnoopposing bladesn',

382 . Occlusion, relation between premaxillary and mandibular dentitions (Andrade et al., 2011): Interlock = interfingering sensu Brochu (1999). 0. either match the mandible or slightly cover it, as upper teeth overbite the dentary teeth 1. premaxilla widely overhangs the mandible, with premaxillary ventral margin covering the alveolar margin at anterior mandible ',

383 . Occlusion, relation between maxillary and mandibular series at mid dentition (Andrade et al., 2011): 0. in-line or interlocked 1. maxillary dentition overbites mandibular dentition',

384 . Occlusion, relation between maxillary and mandibular series at the posterior dentition (Andrade et al., 2011): 0. in-line or interlocked 1. maxillary dentition overbites mandibular dentition ',

385 . Premaxillary teeth, presence of an hypertrophied tooth at penultimate or last alveolus (Andrade & Bertini 2008a, ch125mod): 0. all teeth subequal in size 1. one enlarged tooth, longer than the other premaxillary elements, usually not higher than the symphyseal depth 2. one fully hypertrophied tooth, much longer than the other premaxillary elements and at least as high as the symphyseal depth, also with a much

larger cross-sectional area at crown base',

386 . Premaxillary enlarged tooth, size relative to largest teeth at maxillae and mandible (Andrade et al., 2011):n0. premaxillary tooth smaller, with shorter crown and shorter-narrower alveoli, or subequaln1. premaxillary tooth larger than any given tooth at maxilla or mandible, with higher crown and longer-wider alveolus',

387 . Premaxillary alveolar margin, orientation (Serenio et al. 2001, 2003, ch68mod; Turner & Buckley 2008, ch239mod):Note that scorings strongly diverge from the original. 0. vertical, dentition is procumbent or not 1. inturned, dentition is not procumbent ',

388 . Premaxillary alveolar margin, projection relative to the maxillary alveolar border (based on Wu et al. 2001b; after Serenio et al. 2001, 2003, ch71):0. absent, alveolar margin of premaxillae and maxillae continuous, usually in the same plane 1. present, premaxillary alveolar margin is ventrally offset',

389 . Premaxillary alveolar margin, distinction relative to the maxillary alveolar border, in lateral view (Andrade et al., 2011):0. alveolar margin is continuous, and maxillary dentition is no more than slightly offset ventrally 1. premaxillary and maxillary alveolar margins are separated by a extremely deep notch, with maxillary dentition distinctly offset ventrally ',

390 . Premaxillary alveoli, disposition in ventral view (Serenio et al. 2001, ch69mod; Turner & Buckley 2008, ch240mod):0. alveoli set in the alveolar margin to form an arched row, curved posteriorly from midline and poorly diverging from medial line, usually angled laterally at c. 90 degrees or less 1. alveoli set in the alveolar margin to form a straight to poorly arched row, strongly diverging from medial line and angled laterally at c. 120 degrees ',

391 . Last premaxillary tooth, relative position in the horizontal plane (Serenio et al. 2001, 2003, ch70mod; Turner & Buckley, 2008, ch241mod):0. strongly anteromedial to first maxillary tooth 1. anterior to first maxillary tooth, or slightly altered relative to it 2. evidently anterolateral to first maxillary tooth',

392 . Maxillary dentition at anterior maxillae, presence of an hypertrophied caniniform tooth (Andrade & Bertini 2008a, ch130mod): 0. absent, no enlarged caniniform is present, with maxillary dentition usually isometric to subisometricn1. present as an enlarged tooth slightly larger then (but not contrasting with) neighboring teeth, with maxillary dentition anisometricn2. one hypertrophied tooth, much larger than

neighboring teeth and contrasting in size with them, with maxillary dentition strongly anisometric',

393 . Maxillary dentition, morphology (Andrade & Bertini 2008a, ch130mod): 0. all maxillary teeth caniniform, or last teeth lanceolate (isomorphic or subisomorphic) 1. acute caniniforms anteriorly, followed by blunter caniniform teeth 2. caniniform teeth anteriorly, followed by molariform teeth 3. most or all teeth molariform, but teeth 1-2 eventually weakly caniniform to conical',

394 . Maxillary tooth row, extension relative to anterior border of suborbital fenestra (Ortega et al. 2000, ch18part): 0. does not reach the anteriormost border of the suborbital fenestra 1. reaches the anteriormost border of the suborbital fenestra 2. extends posterior to the anteriormost border of the suborbital fenestra',

395 . Maxillary tooth row, position of last maxillary tooth relative to posterior border of suborbital fenestra (Ortega et al. 2000, ch18part): 0. far anterior to the posteriormost end of the suborbital fenestra 1. at the same relative position of the posterior border of the suborbital fenestra, or very close',

396 . Maxillary/dentary teeth, implantation of anterior to middle elements, at maturity (Ortega et al. 2000, ch19mod; Turner & Buckley 2008, ch164mod): 0. teeth set in fully isolated alveoli 1. at least part of the teeth set in a groove, not separated by septa',

397 . Maxillary/dentary teeth waves, in non-tubular-snouted forms (based on Clark 1994, ch79; as in Turner & Buckley, ch79mod): 0. absent, no tooth size variation 1. one wave of teeth enlarged, at mid snout 2. enlarged teeth in two waves 3. one wave of teeth greatly enlarged, at the end of maxilla/dentary',

398. Symphyseal dentition, alignment of anteriormost alveoli relative to the medial line (Andrade et al., 2011): 0. alveoli 1-4 not transversally aligned at anterolateral margin 1. alveoli 1-2 transversally aligned, and following alveoli set posteriorly to them 2. alveoli 1-4 transversally aligned, so the fourth alveolus is lateral (or lateral and slightly posterior) to first alveolus, and following alveoli are posterior to them',

399 . Symphyseal dentition, position of fifth alveoli in dorsal (buccal) view (Andrade et al., 2011): 0. distant, or at least both alveoli moderately apart 1. close to each other, next to the medial line of symphysis',

400 . Symphyseal dentition, presence of a complete symphyseal tooth battery (Andrade & Bertini 2008a, ch141): 0. absent; 1. present, teeth from each pair closer to each other than to other teeth in the same hemimandible',

401 . Symphyseal dentition, presence of highly procumbent teeth (Andrade & Bertini 2008a, ch140mod): 0. non-procumbent to mildly procumbent 1. first symphyseal pair highly procumbent, crowns nearly horizontal 2. pairs 1-2 highly procumbent, crowns nearly horizontal',

402 . Symphyseal alveoli 1-2, confluence (Andrade et al., 2011):Based on Brochu (1999, ch52). 0. well-separated, usually as much distant from each other as from other mandibular teeth 1. alveoli 1-2 confluent, separated by a thin alveolar wall, and clearly apart from neighboring alveoli',

403 . Symphyseal alveoli 3-4, confluence (Brochu 1999, ch52mod, part):n0. well-separated, usually as much distant from each other as from other mandibular teethn1. alveoli 3-4 confluent, separated by a thin alveolar wall, and clearly apart from neighboring alveoli',

404 . Symphyseal alveoli 3-4, relative size (Brochu 1999, ch52mod, part):n0. nearly same size, or third alveolus largern1. fourth alveolus larger than third '405. Symphyseal alveoli 3-4, relative position (Andrade et al., 2011):n0. tooth 3 medial to tooth 4n1. tooth 3 anteromedial to tooth 4n2. teeth 3-4 set in tandem',

406 . Symphyseal alveolus 1, relative position (Andrade et al., 2011): 0. not in line with alveoli 3-4, closer to the medial line of symphysisn1. in line with alveoli 3-4',

407 . Symphyseal alveolus 2, relative position (Andrade et al., 2011):0. not in line with alveoli 3-4 and closer to the medial line 1. in line with alveoli 3-4, as close as these to the medial line 2. not in line with alveoli 3-4, at a more lateral position ',

408 . Dentary tooth opposite to premaxilla-maxilla contact, isometry (Andrade et al., 2011): 0. subequal to other neighboring teethn1. tooth is at least evidently enlarged, anisometric relative to other neighboring teeth',

409 . Dentary tooth opposite to premaxilla-maxilla contact, length (Clark 1994, ch80; Sereno et al. 2003, ch54; Andrade & Bertini 2008a, ch142):0. small to medium sized, but length is no more than twice the length of other neighboring teeth 1. hypertrophied, at least twice longer than neighboring teeth',

410 . Dentary tooth opposite to premaxillary-maxillary suture, occlusion (Norell 1988, ch29;Brochu 1999, ch77mod):0. occludes either in notch at premaxilla and maxilla early in ontogeny, or lateral to premaxilla-maxilla suture, when the notch is absent or poorly defined 1. occludes in a pit between premaxilla and maxilla; no notch early in ontogeny 2. occludes medial to premaxilla-maxilla suture, but not in a pit or a notch',

- 411 . Dentary tooth occluding against premaxillary-maxillary suture (Andrade et al., 2011):n0. third, or anteriorn1. fourthn2. fifth, or posterior',
- 412 . Maxillary dentition, area occupied by teeth and alveolar margin of maxilla, in palatal view (Andrade & Bertini 2008a, ch131mod): 0. proportionally small teeth set in a narrow alveolar margin, marginal to palate/oral cavityn1. proportionally large teeth set in a wide alveolar margin, occupying large area at the maxillary ventral ramus/oral cavity',
- 413 . Mandibular teeth 7-8, relation with the neighboring teeth (Andrade et al., 2011):0. not particularly distinct 1. forming a distinct set, with alveoli closer to each other than to other teeth, and crown from tooth 7 much smaller than crown 8 2. teeth 7-8 are distant from each other, but alveoli 6-7 and 8-9 forming isolated sets, and alveoli 7-8 smaller than other alveoli ',
- 414 . ORD Maxillary teeth, occurrence of bilateral paramesial rotation (Pol 2003, ch137mod; Andrade & Bertini 2008a, ch133):0. absent 1. bilateral paramesial rotation up to 30 degrees from the original plane 2. bilateral paramesial rotation clearly over 30 degrees from the original plane ',
- 415 . Middle and posterior mandibular teeth, occurrence of bilateral paramesial rotation (Andrade & Bertini 2008a, ch144):n0. not oblique or slightly alteredn1. oblique (more than 30 degrees).',
- 416 . Middle and posterior teeth, occurrence of bilateral paradistal rotation (Andrade et al., 2011):0. absent 1. bilateral paradistal rotation present, teeth obliquely implanted, with rotation of at least 30-40 degrees from the original plane ',
- 417 . Middle and posterior teeth, presence of cingula with accessory cusps (Andrade & Bertini 2008a, ch149mod):n0. absent; 1. present, cingulum bearing a series small of cusps, set labial/lingual to the main bodynof crown',
- 418 . Posterior teeth, presence of rings of undulating enamel on crown surface (Gasparini et al. 2006, ch242):n0. absent; 1. presentn',
- 419 . Vertebrae, presence of strong procoely (Andrade et al., 2011): 0. absent, vertebrae no more than feebly procoelicn1. present in all cervical, dorsal and proximal caudals, with degree of procoelynprogressively decreasing in distal caudalsn',
- 420 . Presacral vertebrae, morphology of articular surfaces (Clark 1994, ch92+93; Brochu 1999, ch18):0. all amphiplatic or amphicoelicn1. presacral series includes at least gently procoelic vertebrae',

421 . Presacral vertebrae, presence of a ventrally projecting laminar process (hypapophysis) ventral to the centrum (Wu & Sues 1996, ch37m; Clark 1994, ch91mod; Andrade & Bertini 2008a, ch158+159): 0. absent or incipient, but neither laminar nor projecting ventrally, no more than a sagittal ridge 1. present as fully projecting laminae',

422 . Caudal vertebrae, morphology of articular surfaces of proximal elements (Clark 1994, ch94mod): Further data from Buscalioni & Sanz (1990), Ortega et al. (2000), Schwarz (2003). Biconvex first caudal so far identified only in the Fruita Form. 0. amphiplatic or amphicoelic 1. all at least gently procoelic, only with first caudal eventually biconvex ',

423 . Axis, proportional length of the main body of the centrum relative to its height (Andrade & Bertini 2008a, ch151): n0. short, length and height of centrum subequal n1. long, centrum evidently longer than high',

424 . Axis, development of neural spine laminae (Andrade & Bertini 2008a, ch152): n0. poorly developed, limited to the posterior half of the neural arch 1. well developed, occupying the dorsal surface of the neural arch and projecting anteriorly and posteriorly to it, due to the presence of prespinal and postspinal laminae',

425 . Axis, morphology of posterior half of neural spine (Brochu 1999, ch3; Turner & Buckley 2008, ch258): n0. widen 1. narrow',

426 . Axial hypapophysis, presence of deep fork (Brochu 1999, ch19; Turner & Buckley 2008, ch259): n0. present n1. absent or feeble',

427 . Third cervical vertebra (CIII), development of prezygapophysis (Andrade & Bertini 2008a, ch155): n0. poorly developed, slightly projecting anterior to the vertebral centrum n1. well developed, clearly projecting anteriorly, beyond the vertebral centrum',

428 . Anterior (postaxial) cervical vertebrae, development of neural spine laminae [Clark 1994, ch90mod; Pol 2003, ch90mod; Andrade & Bertini 2008a, ch153rev]: n0. laminae absent or poorly developed, with neural spine rod-shaped or poorly flattened n1. prespinal and postspinal laminae well developed, with neural spine occupying at least most of the dorsal surface of the neural arch',

429 . Posterior cervical vertebrae, development of neural spine laminae [Clark 1994, ch90mod; Pol 2003, ch90mod; Andrade & Bertini 2008a, ch156rev]: n0. laminae absent or poorly developed, with neural spine rod-shaped or only slightly flattened laterally n1. well developed, laminar, occupying at least most of the dorsal surface of the

neuralnarchn',

430 . Anterior cervical vertebrae, structure of the base of neural spine (Andrade & Bertini 2008a, ch154):n0. gracile base, with neural spine clearly distinct from the neural archn1. robust base, with the development of spinozygapophyseal ridgesn',

431 . Posterior cervical vertebrae, structure of the base of neural spine (Andrade & Bertini 2008a, ch157):n0. gracile base, with neural spine clearly distinct from the neural archn1. robust base, with the development of spinozygapophyseal ridges',

432 . Sacral vertebrae, number (Buscalioni & Sanz 1988, ch44mod; Pol & Apesteguia 2005, ch115mod): 0. two1. three, being the third the first caudaln',

433 . Sacral vertebrae, orientation of the transverse processes (Gasparini et al. 2006, ch255mod; Young & Andrade 2009, ch82mod): 0. horizontaln1. arched ventrally, at least in the first sacral',

434 . Sacral vertebrae, relative position of lateral end of transverse process (Andrade et al., 2011): 0. level with the vertebral centrumn1. ventral relative to the vertebral centrum, transverse processes of both sacralnlateroventrally directedn',

435 . Caudal vertebrae, relative height of neural spine (Andrade et al., 2011):0. larger spines are up to 2.5 times the height of vertebral body 1. average spines are 2.5-4 times the height of vertebral body ',

436 . Tail, vertebrae morphology near distal end (Young & Andrade, ch61):State (1) is putative apomorphy of Metriorhynchidae. 0. non-hypocercal, distal vertebrae isomorphic to poorly heteromorphic 1. hypocercal, caudal series clearly heteromorphic, with a section of the distal vertebrae defining the lower lobe of a tail fin',

437 . Atlantal ribs, presence of very thin medial laminae at anterior end (Brochu 1999, ch16):n0. absent; 1. presentn',

438 . Scapulocoracoid synchondrosis, precocious closure during ontogeny (Brochu 1999,nch24):n0. absent, synchondrosis closes very late in ontogenyn1. present, synchondrosis closes relatively early in ontogenyn',

439 . Scapula, symmetry (Clark 1994, ch82; Brochu 1999, ch22; Ortega et al. 2000, ch120mod; Lauprasert et al. 2007, ch66):n0. symmetrical, anterior and posterior edges similar in lateral view, with dorsal endnpoorly flared 1. asymmetrical, anterior edge strongly concave relative to posterior edge, with distal end strongly flaredn',

440 . Coracoid, length relative to the length of scapula (Clark 1994, ch83; Ortega et al. 2000, ch121; Lauprasert et al. 2007, ch67):n0. smaller, approximately half the length of

the scapula 1. subequal',

441 . Ilium, relative length of anterior and posterior processes (Clark 1994, ch84; Lauprasert et al. 2007, ch68): 0. subequal, anterior and posterior processes similar in length 1. unequal, with anterior process relatively small, one quarter or less than the length of the posterior process',

442 . Ilium, presence of indentation at the dorsal margin of iliac blade (Brochu 1999, ch28mod, part): Character divided to separate diverse aspects of the morphology of the anterior end of iliac blade. This character samples the indentation at the dorsal edge of the anterior process. 0. absent, dorsal edge convex or straight in lateral view 1. present as a shallow or modest dorsal indentation 2. present as a strong dorsal indentation ("wasp-waisted")',

443 . Ilium, morphology of anterior process of iliac blade, in lateral view (Brochu 1999, ch28mod, part): 0. very narrow relative the main body of the iliac blade 1. rounded and moderately broad relative the main body of the iliac blade 2. very broad and deep, at least half the height of the main body of the iliac blade',

444 . Ischium, presence of pubic process (reformulated from Clark 1994, ch86): See Andrews (1913). 0. pubic process absent, or incipient and small, not restricting the participation of the pubis to the acetabulum 1. anterior process well developed, robust and with a round head, at least partially restricting the participation of pubis in the acetabulum',

445 . Pubis, exclusion from acetabulum (Andrade et al., 2011): Based on Andrews (1913) and Clark (1994, ch86) 0. pubis not excluded, participating at least marginally of the anteroventral rim of acetabulum 1. pubis excluded, acetabulum composed exclusively by ischium and ilium',

446 . Pubis, presence of exclusive proximal contact with ischium (Andrade et al., 2011): Based on Andrews (1913) and Clark (1994, ch86) 0. absent, pubis supported by both ilium and ischium 1. present, proximal head of pubis contacts only the ischium',

447 . Pubis, expansion of distal end (Clark 1994, ch85): 0. absent, pubis rod-like 1. present, paddle-like',

448 . ORD Limb bones, length relative to trunk, at maturity (Brochu 1999, ch33mod): 0. limb bones relatively short 1. limb bones moderately long 2. limb bones very long',

449 . Limb bones, general structure (Brochu 1999, ch33part): 0. limb bones robust 1.

limb bones overall slender, but not weak 2. gracile',

450 . Limb bones, relative length of forelimbs/hindlimbs (Brochu 1999, ch33part) :0. forelimb much shorter than hindlimb at maturity1. forelimb slightly shorter than hindlimb at maturity2. forelimb and hindlimb subequal in length at maturity',

451 . Limb bones, general morphology of manus and pes (Andrade et al., 2011):n0. plantigrade or digitigraden1. paddles',

452 . ORD Limb bones (forelimbs), proportional length of ulna relative to the humerus (Andrade et al., 2011):State (2) is putative apomorphy of Teleosauridae, where humerus is almost twice the size of ulna.n0. ulna clearly longer than humerusn1. ulna subequal to humerus (distal/proximal = 75-125%)n2. ulna clearly shorter than the humerus',

453 . ORD Limb bones (hindlimbs), proportional length of tibia relative to the femur (Andrade et al., 2011): 0. tibia subequal to femur, or only slightly shorter (distal/proximal >74%)n1. length uneven, tibia evidently shorter than the femur (distal/proximal c. 50-74%)n2. length uneven, tibia much shorter than femur (distal/proximal < 50%)',

454 . Humerus, relative orientation between the proximal and distal heads (Ortega et al. 2000, ch181): 0. unaligned, each turned more than 30 degrees 1. mostly aligned, each turned no more than 30 degrees',

455 . Femur, relative orientation between the proximal and distal heads (Ortega et al. 2000, ch149):n0. femur with light torsion, proximal and distal articulation facets approximately at 30 degrees or less from each other1. femur with evident torsion, proximal and distal articulation facets approximately at 60 degrees from each other',

456 . Humerus, presence of common insertion for M. teres major and M. dorsalis (Brochu 1999, ch29; Turner & Buckley 2008, ch261):n0. absent, separate scars can be distinguished dorsal to deltopectoral crestn1. present, insert with common tendon, with a single insertion scar',

457 . Ulna, morphology of olecranon process (Brochu 1999, ch27; Turner & Buckley 2008, ch260):n0. narrow and subangularn1. wide and rounded',

458 . Proximal carpals, general morphology of radiale and ulnare (Clark, 1986; Wu & Sues 1996, ch40; Ortega et al. 2000, ch129; Pol & Apesteguia, 2005, ch110; Turner & Buckley 2008, ch110): 0. radiale and ulnare short, almost spherical 1. radiale and ulnare at least poorly elongated',

459 . Proximal carpals, relative proportions of radiale (Ortega et al. 2000, ch127):n0.

slender, much longer than wide 1. broad, proximal width subequal to length',

460 . Proximal carpals, length of radiale relative to length of metacarpals (Andrade et al., 2011): Based on discussion by Sereno & Larsson (2009). 0. radiale is shorter than metacarpals, or subequal 1. radiale is evidently longer than metacarpals',

461 . Proximal carpals, relative length of radiale and ulnare (Ortega et al. 2000, ch128): 0. radiale and ulnare subequal in length 1. radiale evidently longer than ulnare',

462 . Proximal carpals, relative expansion of proximal and distal heads of radiale (Buscalioni & Sanz 1988, ch54; Ortega et al. 2000, ch150; Pol & Apesteguia, 2005, ch117): 0. almost equally expanded 1. proximal head wider than distal one',

463 . Proximal carpals, presence of a facet of articulation in the radiale, for reception of the ulnare (Pol, 2005): 0. absent; 1. present, facet evident, near its proximal end',

464 . Femur, general shape (Andrade et al., 2011): Based on Andrews (1913). State (1) is putative apomorphy of Thalattosuchia. 0. poorly sigmoid 1. strongly sigmoid',

465 . Pes, relative length of digits III and IV (Wilkinson et al. 2008, ch77; Young & Andrade 2009, ch77): 0. digit III is longer than digit IV 1. digit IV is longer than digit III',

466 . Calcaneum tuber, presence (Young & Andrade 2009, ch74rev): 0. absent or vestigial 1. present',

467 . Metatarsal I, morphology of proximal end (Young & Andrade 2009, ch76): 0. proximal end not enlarged 1. proximal end moderately enlarged 2. proximal end greatly enlarged',

468 . Dermal armor, presence and distribution (Clark 1994, ch100mod; Brochu 1999, ch39part): 0. absent 1. dorsal osteoderms present, but ventral osteoderms absent 2. dorsal and ventral osteoderms present',

469 . Presacral nuchal armor, relation of nuchal osteoderms with the remaining dorsal armor and skull (Brochu 1999, ch38mod, part): 0. large nuchal shields continuous from postoccipital region to trunk armour, with any given osteoderm contacting the anterior and posterior elements (except for the first postoccipital shield) 1. large nuchal shields continuous with trunk armour, but not reaching the postoccipital region 2. large nuchal shields discontinuous with dorsal trunk armour and absent from postoccipital region',

470 . Presacral nuchal armor, number and arrange of nuchal shields (Brochu 1999, ch38mod, rev, part): 0. four paramedian nuchal shields, sided by two accessory shields, all enlarged relative to the remaining neck dermal armour 1. four paramedian nuchal

shields enlarged relative to remaining neck shields, and no accessory shield enlarged 2. eight (or more) shields, arranged in two paramedian rows, enlarged relative to remaining neck shields, with no accessory shield enlarged 3. ten or more median osteoderms, combined with several lateral osteoderms, composing a distinct cervical shield ',

471 . Presacral nuchal armor, morphology of nuchal shields relative to the remaining trunk dermal armour (Brochu 1999, ch38mod, part):n0. nuchal and dorsal trunk shields undifferentiated, morphology grading continuouslyn1. nuchal shields clearly differentiated from dorsal trunk shields by size and generalnmorphology (regardless of contact between nuchal and trunk series)n',

472 . Presacral dorsal armor, number of contiguous longitudinal rows of paravertebral osteoderms (Norell & Clark 1990, ch12mod; Brochu 1999, ch37mod; Ortega et al. 2000, ch107):n0. two paravertebral medial rowsn1. four continuous rows, two paramedian and two lateraln',

473 . Presacral dorsal armor, presence and number of accessory ranges of osteoderms (sensu Frey, 1988) in addition to the dorsal rows of osteoderms (Norell & Clark 1990, ch12mod; Brochu 1999, ch37mod; Ortega et al. 2000, ch107): 0. absent (total of up to four dorsal rows)n1. present, two accessory rows (total of 4-6 dorsal rows)n2. present, no less than four accessory rows (total number dorsal rows usually eight ornmore)',

474 . Presacral dorsal armor, type of contact between elements in a row (Clark 1994, ch98): 0. imbricated, any given anterior trunk osteoderm partially overlays its following element 1. sutured, osteoderms do not cover adjacent dermal elements, and are sutured if in contact ',

475 . Presacral dorsal armor, general proportions of medial elements (Clark 1994, ch95mod):n0. at least as long as wide n1. evidently wider than long',

476 . Presacral dorsal armor, surface of paravertebral osteoderms (Andrade et al., 2011): 0. mostly straight, forming a plain flat scute, either keeled or not 1. scutes strongly curved, with convex surface, partially embracing the vertebrae from side to side ',

477 . Presacral dorsal armor, presence of an anterior process to articulate with the anterior adjacent scute, in medial dorsal elements (Norell & Clark 1990, ch13rev; Clark 1994, ch96; Brochu 1999, ch40rev; Ortega et al. 2000, ch113rev):n0. absent; 1. present',

478 . Presacral dorsal armor, presence of an anteroposteriorly directed keel on the dorsal surface of paramedial elements (Buscalioni et al. 1992, ch22; Clark 1994, ch101part,

rev; Brochu 1999, ch35):n0. absent; 1. presentn',

479 . Presacral ventral armor, presence of ventral collar scales (Poe 1997; Brochu 1999, ch156): 0. absent, no shield enlarged relative to other ventral scales 1. present, forming a single row of enlarged scales 2. present, forming two parallel rows of enlarged scalesn',

480 . Presacral ventral armor, presence of paired ossifications (Buscalioni et al. 1992, ch21; Brochu 1999, ch39):n0. single or absent; 1. present, pairs sutured togethern',

481 . Postsacral armor, distribution when present (Clark 1994, ch99mod):n0. a pair of rows, covering the vertebral columnn1. several rows, enclosing the tail surface',

482 . Postsacral armor, presence of an anteroposteriorly directed keel on the dorsal surface of paramedial elements (Clark 1994, ch101part, rev):n0. absent; 1. present

483. Tongue, presence of keratinized surface (Brochu 1999, ch159):State (1) is putative apomorphy of Alligatoridae/Alligatoroidea, but unknown in all fossil taxa. Originally based on Taplin & Grigg (1988), apud Brochu (1999).n0. absent; 1. presencen',

484 . Functional lingual salt glands, presence (based on Taplin 1985, Taplin et al. 1989, Brochu 2007):0. absent; 1. presentn',

485 . Internal hypertrophied salt glands, presence (Andrade et al., 2011):n0. absent; 1. present',

486 . M. caudofemoralis, morphology (Frey et al. 1988; Brochu 1999, ch160):n0. with single headn1. with double head (longus and brevis)' ;

MATRIX

Gracilisuchus

10001210000-----??00??0?00000-000020100011101311002000100002?00-----?2010-
00?10000?00000100001010000000000124??000001000000?????0100000010000001
0?200000100?20001000---1?1000000111000??????11100??00000?-0--00?00-----?-1---
??-?-----1-000?--??0??0??1000000?0000000-0010?????2?0??0000??00?0??1?
?00--0020021000000010?00?00000020000?00-000001??0102000-0--0??00000000000
?0001110000001101001000000010000(12)?00000000000011?1110??0000??000?0000
?12001?00?????????00101??0000?11??0?????

Pseudhesperosuchus

040012010?0-----?0?0??0?00001-000020?0001110130?002001101002000-----?21101
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?2?0000100020110000---1??000000110?00?????01100?????00?-??-00000-----?-1-?-?

?-??-----1-0???-10?0?00?000?00?0000000-0010????2001?0010?0????1??
00--?021100?000000?????0?00?20?0?????00???1?0?02000-0-???00?00000000??0
0011?0000011010010000???????(12)?0?00000000011??11100??00?00???????2200
0000??10010000??1????????????????

Sphenosuchus

040012010?0-----?000?0?00001-000020100011101300002001??1002000-----?21100
00?10-0000000010000101000100?1201200??0000000100000-1-?01101100100012100
?210000100?20110010---111100000110000?????11100?0-00100?-0--00000-----?-1---?
?-0-----?-?00?--1000?00?1000000?0000000-001001???2001000000?00?0??1?
?00--0021100000000010??1?01000020200000-01?001???102000-0-?00?00000000000
10000110000001101001000000110010(12)10000000000001??1110000000?0000?000
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Junggarsuchus

000012010???????????0?0?00000-0000??00011100200002000101002000-----?211
0000?10000?0000010000111000000?010120??00000?010000?????0110110010001??
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01000011000000110?0?010000????????(12)?0?000000110?????100?00?0???????????2
2?0?0?0??100???????1????????????????

Protosuchus

000001?10???1?????110110001000-000020100011100100002001100002100-----?211
0000?20-0-00000010000111000?0000001000?0001000100000-1-?011000000000110
00?000000000010101010---111000000100000212??111000?0?0101?-0--00000-----?-1-
--??-0?-----?-????-1?00?0?0?10?0000?1100101000?01???2000110011101?0??
1?00--00210500000000010?00?01000?20201000-000001?0102000-0--00?0(01)(01)00
000000?1000?000000100?000000001???1001000000000?0?????10?00000??100?0
1??011101000??100100001020200001?11??1???0?

Hemiprotosuchus

000001010?1?1110????10?0?00000-000020?0001110010000200110?002100-----?211
0100?20-0-?0000010000011000?00?0001000?000101010000?????011000000000110
00?000000000020101010---111000000100000212??111000?0?01?0--0?00-----?-?-
--??-??-----?-????-??00?00?1000000?1100101000???1???200?110011?0?0??

1??00--?0210(01)00000000??00?0100??2020????00?001??0?02000-0--??0??00000
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Gobiosuchus

100001010?????????000????0000-000020?0001110010?11?1?0-000021000---021??
100?(02)0-0-?0000010000100000000?-101000??0001000200011?00??11020001?1000
0?00000000011010000110---1?1000000?1100021?1(12)1100?0??01101?-2000??00--
10?00-0-??-0---01-0000021001-0000001000-?00000?0000?1?00011?000?????2000?1
0011101?0??1??2?0??00---??????(01)0??????????0??000-??????0?0?01000?00
?011?0000000??????0-00001002010?00??????11(01)?0?0??0000??????????????0?
?0??????111?0????????????????2???1001?01??11????

Hsisosuchus_chowi

100011110011011111?00??10?0?000-??0?????0?????????2111100????03??????211
2100120-01??0?0100?010100000?00000-001?00010(01)02000(01)?????10101?0010?
01100??000000010020000110---111110010????00(12)1(01)??11011??00101?-1000?
110?--??1??-0-??-0---01-000??10010000000?1000?1101100000?0111011?0?00?????1
00011201111?0?0?1??2000?0?????0000010?0?00?001(01)00200??110?1?001?0?020
10001200?00?01000000100011100110?11(01)00?100??????????0?000000010?????
11000??0?0?10??1??1?01?????110111????2??00001000?0?0????

Hsisosuchus_dashanpuensis

10001111001101111??00?110?00000-0?0020?001110010?012??1100002?030---?21?
210012?-01?1010010010101?0000?00000-000?00010(01)02100?????1?10110010001
100000?0000?10020000110---111?100?0?11000??(0
1)?1?10110?00101?-100011100--10000-0-??-0---01-0000021001000000011000?1101
100000?0111011?0?00?????10001120?11?1????1??2000?????????????????0?????
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Hsisosuchus_chungkingensis

1000??010011011111?00??10?0?0?0?-?????????1110010101211???00?????????????12
?00120-01?1010010010101?0000?00000-000?00010(01)022000?????10101000100011
00(01)0000000010020001110---111010001?11000(12)1(01)??11011??00101?-1000?1
100--????-0-??-0---01-00000?100?0?00000?100??1?01100000?0110011?0????1???10
001120?111?0?0?1??2000?0(01)0????000010?0?00?00??0?0?0??110?0001?0?0201

000?200?00?010000001000?11?????11000?10?????????????0?0000000?????????????
?0????0?????????????????????????????????02000??????????????

Platysuchus

1000211?0010110?????01110000001000010-0000???000???0101201002103?????00
10100100-0-?00000100101110000-0?22012001?00000?022000?????11101000000012
0000110000020010100020---0101?00001110000?---111100??12000?0?00111???00???
?01?????0????11?????????00?-?????????00?0?00?0000??100?11?10?????????010?200?0
?0?0?0?????20?0??220(12)0100001?0?0?00210?0?0?1?01?00???0?0?011200010?0
11000002001100000100000100?0-000001020110010?0010000?0?????????01000?01
1000?0?02002?01??100100101020-01001011?0?????

Steneosaurus_herberti

1000211200101???00?0?0010100100-0-?0000000012100011000002001121000?00001
1?010000?????20101200?0?00?0?0?02011200010?0110?????????????????????011100
00001000010-00001100000111010120100210310?1(01)100101110000-0?22012001?0
0100?022000?????11101?0010100020---0101100001110000?---1111001112000?0210
01001120200101000-0000011000?1000010010?1100?11?1000?????21000?220101000
01110?00002100?0101?12001?00?00002001100000100000100200-0000010201?0?10
000100?????????????????????????????????-?????????????????

Steneosaurus_bollensis

1000211?0010110?????001110000001000010-0000???000???010120100210310?1(0
1)?0010100100-0-?00000100101110000-0?22012002?00000?0220000-???1110?0010
00120000110000020010100020---0101100001110000?---111100??12000?02?0011210
00?000011?0100000011?0200101000-00000?0000?1000000000?110001111000?????2
0101200?0?00?0?????2?000?220(12)01000011?0?00002100?0?0?012001?00???0?02
011200010?01100000200?100000100000100200-00000102011001000010000?0??????
???01000?011000110102002101??100100101020-01001011?0?????

Pelagosaurus

121121120010100?????001110000001000010-00001111000011010120100210010110?
0012100100-0-000000100101110000-0?12012000?00000?0220000-0??111011001000
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?00101112000000011202002?1000-0000011000?1000000000?110001100000?0???201
0120000?00?0?????21000?21021100001110?00000200020000012001000???01020112
00010?01100000000?100000100000100200-00000102?110010000?000000?????????0

1100??110001101011011????1?0???101020-01001010??0???0?

Cricosaurus_araucanensis

03102110000-----00111000001131001301001112100111121001010021011?111?00
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00001100000001201000?0---1000000001110000?---11100???12000?02?001121000?0
0001112100000011?0200101000--?000???0??1000000000?1100011?1000?????201011
0000?0?0?0???11000?00---000001011?0?002000200-0012001000??0?0201020001
0?011000000000100000000000100200-000000020000010000?000000?????1000?01
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Cricosaurus_suevicus

03102110000-----?11100000113100130100111210011112100101002101?????001
2100100-0-?00000100100010000-0?220120?2?00?00?022010?????1110110010101100
001100000001201000?0---1000000001110000?---11100???1200???2???11?????0????
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0?????1?00?00---000001011?0?00200?200-0?????1?000?0?020102000?0?0110000
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Rhacheosaurus

13102102000-----????100000013100130100?11210011112100101002101?????????2
10010?0?000001??1000?000000?22012000?00000?022?10?????1110210000001100
00110000000?201000?0---1000000001110000?---111000?12000?????????????????
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0?????10?000---0000010???0?0020?0200-0?120???????0?02?102000?0?01100000
0001100000000000100(12)00-0000?0?0?000?000000?????110001101??110??1
10100111201??10000011110-----0--???

Metriorhynchus

13101110000-----0?11100000?1300010-0001112100111121001010021011??1(01)?0
012100100-0-?0000010010001000000?22012002?000001022010?????1110110010001
100001100000001201000?0---1000000001110000?---11100?1?12000?021001121000?
0010111210??0?01?20???1010?0?000001?0???1?00000000?110001111000?????201?1
200?0?00?0?????11000?00---000001011?00002000200-0012001012???01020102000
10?011000000001100000000000100200-000000020000010000100000011???1100011
01?011000110100111201??01000011100-----0--?1?

Dakosaurus_carpenteri

????11?0000-----0???00?00?1300010-000111?1001?112100101002101????00012
100100-0-?00000100?00?000000?22012012?000001022010?????11011001010110??
?1100??00?20?????????????00?????00?---???????12???0????11?0-????0????
?????????0?????0????????????????????????1???0????????????????????????
??0??00---?0???0???0?0???????-???????????0?02?112?0010?01?00000200110?
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???????1???0-----0--???

Dakosaurus_maximus

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??0?00---?00001011?00?00100?200-0?120?0?11???0?020??00???000000000001000
0???00000100(01)00000000002?000?10000101????????????????????????????
?????????????0-----0--???

Dakosaurus_andiniensis

03101200000-----00?110100001300010-000?11210011102100101002101?????0001
?100100-0-?0000010010001000000?22012012?00000?022010?????111011001010110
000110000000120100020---1000000001110000?---111000??12000?0?001121?0?00
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000?0?0?????1100?000---000001011?0?0010??200-0?????0?110?0?02?102000???0
000000000010000?000000100(0
1)00000000002?000?10000?01????????????????????????????????????
???????????0?????

Geosaurus_giganteus

????1?00000-----0?111000??1??????-?0??11210011112101201???????????001210
0100-0-?00000100000010000?0?220?2?1???0?0???2?1?????11101100101?1?????1?
00??00012010?0?0---1000000001110000?---11100???12000?02???????000?0???11??
???0?0??0?????0?????000????????????00???????????????????????0????????
???????00---000001????00?00???200-0?????1?12???????0???0???00011000000100
0?00?0?000?000000?00?0?20010?10000101??0????????????????????????????
???????????0-----0--???

Geosaurus_grandis

03101200000-----?01110000?11300010-000?11210011112100101002101?????001
2100100-?-?00000100?00010000?0?22012012?00000?022010?????111011001010110
00011000?001201000?0---100000000111?000?---?1100???1200?02?00?????????
1????????????????????????????00?0?000000???100?11?000?????????0?(12)00?0
?????????1?00?00---000001011?0?0010??200-0?120?1?12???????0102000?0?0001
10000001000?00?00000100?0000000?020(01)000?0?0010???0?????????????????
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Notosuchus

14000101010-0----0000110001000-00100-0100110001000021101010001001(1
2)0011201100?100-0000000010000?0100010010001100(02)?0001010010001000?111
011001000110000000000111010101110---110100011100000210000001100?01100?12
00011210102000100000010000121010111101001?0001111011111010000?110001110
000?1???1000111111111?1?01?022000022010000110020?0000110012010001011011
20??1010010001200?02000000010021?0112100001031011000?000201002?00100000
00?00?00001110000??101?0???111201000??1101010010(1 2)?0000?????????0?

Mariliasuchus

14000101010-0----0000110001000-00100-010000--00----21101010001000----120110
01100-0000000010000?01000100?0000-300?00010000100010???1110110000001(0
1)0000000000111010101110---110100011000000210000001100?01100012000112101
0201010000001000012101011110100130001110011101010000?110001110000?????1
000111111111?1?01?022000021100000110020?00000100120100?101101120??10100
1000120??0200000040002000112100001031011000100020100210010000000?00?00
01110000??1??????111201000???????00??(1 2)?0000?????????0?

Yacararani

14000101110-0----?00011000?000-0010??110000--00----21101010001020----?2?1?00
?100-00?000000??0?0?000000?0100-301?000101001000?????1110000000001100000
000001110101011?0---1100000000000112????000110??0?100?020001121100?010?10
0000100?212101002?101011000011?001?1?1010000??10??1?00?0?????10001111???
???1?01?02??0021000000110020?00000100120100?101111000?????10?1000120??12
00000000012110002100001031011010100021100200021000?????????????????????
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Adamantinasuchus

0???01?1110-0-----0???0110001000-00100-010000--00----2110101000102??????201?0
01100-00?0000000000?01000100???0?0000?00?1???001000?????1110100010?0?????
0?0000?1?01010?110---111000000000010??(01)?(01)0001100?0?1?0???0??1?21????0
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??11??????2???002110000011(01)020???0010??20100?1(01)?10100????0?0?0?????
???02?0000?0000200000210000103?0110??1???211002?002100000?????????????00
????????????11?0????????????00????????????????????

Armadillosuchus

0???0101?10-0-----0????????1000-00100-0?0000--00----211010?000?02??????20111?
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000001100?01011?0---110100010?000?02111?0011???0?1????????????????(12)?????
??0?0?????1????111?0?1?????
???2?????????000?????????0100?2?????1????????????????????????02?00?0101??2
1?00?210000103???1011100021100201?21000????????????????????????????????0??
?????????????(1 2)0310001?00????????

Sphagesaurus_huenei

0(04)000111110-0-----?0?01100?1000-001?0-010000--00----21101010001020----0201
?1?0100-00?000001?00?0?000?????????00?00001????00?????1110?00?0?0?1???0
0?00??110010101110---110100010010010?????00011???0?1?0?02001112101020?010
00000100101?0?1????10100?????11?0??11?0?0?10???1?0?1110?????????1?0?1111?0?
110?????2???1?????000?????????0100?20?????????????????????0?0?????0220000
101002110002100001031001011000021100201?2100000??10?????1????????????????
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Sphagesaurus_montealtensis

0(04)000111110-0-----?100110001000-00100-010011000000002110101000102?-???02
011000100-00?0000010000101000100?01011000?000100000000?0?0?111011001000
111000000000110010101110---10000000001001021(01)???0011?0?0?0?0?020011121
010(12)010?000000100?0121010111101002?00011000111?1010100?11???1110000??
???1?00111?0111???01?02200?02(12)?0000011?020???0?010002000?110110112???
?0?0?0???????0220000??10021100021000010310?101100002?100201021000??????
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Comahuesuchus

04000111010-?------?000?0?0?00-00100-?10000--00----210010100(01)100??????201

1000?10000?00000000001000000000(01)00-000?0001?10(01)?000????1000000000
0010000?0?00001100101011?0---11?(01)100?010000?????0011?0?0?1???0200?112
1010?0?000000001000012101011110?0???000110001?111010?00??100?11?0000????
?10?0?11110?11?1?????2200002(12)?0001110?02???0?000120?0??10111?0?????
?0???????000000000000100011000000010000?(12)00000010000-?0000?00???????
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Baurusuchus

040022?0010-0-----0100110001000-001020110000--00----20012210021000----121111
??110000?000001000000000010001201240??00010000100?????11101000100011001
0010000000010101110---1111100201?12002111110011??01101?0200?11210102000
00000002?010121010111101000000011110?1112011000?0100?1110000?1???100010
1110011?1?01?02?000021100100000020??00011110100001110?01111??1012010001
20??000000000001000011200000120000100000011001101000000000??10???0???10
000???????111?11201000??1101110010(1 2)????????????????

Stratiosuchus

040022?0010-0-----0100110000000-001020110000--00----210122100210010142?2111
1???10000?000001000000000010001201240??00010000100?????1110110010001100
10010000000010101110---1111100??1?12002111210011?0?0?101?020011121010200
000000002?010121010111101001000011110?1112011000?0100?1110000?????10001
011?0?11???01?02?0000211??100000?20???0?1???10???????0?11???1?120???????
?00?0000000010000112000001200001?000?????1101000000000?????????????00??
?????111?11201?00??1101110010(1 2)????????????????

Malawisuchus

000001110?0?0???0?00?100?1000-0??02?1(12)0011010000002100101??1100?????0
21??101110000?000001000?101000000000010000?00010100?001?????111?200010?0
10000000000?110010101110---110100010?00000211(01)?00011???0?100?02?001121
000?0000112000??0?0??100?0?110?0??000??00?1?0010?0?0??100?1110000?????1
000?(12)1?10?1??1?????220??02203?0?000002???0?0010?120201?110?0?000??1?100
10001200?00?001000010100111(12)01000?22?01100?????????02?000001000?0?????
??????0???1????????11?0????????????0010(1 2)?????0?01????????

Candidodon

000011211012011????0001100?1000-0?100-?10011000000002100101001100?????02
110?000?0-00?000001???110?000000?00010000?00010???100??????1110110000?010

00000?0000010010101110---11010001011?000????00011???0?10?02?00112100020
0001????0000?0121010(01)(12)1101000000011?01?10?1010000??100?11?0000?????1
0001111?0?11?0?????2200?0??????000?????????010??20?????110?????????????0?????
????00?0010?000100???10000012220110?0?????111???0?0?010?????????????????
??????????11?0?????????????0??? (1 2)??????????????????

Uruguaysuchus

0000112110120111??1000110001000-0?100-0?001100010?0021001010011001?0??02
110101010000?000001?01100000000000010000?00010100100?????111020001000
1000000000000100101011?0---110100000100000(12)1??00011???0?1???020001121
000(12)0000100100010?01210100211010000000?001?10?10(01)00?0?0100?11?0??
?????1000?11110????0?????2??0021000010001000???0010?1?0?0??11010?0???10
110100012???000001000000100?1110000012220?1000000?1??1021000000000000????
?????00000????1??111?11101??????????0???1??000000?-0??????

Araripesuchus_patagonicus

10001111001201000?1000??001?00-0??02?1(1
2)001100010000210100100?100??????21000000?1?0??00000100001?1000000000010
000?000101001000?????1000000010001000000?0000010010101100---11110001111?(
01)002101(01)000110?0?11?01020001121000?0000100000000?011101022110101110
00?100111001000000?0100?11?00????????1000111110?1??0001?02?00?0210310?000
1010??0?0?10?1?02?10110?0?100??1?11010101100?01?000000000????11100000012
20?100?????????0(12)?0?0?00000?????????????0???1????????111?1001?????????0??
10200001100-0??????

Araripesuchus_gomesii

1000111100120110011000101001000-0000211200110001000021010010011000----?2
100000011000?00000100001210000000000010000?0001010010001101?100000001000
1000000?0000010010101100---11111001211110021010000110??01110102000112100
010000100000010001110102211010111000?100?11001000000?0100011?0000?1???1
000111110?11?0001?02(03)000021031010001010??000010102021??11010?100??101
1010101100?01?000000000000111000000012?011000000010010(12)100000000010??
???00??10000??111??111111101001?0?????001010200001101-00?????

Araripesuchus_wegeneri

1000111100120110?11000101001000-0000211200110001000021010010011000----12
100000011000?000001000012000010000000-300?0000010010001101?100000001000

100000000000010010100100---111110011(12)11100210??00011?0?011?01020001121
000200001000000100011101002110100110001100111001000000?0100?1110000?1??
?1000111111?1??0001?02300002(12)??01000??????0?00000102???11010?0?????
??????????00000000(01)00000011110000001220120000001100102100000000000??
?????????00??????????11101?0???10110?0101?????????-011??0?

Araripesuchus_buitreraensis

1???11110???0?????00?????0000-0?0??120011?00100002??100100?10?????????
10??1100??000001??????0000000(01)(01)00-3?0?0000?1001?00?????100001001000
100?000?000??100?01?01?????1??1000?(01)???00(12)1???0011??0?1??02000112
1000?000010?000010?01110100211010110000?1001?10010000???0???1???0??????
1?0??11?1??????01?0?????0?????01000?????????010?120?00111?0?????????????
?????0?00000000?????????0100001?(12)01?00?0???0010(12)10?0?00????????????
??

Araripesuchus_tsangatsangana

00001112001?01100??000?10000000-0?00??12001100010?002??100100?10?????0??
??10??1000??00000101001?00000000(01)(01)00-3?0?000001001?001111?100000001
000100000010000010010100100---11110001(12)10?0002101(01)0001100?011101020
0011210???0?00??000??0011(01)0(01)00211010000000?10???10?(01)0???00?0100
11110000?1???1000?11110111?0001?023000011100010001?10??0000100120001011
0100??0??1011?1110?0?0?0000000000001000??10100001220110000000100101(12)0
000000000000??1?11?00000??1?1(01)01111?11010???101101?????????????????
0?

CratoForm

?000111100120110001000110001000-000021120011000100002100101001100?????
2100000111000?000001000011?000100?0000-301?000101001000?????11101?0010?0
1100000?00000?0?????????---11???00??1???00?????????????????0200011210???00
00?????0?0?0121010011?01?000000?1?01?10?10000???0?????????????????1000?1???
??1?????????????0?????0?00010??????010???0(12)???110?1?????1???0?00?????00
?000000000?0?111000000012(01)011?00???????02?0?0?0000000????????????00????
???????11?01?????0?0?????1020000?00-?01???

Libycosuchus

0000111100120111???00011000?000-00102112001?00?00002100101001100101???2
1?0100100000?000001?00010?000000000011000?000101??100??????1110?00?0??1

000000?0000010010101100---11?110001111000????11011?0???1?0?0200?1121?000
0?00100000?10001?10?00(12)110?????00001001110?1000000?0100?11?0000????10
001111?0?1100??1??2?0000210310001010?0???001000120?01?111?11100??1001010
001200?0??????????10?111?0000101?1011?0000001000?0000?-??00?0??????????
??

Lomasuchus

000011100010?111???000?000???00-0?????20?11?0010?00210122111210??????21
10100010100?0000010100100000000001012000?0?01010020001?01?1110100010001
000100000000100101011?0---1111100011???002111210011(12)?011?0?02000?1210
0020000100200010001(12)1010011101000000011?0??1001001?00?010001110000??
??1000111?10?1???01?0?0????????10?0??(12)????????????????1110??????
?????????0000000000001000?11?0?0??1(12)120?1?????????110?0?00000?????????
????????????????????0????????????????????????????????

Montealtosuchus

000011100010011111100?100001000-00?02112001100010000210122111210010152?
2110100010100?0000010100100000000001012000?0001010020001????11101000100
0100010000000010010101100---11111000?1111002111210011(12)0?0?100?0200011
21000200001002000100012101001110100000001100111001001000?010001110000??
???1000111110?1100?01?023000021131110001020???001011?110210?110111100???00
020112001000000000000000100011110001012120?100000011001101000000000????
?????????0?11??????11?01?0???110111????2????0??????????

Uberabasuchus

04001111001(12)0111111000100000000-000021120011000100002101221112100????
?02110100011000?000001010010000000000101240?0001010(12)2?0(01)????11?02
00?100?100010000000010010101110---11111000(01)?112002111210011(12)1?0?1?0
?02000112100??0001????????0????????????????????????00?0100????0?
?????(12)00??11010?11????????0?0211311?0002120??0?1011?110211111?11110
??0??2?11210???01100010?00?00111200010?212001?000??1???11010?0000000?0?
?????????0????11???1?111(1 2)01????1101110???2(0 1)20?(0 1)01001??????

Cf.Hamadasuchus

0500221100100111???000000000000-00012112001100000001210122110210310052?
2110100010100?0000010010101000000?01012000?000101002?00????11101000100
0100010000000010010101100---111110021?11000(12)111?100110?01100?02000112

1000100011002000?00010202002010100000001100?11002?01100?0100?11?0100?1?
??100?1120?0?1110?01?02300?????11?????????0????????????110?????????????
??????01?000000001000???(12)0000012120?2000000110011010?0?000??????????
??

Caririsuchus

????2111001?0111?1??????????100001201?000---00---(12)?01211002100??????21
10100010100?0000010010101?00000?0001?0?0000101001?00?????11101?00100010
001000000001001010110?????11111001??100002111?100110?0?1??????????1?????
??0?????????????????????121?0?1
????01?02?????2(12)1(03)?110001100?0?01??(12)?(02)?1??????????0??(12)?1?2
0?0??00?01000000100?0?(01)00000?11(12)001?000?????110(12)0?0?000?????????
??????00?0??1?????1111020?????0??0???20200001000??11????

Sebecus

0500121?1012011111?0?0000000001000?1(12)0100??????????2101211??21?30----?
21?0100020-00?00000100?0?01??0100?010???0?00?10100?00?????1110210010?01
00010?00000(01)001010110?????111110021?10000(12)111?10011?1?0?1?0?02??011
210?0100001000000?000?1101???110?0??0001100?01??2????????100?11?0000?1??
?100?11(12)110?1110?01?0?30000201??1000011?????01011?020???1?01??????00
21112?0(01)?0?000010000001000011(01)00000110(12)0?10000000211110100000000
0??

Anatosuchus

1???102100110110111000110001000-0?00211200110101000021?0101002100?????12
(12)?0100111000?000001011?1000001000000(01)000000001010010001??1?1010100
01000100000010000010010001100---111110011?100002???00011???0?1000020001
121000?000010(02)(01)000100010202002?(12)0110?000?100011001100000?0100?1
1?00??????1000111010?1100?01?0200?0020131??110001???0?01000020?11?101?0?
100??1002111001?0??011000000001100111000001010(12)0?1?000000?000011000?0
00000????-?00?????????11???????11?02?????11011?????(1 2)100000(0 1)001???????

Kaprosuchus

0??030210??1011000?00011000010240100100100110101010121012110021000---02
110010011100?000001011?100(01)0010000200?0000000111002101?????1011200010
00110000010000010010101100---110111121211100?????10011?????1?0?0200011210
1011000102000010001020202001011113000110011100210000????????????????1???1

????120?0??00????????20??011100010??1?110??0201?1??0?110??10?201100
1?0??000000000001(01)000012000011202002?000000??11000000000?????????
??

Mahajangasuchus

1??0?0210??011001100??10001?0(12)??0??????11010100012100101???00?????
?(12)?0?1001?000?000001011?10020000000201240100001110011011?01?101021001
000110010000020010010101110---110111121?11200????10011(12)?02100?02000?
12101?000?1?2??0010?011202?1112011012000110010100210000?0100011101001
1???1000?12000?1100?01?02300??20131011100010??0?11000021011100-00??0??10
0211(01)101?0?00?00000?00?0000??0000??1(01)1001?000000(12)0011(01)000000
000000????1110000000??111??1111112010?1??1101110???(12)(01)?0000001?????
??

Theriosuchus_pusillus

1(12)?100110011011?1?1001?10000001?00002010001??0?00001101211002100?????
?2100100011101000000100001010001111000110?0?000101010?001001?10011?00?0
0010000?0?000101001010110????11100000(01)10000011???0011???01110?0200011
21010?00001000000000011102102010?10000001100011001000000?0????11??0??1?
?01000122?10011?0????230(01)0000-??1200011???0?0000??10??0110?00????00
0?????????0?000000000000100011100000112200(12)0000000??100?00000000????
??????????00??1??????1(0 1)010??1?010010?00102(01)?000010??011????

Theriosuchus_guimarotae

1???001?0011?11?11?00??100?0001?0??02010?0110001000011?121?00?10??????21
00?01011101?000001000010000011??000?0?0??1?1010000????10011?00100010
00?0??00?1?1001010110????11100000(01)1000?011???0011?00?111?02?00??210??
?0?0?1?????00??1110???(12)0?01????00??1?0??1??10000??????????????????0?
22??0??????????????0200?012??1?00?0?001???10201????0?00????????(12)??
???0000000??0?100??10?000?122?01000?0001??100?0?0?0001??????????????
??

Stolokrosuchus

12113?11001?0?????0??????100100011201(12)0011?1020001210120100211012111
?11??100?010?1?000001001110100000000100-300?0001010100001?01?100?1000100
0110010000000010010101100---111110?2(12)?11000????00011011011000020??112
100120?0011100000?00??0?????0??????011?0??10??00100?0100?1110000?????0

000122000??1?0??1??2301????????????????????????????1??0?????????????????
???01??00??0?100???1?000011?1001?????????????0?0?0?00?????????????????
??

Calsoyasuchus

1???3011001101????0??1101?0001000010-0000111102110101012010021030---011
1210010100101001010010101000000000012000?0001?1000?00?????110011?010001
00?0?0100???100101?????????11??10?0?11000??(01)(01)?10011?110111??2????112?
???1???0101??0?????????????????11000?0?0?????????????????????????????????
?????????????1???01??
00?02?0?0???10000011?2001?????????????00?????????????????????????????????
???0?

Eutretauranosuchus

1???101?0010011111?001?10?0?0?0?????????0?000--00---110120????10??????11001
00?10001?100101001?1?1??000100011001?00010100000011???11001100100010000
00?00000100?010110????1111100?(12)?1?0?0?0?(01)1?0011??011?0?220001120001
(12)000010210000000111021020101000000011?00?1001000100?0100?11?00??????
00001220?0?1??0????2??0?21100110001100?0?00110?10?0?111????1???0?02?10
100000?0???0?02?01???0???0?0?1(01)2001000001020110?100?????????????????
?????????????????????????0????????????????????????????????

Sunosuchus_junggarensis

1???201?00100111??100??10??0002000010-00?000--00---?101201002103101??0110
0100110001?100101001?1??000100?00011000?000101000000?????110011001000100
0000?000001??1010110????1111100?(12)?110?0101(12)-?0011??01110?220001?2?0
??200001021000000011102?020101000000011000?10010001?0?0100011?00???1???0
000122010011?0?????2?01002(12)?001?00001100???001100102?1?110?0?100??0002
010100000?011000002001?0?0??(01)0000011020?10000????01100?0000?000000?11
???????0?????1?????1(0 1)010???1??1101110???2??00001010?0?1???

Sunosuchus_miaoï

1211(12)00(12)001?011111?00?????????0?????????????00--00---?????????????????(1
2)?0?00?????-?100101??????000000?0000-000?0001010?0000?????1100100010??1
000000?00000100?010110????11111001(12)????0??(01)(12)?10011??0?1???22000?
1210???00??10???000?01110200201010000000?1000?10010?0100?01???11?0?0???
??0000?220?0?11?0?1??2??1?021141??0001100?0?00(12)?????01?1?0?1?00??000

2010100000?01??0000200??0???1????????20??0??????????0?0?00??????????
??

Sunosuchus_thailandicus

???(12)????1????11??
??0????????????????????????????????
??
??2(
12)?41???01100???00??????01?1???1?0???0??20101000?0?????????0?????????
????????????????????????????????0??
????????????????????????

Siamosuchus_phuphokensis

1(12)?1101?0010011????10???0??010200?010-00?00-----?1?1211002103?????0210
0100?11101?1001?100101?1100100?(01)(01)0??(03)?0??0010?0?000?????1110???0?
0??10000?01?00?0???1?1?????????11??1?????1??????????0011?????10??0???1121??
????01????????????(12)0????????????????????????00?0100?11?10??????000?1
220?0011?0?????2?0???01
?000102001100?00(01)000002112?02?000?????1?0?0?0?0?001011??11100???0??
?1??111?00??10?1???????0??2?0?0?01011???1???

Amphicotylus_lucasii

12111011001?0111??001110?0010200?010-001000--00---1101211002104111?0110
0000?11101?1001010010101101000?0100-300?00010110?10(01)1????1110111010?0
10000101100001001010111????11110012?11000??12-10011???0?1?0?02000112101
120?001000000000??? (12)0??????0?????????1?00?00?000100?0100?11??000?????0
001220?0?11?0??1??2001?????????????????????0????????????????????????????
??01?0001020011000?0101?002112002?0?0?????1?0?0?0?10????????????????????
??

Amphicotylus_stovalli

---1101100-00111????011101?0-02001010-00-000-----10121100210410032-11001
001-1-01-1001010---1---0-000--100-100-0-0101--1-----1110--101-0010000101--000
1-0-01011-????---110--2----01----1-0-1---0-1---0-0??112000-20?0-100000000-?1?0??
1020????????????????????????0-0100-11--0-----00-?220--01--0-----?????????
??011000102001100-00-000--211200-
????????????????00-?-00??

?????????

'GMNH-PV0000229'

1???10-?001001111110011101-01-2-011?0-0010-----1101211002104100--011000
00111-01-10010100101011010001-100-100-000101021-0-----1110?01011001000010-
1000010010101100---111110012-110001-12-10011---011---020011120001-0?0-10(0
2)(12)00000-?1200110201011--000?--00011001-00100-0100-11--0-----0001220100
1--0-01--200100101-11-0001100---100(01)10-10-0-1110(01)-----0002010100000-011
000102001100-00-000--21120020000010(12)00100100---00000011101110000000001
11001111(0 1)02010-1111001110(0 1)11(1 2)-{0 1}-0-01011-----

Nannosuchus

12111011001?0111??1??1?101?0002001010-00?000--00----110121100210(34)?????01
100000111101?0000010000101101001?0000-000?00010?021101?????110211010101
000010110000100(01)0101101???111?000?(12)1100?01112-10001???0?1??????????
??100?00?0100?11?1000?????0??
?220?????0?????2??1?0?????11000?????????00?0?10???110?????????????????????0?
?1?000002001100??????0?10?????0????????1????????00?????????????????????
??

Goniopholis_simus

1211101100100111111001110100102101010-001000--00----110121100210410132011
000001111010100111001010110100011100-101?0001020211011?01?11102(01)11111
01000010110000100011011011?1111110012?110?01112-10011(12)?011?0?0200011
21001200?0102100000001110210201010000000?00??1001000100?0100?1111000??
?000001220?0011?0?01-020010010110110001100?0?00010010201111?010100?00
02010100000?01100010200110000010000021120021000110200100100001000?????
?????00000??1?1?????00101011????????0???2(01)?00001010????????

Goniopholis_kiplingi

1211201100100111??10??1101?0102101010-001000--00----110121100210410132011
0000011110101001110011101101000?1100-100?000102021101?????1110201111101
0000101100001000110110?????111110012?110001112-10011(12)1?0?110?20?0?11210
??2000?????????00001??02102??0?????000??????0?100?100?0100?11?1000?????00?
?220?00??20?????20?1????????????????????0?????????????????????????????
1?00010200110000?1000002112002?0?0?????1?0?0?0?100?????????????????????
?111??0?

Goniopholis_baryglyphaeus

1???101100100111111001?10100?0????10-?01000--00----110121100?1????????1100
0001111010100111001010110100010100-100?00010102?101110??111020101110100
00101?00001000110110????11?11001221?000??12-10011?100?110?02000112100??0
???1?????00?00111020020?01000000011?00??00100?100?0100111?1000?????000??2
20?00?1?0???020010?00---110002100??0?00010?10?-1?1??000100??0?02010100?00
?011000?020011000?010?0002112002100011020010010000?00001?????????00????
????????????????????????????2???0?01010????????

Hooleygoniopholidid

1211101100100111111001?10100?0????1?????00--00----11012??00???(34)?????11
00000111001?100111001010100000011200-300?1?0101020102?????11102110101010
00010121000200001011?1???110100002?110001222?10000??0?1?0?02000?121011?
00?011210000100111020020101000000?11000?10?1000100?0100?11?1000????0000?
1220?0??1?0??1-?20010000---1?0002100???0001?010?-1?11100000??0?02010100?
?0?011000102001100?0?????0??112002200011000010?100001000?????????????0??
?????????0????????????????2???00010?0????????

Dollo_goniopholidid

12111011001001111110?111010010200?010-00?000--00----1101211002104?????0110
0000111101?100111001?10100000011200-300?10010?020102?????1110210000?0100
0010?210002000010110????110100002?110001222-10000??0?1?0?020?011210????0
0??1?????001001?10?0020?01???????1000??0?1000100?0100?11?1000????00000?22
0?0??00?01-02001?000---110001100??01?00100102-1?1??00?0?????0?020101000000
011000102?01100?0?10??0211200220??11000010??0000?00000011??1110000000??
111?1111(0 1)01010?1??1001000??2???0001010??01????

Hulke_goniopholidid

1211301100100111??001?101?0102001010-001000--00----1101211002104(12)00??0
1100000111001?1001110011101000000?1200-101?10010102010111?1?11101100101
011000001100001000110110110?1101100022110001112-10001(12)1101110?0200??1
21011200001111000000011102002010?100000011?00?10?10001?0?0100?11?1000??
??00001220?00?1?0?01-02001?????????????????0????????????????????????????
??????01?000102001100?001000002112002?0????????1?0?0?0?00????????????
??

Pholidosaurus_schaumburgensis

1000300200110111??100??00-0?02?????-?0?00--00----1101101?????(3 4)1????(0
1)100100?0--0-?0000010010101000000?1200-100?000100021101?????111011001010
11001001100001001010?101101110100002211000??12-10000?1?01110?02?00?1210-
??0001111000000?01110200201010000000110001100?000100?0100?1111000?0???0
000122000?11?0?010020010?????010000111?????00210010?0?012?000?0?0?002011
200100?011000102001100?00?0?0(01)200-0000010202???1?000100011?????????
?????0???11?????????0???1?????????????(0 1)???0???1?????????

Sarcosuchus_imperator

1211201200110111111001??0?00001000010-000000--00----01011010021131001001(
01)0010000--0-?00000100101?10?000001100-300?1001020001001?00?110111001011
1000100?210002001010?100---1111?0012?10000?(01)1-11000?1?01100?020001121
0010010011100000000011102001110100000001100?11001000100?0100011?1000?0??
?0000122000?11?0?010023010010100000001110????002200000011120010101???002
010100000?0110001030011000001111012001000200211000000020000100000001???
00??000?0??1?100111100?010?1?????????0???21200001011?000???

Elosuchus

1211211200110111??1001??0?0002000010-000000--00----11011010021131(0
1)04201100100011011?0000010010101000000?2200-200?10010101010?0?????110111
0010?01000100111000210(01)010?100---111110022111000??(01)1-11011?1?0111??0
20001121001200001120000000011202001?20100(12)100011000110?1000100?0100?
11?1000?????00001220?0?11?0?01002301??22100?????11???????02??01?0?0?1?01?
?0???????0??200????01?00010(23)?01100000(01)0000021(01)2001?000???????0?0?
0?10?00?0??2???00010?1???????

Vectisuchus

1(12)?121020011011111??01?10?-000???????-??0000--00----110110100?11(34)?????
1100?00000-?-??0??01????10?000000?2200-201?10010?0(12)0?0?????1101?0010?0
10001?0111000210?010?1?????11111001211?000????-11000?1?0?????02000?1210??
?0?0???????0000011202001020100?000?1?00?10?1000100?0100?11?000?????0000
1220?0?11?0???????0100?20101000011?0???002??010001?120?0?10???1?02011100
100?011000102001100?00???????0(01)(12)00-(01)00???????00010?0010000?0?1????
????????????????????11?0????????????0???2???0?01011?0??????

Dyrosaurus_maghribensis

13102112001101110010010000-0002000010-000000--00----010110100211311010011

00110000-1-?0000010010101000000022012000?000101010000????110?1100101011
0010011100?200101011011011111000221000010(01)?-11000?1?0?100?0200011210
01200001110000000011202001?20100000001100011001000121?0101?1111011?0???
01101220?0?11?0?010023010110?00000001110?000023001020?0120000000??1002
112210111?011000002001100?00000000100200-0000000212100101001000010?????
???00010??1???0???00?0?011??11011100102???11010??????????

Dyrosaurus_phosphaticus

1???(2

3)1120011?111??10?10000-0002000010-000000--00----0101101002113???100110011
0000-1-?0000010010101000000?220?2?0?00?1???000?1100?110?11001?1?1?001?0
???00?(12)0010?????????11??100??21000010????10??(12)???1???0200?1121?01???0
01110000000????0????????????????11????????1????????????????11?11??????????220????
????????????101?????000001??????????30????????120?0????????????12?1?1?1?0110000
02001100?00000000100??0-000?00021210010100100????????????????1????????????
??

Congosaurus

1???(2

3)1120011?1??1110?10000-0002000010-0?0?00--00----01011010021131?0100110011
0000-1-?000001001?101000?00?????????00????????????????1??11????1??????0???
??? (12)0010?????????1??100??2100?0??????????????????020??1121001?000011100
0???0???0????????????????11????????????????????????????????0????????????
???00?????000011?????1??0??????120?0?0?1???112?1?11?01100000200110
0?0?000000100??0-00??00021210010100?0?0010?????????00010??1???111?00?01?1
1??11011100??????11????????????

Guarinisuchus

1310111100110111??10010000-0??2000010-000000--00----0101101002113?????0110
0110000-1-?0000010010101000000?22012001?001?0?0(12)0000??????10?110010101
21010011100?2001010110????111110002?10000?(01)0-11000??01100?0200011210
012000011100000000112020010201000000011000?1001000121?0101?11?1011????
11101220???11?0?0100230100????0?0000??1??????2?0010?0??1200???0???0???12
???1???01100000200?100?00000000100200-?0??????1001010010?00?0?????????
?????????????????0?????????????2????????????????

Rugosuchus

1(12)?1200?0011011111100??00?000(12)?0?0020?0000---00----(01)1012(01)100(12)
10(03)1???02100100010101?11000100101(01)1000111?00011000??010101?00???

??1001010010?010001?0??0000(12)00(12)010110????1111100(12)2?11000??? (01)?10
011???0???0?020001121010?0?0?1120000000011102102020????0000???0???100?1
00?01000110?00?????0000?(12)2??0?1100?????2??00000---??00011?????0001?010(
01)?1?110???????0?0201(01)(12)?0100?0(01)(01)00000?00?100?1110000011-2002?0
00?????????0?0?00??0????????0000????????????????????????????2???010??
????11???

Bernissartia

1101001100110111111001?10000002000010-000000--00----0101211002103?1???011
00100011101?0000010010100000000?0(01)01(01)00000001010(12)20001?01?100111
00?0001000010?000001001010110100?111110012211000??(0
1)0-0001121?011?00020001121010001001?100000000?020(12)0?(12)020?0???00011
000010?100?10000100011?1000?????000?122000?110000?0023010000---1200011101
?01000000100-0?10?000?00??0002010100000000000000(13)000100?1110000011121
02000?0011001001000000000?1??10?????000?0?01?10111110010101100?????0010
21200101001?001???

Susisuchus

1101202100110111001??1?100-0002200010-000000--00----0100101002100?????0210
0101002-0-?0000010010101000000000010000?00010??0000?????10012000100?100
000000000?10010001111001111?100???00000??(01)(01)-000?11??0?1?0????????????
??00???????1?00???????0???220
?0?????0000230?????????????1?0?0??0?0??0?1??1????0?????????01?000?????0
?????????????????00?10?????????????????0?????0?010?????????000???1???????0
0?01?????110110????20211100001???????

Isisfordia

1101201100110111??100???0?-0002200010-000000--00----0100101002100100420210
0100?02-0-?0000010010101000000000012000?000101010000?????100120001000100
000000000010010101101001111110012?11000??(01)(01)-0001111?0(12)1?0?020001
12101100100112100000001120200103010-??00011000110?10001?0?0100?11?0000??
???00001220?0?11?0000002300?02(12)?(01)0???????0???0?????1?20?????00010???
????0?????????000000000001100?1100000010020?0???????????0?0?000000101???
?????????0?1?1?????001010?1??1?0???0???222?1100001??1?????

Allodaposuchus

1??1101?00110111??00?????0?0002000010-000000--00----0100101002100100420210

0100?12101?0000010010101000000100012402?000101012000????10012100100010
001001000001001010110????111110012?11000?(01)(01)-00011?110(12)1?0?020001
12101?10100100000000?000212???031?0???00001????10??0??00?0100?11?1000??
?10000?22000?1?0000?-02000??
??????0110000010011000001000001112102?0?????????1?0?00000????????????
??

Iharkutosuchus

1???001(0

1)00110?????00????0?0002000010-000000--00---01001010021001004202100101?0
2-010000000110010000000--002-----?000101012000?????10010000100010001000000
00(12)001010110?????1111001??00?00?(01)(01)-11011?1?0?110?011001121010001
00100000000?00021200103100-?00001000110000100?0?0100?11110?0?????0000?2
2100????00????2?0?0000---000102111?0?000000201-1?00-10000???0?0201????????
01100010002010000000000110221030000000010000?10000000????????????????
??

Hylaeochampsia

1?0???1?0?110?????100??1?0???0?????1?????000--00---0?????00???????????(1
2)00?00????01?00000?110010000000100001100000001010120001?010100100000000
1000000100000100101011?????1???100??210000?(01)(01)-11011211011?002100?1
21010?010?100000000000021200103100-?00001000?100?0?011000100?11?1000??0
?10000122?00???000-02000??
??????0?????0??????????????00???221?3?????????????0?????11????????????
??

Gavialis

11013102001101000110010000-0002210010-000000--00---010110100211310010001
00100000-1-00000010011101000000011012?0?0000111010000111101111110010101
1000001000002001010110100111011001221100010??-1101121101110002000112100
100100111000000000021200013100-0000001000010000001001010001110100110000
01012200001100010002310002110000000110000000023001000101200001000?1002
0112100100011000001001100000000000100200-000000020200010000100111111111
11010000000111011111000010110111011000101110101000100110?00

Piscogavialis

1101311200110100??10010000-0002210010-000000--00---010110100211310010001
00100000-1-?000001001110100000001101220000001100100001111?1000110010101

1001001000002001010110100?110110012211000???-1101121101110?02000112101
100100111000000000021200113100-00000010001100100010010100?1110100???000
0001220?0011?00100023100022?000000?100???0023?010?0?01200?01???0???0??
??????011000001001100000000000100200-00000002020001000010011?1?????????
??0??????????100?0?0?1????????0010????101000?????????

Eosuchus

1101301100110101?110010000-0002210010-000000--00---010110100210310022011
00100000-11?000001001110100000000001000000001100120001111?1000210010001
1000000000002001010110100?111110012211000??(01)1-01011?1101110?020001121
01100100112000000000021200113110-?000010001100100010010100?1110100???1
?00001220?0?11000100023100022?00000001110???0?0200020?0?0110????????1????
112??????011000001001100000100000100200-000000020100010(01)0010011111111
11100????????????????0????????????????????1101?10001?????????

Tomistoma

11013012001101100110010000-0002210010-000000--00---010110100210311021011
0010001101100000010010101000000000010000000011101210011111100121001000
1000100000000100101011010011111100122110001001-000111110111000201011210
1100100110000000000021200103100-00000010001100100111000100011?0100??111
0000122010011001100123100021100100001111001000230020201011000010000100
2011210010001100000100110000000000011020010000000212100100001001111111
01110?0000001111111110010??1111110110001011(1 2)1111000110110101

Crocodylus_niloticus

1101201100110111111001000010002210010-000000--00---010121100210311021021
0010001111110000010010101000000000012000001011000(02)100111111011210010
001000100000100100101011210001111100122110001000-0001111101110102020112
101100100112000000000021200113100-0000001000110010011000010001110100111
110000122010011001100123100021100120001110101110010012201000-0001010110
0201121001000110000000011000001000001102102000000110010010000000111111
10111010000000011211111001010111111011000101201111000110110101

Crocodylus_porosus

1101301100110111111001000010002210010-000000--00---0101211002103110210??
00100011111100000100101011000000?012000001011000(0
2)10011111101121001000100010000010020010101121110111110012?110001000-00

01111101110102020112101(01)00100112100000000021200113100-00100010001100
100110000100011101001111100001??0100110011001231000211001200011101011?0
010012201000-0001010110020112100100011000000001100000100000110210200000
01100100100000001111??10?11??0000000112111110010??11111101100010120111
1000110110101

Osteolaemus

11011011001101111110010000100020100110100000--00----?1012110021031100002
100?00011111000000100?010110000000011000000?0111010100111111?0121001000
1000000000000100101011211101111100122110001000-000111110111000202011210
1100100011000000010021200003100-??10101000?10010011(01)00010001110100?11
110000122010011001100123100021100120001110101?10000010201?00-0001010110
0201120001000110000000011000011000001102102000000110010010000000111111
1011101000000001111111100101011111101100010(1 2)211111000110110101

Voay

1101101100110111111001000010002010?10-000000--00----?101211002103110000(1
2)100?000111110000001001010110000100011200000?011001010011??11?01210010
0010000?000020010010101120---111110012211000??(01)0-000111110111010202011
2101110100112000000010021200103100-??11101000?10010011?000100?11?0100??1
1?0000122010011001100123100021100120001110100?1000001020?00-0001010110
0201120001000110000000011000011000001102102000000110010010000000111111
?01110?00000??111111111001010111111011000??(1 2)???101000?????????

Brachychampsia

1101101?00110111111001000010002200010-000000--00----010010100210021152021
00100012101000000111?0100?00000100120000000110012001?????1001210010001
0000000000001001010110111011110012211000??(01)0-0?011111011100020?01121
001?000010210001?00021200103110-??010?1?00110010011(01)?00100?1110100??0
?10?00122010011100101123100?2(12)?00121100110100?00000010201?00-?0?1100?
100201120001010110000?00?100011?0100011021020000001?0010110000?001?????
0??????????00?????????0????0?1?????????????1112????1?0??????

Diplocynodon

1101101100110111111001000010002010010-000000--00----010121100210011000011
0010001210100000010010101000000000010000000011001000011???1001200010011
00000000000010010101101110111110012211000????-0001111101110002000112101

1?0000112100000000021204113110-??01011000110010011000010001110100??0110
000122010?1110010012310002(12)?00120001110100100000010201000-0001100?10?
20112?00?0101100000000110000010000011021020000010100101100000001?????0
???????????0???02???0???0???1?????????????????????1?1???0?

Alligator_mississippiensis

11011012001101111110010000100020100110100000--00----01001010021001100002
1001000121010000001111010010000000001000000001100100001111110012100100
0100000000000010010101100---1111100122110001000-000111110111000200011210
1110000112100000000021203103110-000101100011001001100001000111010011011
000012201001110010(01)123100021100121101110100100000010201000-000110011
0020112000101011000000001100011100000110210200000011001011000000011111
100111010000000011111111001010111111011000101111121000110111001

Caimancrocodilus

1101101200110111111001000010002010010-000000--00----010010100210012000021
001000121010000001000010111000000010-0001000110000000111111001210010001
0000000000001001010110(01)1101111100122110001000-0001111101110102000112
101110000112100000000021203003110-000101100011(01)010011002010001110100
110110000122010011100101123100021100121101110111?00000010201000-0001111
0100201120001010110000000011000111000001102102000000110010110000000111
11100111010000011011111111001010111111011000102101111000111111001

Caimanlatirostris

1101101200110111111001000010002010010-000000--00----010010100210012000021
001000121010000001000010121000000010-0001000111000000111111001210010001
00000000000010010101100---1111100122110001000-00011111011101020001121011
10000112100000000021203003110-00010110001100100110020100011101001101100
00122010011100101123100021100121101110?11100000010201000-00011110100201
1200010101100000000110001110000011021020000001100101100000001111110011
101000001?011111111001010111111011000102101111000121111001

Melanosuchus

1101101200110111111001000010002010010-000000--00----010010100210012000021
001000121010000001000010121000000010-000100011100000011(01)111001210010
00100000000000010010101100---1111100122110001000-00011111011101020001121
01110001112100000000021203003110-00110110001100100110020100011101001101

10000122010011100101123100021100121101110111100000010201000-00011110100
2011200010101100000000110001110000011021020000001100101100000001111110
0111010000011011111111001010111111011000102101111000121111001

Paleosuchus

1101101200110111??1001000010002010010-000000--00---010010100210011021021
001000121010000001001010100000000002--000?000111010000111111000100010001
00000000000010010101110---11111001221100010(01)(01)-0001111?0111010200011
2101110000112101000000021203103110-000101100011001001100201000111010011
01100001220100111001011231000??0012110111?111?00????10?0?0?????1112110
02011200010101100000000?1000111000001102102?000?011??10110?000001111110
011101000001111110111100101011111101100010?121111000111111001

Denazinosuchus

1???101?0010???????0???10???020???10-00?000--00---1101211???1?(3
4)?????1100?00?11??1?????1001010110?000??200-300?0?01?110?01?????111021
101010100???01?00??10000?????????1?????????1??????(01)?????????????????2?????
?????????001?????00????(12)???
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?1?000???00?100?????00??1-2?0??????????1?0?0???0?????????????????????????
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Goniopholis_phuwiangensis

????(01)???010?????????1???0???
?????????????????1??
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???
????1?000?????????0110010?????110?????????????????????????????????????0?????????????????
??-????000001020110?1?0???
????????????????????

Siamosuchus

1(12)?1101?1010011???10?1?0?0010200?010-00?00-----?1?1211002103?????021
00100?11101?0001?100101?1100100?(01)(01)0??(03)?0?001?0?0000?????1110???0
?0??10000?01?00?0???1?0?????????11??1?????1?????????0011?????10?0???1121??
?????01????????????(12)0????????????????????????????00?0100?11?0?0?????000??
220?0011?0?????2?0?00?????1?000?????????0110010?????110????????????????????

?1?000102001100?11(01)000002112?0200000102011001000??0??01011??11100???0
???1??111?00??10?1???????0???2??0??01011???1???a

Measurements of ceratobranchial and internal choana in Crocodyliformes.

Taxonomic group	Category	Genus species	Specimen	Reference	Tortuosity	CB length / Mandible length	Distance between anterior end of internal choanae to skull anterior end /		Distance between posterior end of internal choanae to skull posterior end /	
							Skull Width		Skull Width	
Archosauri formes	Non-Neosuchia	<i>Chanaresuchus</i>	MCZ 4038	Yoshida pers. obs.	1.08	0.36				
Archosauri a	Non-Neosuchia	<i>Euparkeria</i>		Yoshida pers. obs. (MCZ VPR9176. cast)	1.01	0.25				
Aetosauria	Non-Neosuchia	<i>Desmotosuchus</i> <i>smalli</i>	TTUP90 24	Parker 2005			0.76		0.91	

Pseudosuchia	Non-Neosuchia	<i>Erpetosuchus granti</i>	BMNH R3139	Walker 2002			0.76	0.56
Crocodylomorpha	Non-Neosuchia	<i>Dromicosuchus</i>	UNC 15574	Sues et al., 2003	1.04	0.14		
Crocodylomorpha	Non-Neosuchia	<i>Dibothrosuchus elaphros</i>	IVPP V7907	Wu & Chatterjee, 1993			1.21	0.99
Crocodylomorpha	Non-Neosuchia	<i>Sphenosuchus acutus</i>	SAM301 4	Walker 1990			1.76	1.33
Ornithosuchidae	Non-Neosuchia	<i>Ornithosuchus longitundens</i>		Walker 1963	1.05	0.39	1.31	1.15
Protosuchidae	Non-Neosuchia	<i>Protosuchus richardsoni</i>	AMNH 3024	Colbert & Mook 1951	1.07	0.23		
Protosuchidae	Non-Neosuchia	<i>Sichuanosuchus suchuanensis</i>	IVPP V10594	Wu et al., 1997			0.82	0.56
Ornithosuchidae	Non-Neosuchia	<i>Venaticosuchus rusconii</i>	PVL2578	Von Baczko et al., 2014				0.96
Gobiosuchidae	Non-Neosuchia	<i>Zaraasuchus shepardi</i>	IGM1001 32	Pol & Norell, 2004				1.29
Gobiosuchidae	Non-Neosuchia	<i>Cassissuchus sanziumi</i>	MCCML H 7991a	Buscalioni 2017	1.04	0.25	1.73	1.12

Gobiosuchi dae	Non-Neosuchia	<i>Gobiosuchus kielanae</i>	ZPAL MgR-2	Osmolska et al., 1997			0.52	0.43
Dyrosaurid ae	Non-Neosuchia	<i>Dyrosaurus maghribensis</i>	OCP DEK-GE 253	Jouve et al., 2006			0.94	0.56
Notosuchi a	Non-Neosuchia	<i>Anatosuchus minor</i>	MNN GDF603	Sereno et al., 2003			1.19	0.68
Notosuchi a	Non-Neosuchia	<i>Araripesuchus patagonicus</i>		Turner 2006			0.62	0.51
Notosuchi a	Non-Neosuchia	<i>Mariliasuchus amarali</i>	MZSP-P V 50	Zaher et al., 2006			1.73	1.12
Notosuchi a	Non-Neosuchia	<i>Notosuchus terrestris</i>	MLP-64 -IV16-5	Andrade & Bertini, 2008			0.76	0.96
Notosuchi a	Non-Neosuchia	<i>Simosuchus clarki</i>	UA8679	Kleyet al., 2010	1.14	0.34	0.73	0.44
Notosuchi a	Non-Neosuchia	<i>Yacararani bolivensis</i>	MNK-PA L5063	Novas et al., 2009			0.76	0.54
Baurusuchi dae	Non-Neosuchia	<i>Aplestosuchus sordidus</i>	LPRP/U SP 0229a	Godoy et al., 2014	1.02	0.28	0.71	0.60
Sebecosuc	Non-Neosuchia	<i>Baurusuchus</i>	MPMA	Carvalho et			0.76	0.55

hia		<i>salgadoensis</i>	62-0001 -02	al., 2005		
Sebecosuchia	Non-Neosuchia	<i>Campinasuchus</i>	CPP123	Carvalho et	0.95	0.70
hia		<i>dinizi</i>	5	al., 2011		
Sebecosuchia	Non-Neosuchia	<i>Lorosuchus</i>	PVI6219	Pol et al.,	0.73	0.54
hia		<i>nodosus</i>		2011		
Sebecosuchia	Non-Neosuchia	<i>Pissarrachamps</i>	LPRP/U	Montefeltro	0.67	0.45
hia		<i>a sera</i>	SP 0019	et al., 2011		
Sebecosuchia	Non-Neosuchia	<i>Stratiotosuchus</i>	DGM	Riff &	1.11	0.66
hia		<i>maxhecti</i>	1477-R	Kellner, 2011		
Sphagesauridae	Non-Neosuchia	<i>Caipirasuchus</i>	MPMA	Iori &	1.12	0.75
		<i>paulistanus</i>	67-0001 /00	Carvalho, 2011		
Sphagesauridae	Non-Neosuchia	<i>Caipirasuchus</i>	MZSP-P	Pol et al.,	1.09	0.79
		<i>stenognathus</i>	V 139	2011		
Sphagesauridae	Non-Neosuchia	<i>Sphagesaurus</i>	RCL-10	Pol 2003	0.95	0.68
		<i>huenei</i>	0			
Peirosauridae	Non-Neosuchia	<i>Lomasuchus</i>	MOZ408	Gasparini et	0.89	0.54
		<i>palpebrosus</i>	4PV	al., 1991		
Peirosauridae	Non-Neosuchia	<i>Montealtosuchus</i>	MPMA-1	Carvalho et	0.82	0.61
		<i>s arrudacamposi</i>	6-0007-	al., 2007,		

			04	Tavares et al., 2017				
Peirosauridae	Non-Neosuchia	<i>Uberabasuchus terrificus</i>	CPPLIP no 630	Carvalho et al., 2004			1.02	0.82
Pholidosauridae	Neosuchia	<i>Terminonaris robusta</i>	SMNH P24111.1	Wu et al., 2001			0.35	0.37
Pholidosauridae	Neosuchia	<i>Sarcosuchus imperator</i>	MNN604	Sereno et al., 2001			0.49	0.30
Thalattosuchia	Non-Neosuchia	<i>Pelagosaurus lucasii</i>	M1420	Pierce & Benton, 2006			1.01	0.54
Thalattosuchia	Non-Neosuchia	<i>Geosaurus giganteus</i>	NHM 37020	Young et al., 2009	1.00	0.16		
Goniopholidae	Neosuchia	<i>Anteophthalmosuchus hooleyi</i>	NHMHUK R3876	Salisbury & Naish, 2011			0.44	0.42
Goniopholidae	Neosuchia	<i>Eutretauranosuchus delfsi</i>	BYU176 28	Smith et al., 2010			1.22	0.40
Goniopholidae	Neosuchia	<i>Amphicotylus</i>	GMNH PV00002 29	This study	1.31	0.22	0.82	0.30
Goniopholidae	Neosuchia	<i>Sunosuchus junggarensis</i>	V10606	Wu et al., 1996			0.62	0.35

Paralligato ridae	Neosuchia	<i>Rugosuchus nonganensis</i>	IGV 33	Wu et al., 2001	0.83	0.77
Paralligato ridae	Neosuchia	<i>Shamosuchus djadochtaensis</i>	IGM 100/119 5	Pol et al., 2009	0.94	0.59
Paralligato ridae	Neosuchia	<i>Paralligator gradilifrons</i>	PIN3458 /501	Turner 2015	0.72	0.58
	Neosuchia	<i>Hylaeochampsia vectiana</i>	BMNH R 177	Owen 1874	0.31	0.28
	Neosuchia	<i>Iharkutosuchus makadii</i>	MTM 2006.52. 1	Osi et al., 2007	0.34	0.28
	Neosuchia	<i>Isisfordia duncani</i>	QM F44310	Salisbury et al., 2006	0.57	0.37
Eusuchia	Neosuchia	<i>Allodaposuchus precedens</i>	UPUAM A1		0.55	0.46
Eusuchia	Neosuchia	<i>Allodaposuchus precedens</i>	PSMUB B V438		0.43	0.46
Eusuchia	Neosuchia	<i>Allodaposuchus sp.</i>	AM3–15		0.33	0.25
Eusuchia	Neosuchia	<i>Allodaposuchus</i>	MPZ		0.33	0.21

		<i>subjuniperus</i>	2012/28 8				
Eusuchia	Neosuchia	<i>Borealosuchus</i> (<i>Leidyosuchus</i>) <i>sternbergi</i>	USNM65 53	1.15		0.42	0.35
Eusuchia	Neosuchia	<i>Caiman</i> <i>crocodilus</i> <i>fuscus</i>	ZSM 81.1937	1.09	0.17	0.51	0.41
Eusuchia	Neosuchia	<i>Caiman</i> <i>crocodilus</i> <i>palustris</i>	ZSM 517.1911	1.30	0.23	0.44	0.38
Eusuchia	Neosuchia	<i>Caiman yacare</i>	ZSM170. 1933		1.11	0.19	0.33
Eusuchia	Neosuchia	<i>Caiman</i> <i>latirostris</i>	NSM PO 432			0.35	0.26
Eusuchia	Neosuchia	<i>Crocodylus</i> <i>johnstoni</i>	R26850	1.17		0.41	0.32
Eusuchia	Neosuchia	<i>Crocodylus</i> <i>johnstoni</i>	R26887	1.15	0.19	0.42	
Eusuchia	Neosuchia	<i>Crocodylus</i> <i>niloticus</i>	NSM PO 19			0.34	0.26

Eusuchia	Neosuchia	<i>Gavialis gangeticus</i>	ZSM 29.1912		1.16		0.29	0.24
Eusuchia	Neosuchia	<i>Leidyosuchus canadensis</i>	NMC 8942				0.50	0.41
Eusuchia	Neosuchia	<i>Osteolaemus tetraspis</i>	GMNH VR00002 79				0.26	0.12
Eusuchia	Neosuchia	<i>Paleosuchus palpebrosus</i>	NSM unnumbered				0.47	0.34
Eusuchia	Neosuchia	<i>Penghusuchus pani</i>	NMNS-0 05645	Shan et al., 2009	1.06	0.09	0.30	0.28
Eusuchia	Neosuchia	<i>Pietraroiasuchus ormezzanoi</i>	PC-1	Buscalioni et al., 2011			0.37	0.37
Eusuchia	Neosuchia	<i>Purussaurus mirandai</i>	UNEFM-CIAAP13 69	Aguilera et al., 2006			0.51	0.48
Eusuchia	Neosuchia	<i>Purussaurus neivensis</i>	UCMP39 704	Aguilera et al., 2006			0.47	0.41
Eusuchia	Neosuchia	<i>Stangerochampsa mccabei</i>	RTMP 86611	Wu et al., 1996			0.58	0.46

Eusuchia	Neosuchia	<i>Tomistoma schlegelii</i>	NSM-PO 18		1.14	0.12	0.34	0.25
Eusuchia	Neosuchia	<i>Toyotamaphimeia machikanensis</i>	MOUF00 001	Kobayashi et al., 2006	1.14	0.15	0.41	0.33
Eusuchia	Neosuchia	<i>Tomistoma schlegelii</i>	AMNH 113078		1.19	0.13		
Eusuchia	Neosuchia	<i>Osteolaemus tetraspis</i>	AMNH 69057		1.14	0.19		
Eusuchia	Neosuchia	<i>Paleosuchus palpebrosus</i>	AMNH 137161		1.10	0.17		
Eusuchia	Neosuchia	<i>Alligator mississippiensis</i>	AMNH R67134		1.10	0.18		
Eusuchia	Neosuchia	<i>Alligator mississippiensis</i>	AMNH 46842		1.18	0.16		
Eusuchia	Neosuchia	<i>Alligator mississippiensis</i>	AMNH 43314		1.16	0.16		
Eusuchia	Neosuchia	<i>Alligator mississippiensis</i>	AMNH 43315		1.17	0.17		
Eusuchia	Neosuchia	<i>Alligator mississippiensis</i>	AMNH 43316		1.20	0.19		
Eusuchia	Neosuchia	<i>Alligator</i>	ROM		1.17	0.16		

		<i>mississippiensis</i>	R8039		
Eusuchia	Neosuchia	<i>Alligator</i>	AMNH	1.27	0.25
		<i>sinensis</i>	R139673		
Eusuchia	Neosuchia	<i>Crocodylus</i>	AMNH	1.10	0.16
		<i>niloticus</i>	73047		
Eusuchia	Neosuchia	<i>Crocodylus</i>	AMNH	1.18	0.18
		<i>niloticus</i>	118718		
		<i>(suchus?)</i>			
Eusuchia	Neosuchia	<i>Crocodylus</i>	AMNH	1.09	0.19
		<i>rhombifer</i>	57773		
Eusuchia	Neosuchia	<i>Crocodylus</i>	AMNH	1.12	0.20
		<i>rhombifer</i>	77595		
Eusuchia	Neosuchia	<i>Caiman yacare</i>	AMNH	1.09	0.17
			R73622		
Eusuchia	Neosuchia	<i>Crocodylus</i>	AMNH	1.19	0.18
		<i>acutus</i>	7121		
Eusuchia	Neosuchia	<i>Crocodylus</i>	AMNH	1.13	0.20
		<i>palustris</i>	77632		

Table. Hyoid measurements of ornithischian dinosaurs

Genus	Curvature	Relative CB Size	Proximal relative size to mandible		Prox aspect ratio	Height ratio of mid depth / prox		Size (mm)	FAD	LAD	Specimen		Note
											No.		
<i>Lesothosaurus</i>	1.04				1.03	2.14	0.47		201.3	190.8	NHMUK	PV	
												RU B17	
<i>Thescelosaurus</i>	1.07	0.37	0.06			1.41	0.71	111	70.6	66	AMNH		Cast of
												FARB30049,	NCSM
												(Right)	15728
<i>Tenontosaurus</i>	1.05	0.34				2.6	0.39	113	122.46	109	OMNH		
												58340	
<i>Ouranosaurus</i>	1.2	0.25	0.16	1.04		2.28	0.44	165	125	113	Taquet		
												1976	
<i>Jinzhousaurus</i>	1.05	0.42	0.06			2.88	0.35	176	125.45	122.46	IVPP		
												V12691	
<i>Theiophytalia</i>	1.07	0.36	0.11	1		1.06	0.94	148	125	100.5	YPM	1887	
<i>Protohadros</i>	1.18	0.38	0.12	1.36		3.14	0.32	219	99.6	93.5	SMU	74582	
<i>Gobihadros</i>	1.05	0.49	0.13	1.67		1.98	0.51	130	100.5	83.6	MPC-D		
												100/763	

									(Right)		
<i>Plesiohadros</i>	1.05	0.5	0.14	0.86	2.07	0.48	270	85.8	70.6	MPC-D	
										100/745	
									(Right)		
<i>Velafrons</i>	1.03		0.30		1.83	0.55	63	83.5	70.6	CPC-59	
<i>Corythosaurus</i>	1.03	0.48	0.20		3.93	0.25	93	83.5	70.6	AMNH5338	
<i>Edmontosaurus</i>	1.11		0.24	2.86	4	0.25	255	70.6	66	ROM 53541	
										(cast of	
										MR-A1-N)	
<i>Kamuysaurus</i>	1.05		0.13	1.95	1.61	0.62	286	83.6	66	HMG-1218	
<i>Brachylophosaurus</i>	1.08	0.49	0.22	2.95	2.82	0.35	308	83.6	72.1	MOR1071*	*Prox.
											end
											aspect
											ratio from
											CMN8893
<i>Psittacosaurus</i>	1.02	0.4	0.09	1.25	1.39	0.72	57	125	100.5	IGM	
										100/1930	
									(left)		
<i>Leptoceratops</i>	1.02	0.30	0.15	1.39	1.97	0.51	101	72.1	66	CMNH 8889	
										(left)	
<i>Protoceratops</i>	1.02	0.47	0.11	0.85	1.83	0.55	97	83.6	72.1	IGM	

									100/3502	
									(left)	
<i>Zhuchengceratops</i>	1.05	0.47	0.16		2.17	0.46	167	83.6	72.1	ZCDM
										V0015
<i>Centrosaurus</i>	1.01	0.23	0.14	1.03	1.55	0.64	162	83.5	70.6	ROM767
										(right)
<i>Styracosaurus</i>	1.03	0.27	0.20	2.12	2	0.5	180	83.5	70.6	CMN 344
										(right)
<i>Pachyrhinosaurus</i>	1.02		0.16	2.19	1.84	0.54	147	83.5	66	TMP
										89.55.691
<i>Arrhinoceratops</i>	1.01	0.28	0.18	1.59	1.81	0.55	105	83.5	66	CMN 8882
<i>Scelidosaurus</i>	1.04		0.1		1.48	0.67	87	199.3	190.8	AMNH 6798
										(incomplete)
<i>Hungarosaurus</i>	1.13		0.07		1	1	102	86.3	83.6	MTM
										Gyn/404
<i>Pinacosaurus</i>	1.13	0.54	0.12	1.17	1.27	0.79	41	83.5	70.6	IGM
										100/3186
<i>Saichania</i>	1.05	0.71						83.6	72.1	GJ SPS
										100/151
<i>Euoplocephalus</i>	1.08	0.75	0.04		1	1	228	83.5	70.6	AMNH
										FARB 5405

									(right)
<i>Stegosaurus</i>	1.01	0.53	0.09	0.71	1.4	175	157.3	145	USNM 4935
									(left)

Table. Widths of cricoid and mandible

Clage	category	Family	Genus	species	speciemen No.	Cricoid width (mm)	log cricoid width	Mandible width (mm)	log10(Mandible width)
Aves	Aves	Passeriformes	Streptopelia	orientalis	HoUM 30815	5	0.7	12.6	1.10
Aves	Aves	Charadriiformes	Scolopax	rusticola	HoUM 30180	5.2	0.72	22	1.34
Aves	Aves	Cuculiformes	Cuculus	saturatus	HoUM 30332	4.8	0.68	17	1.23
Aves	Aves	Anseriformes	Cygnus	cygnus	NSMT AS33	16	1.2	45	1.65
Aves	Aves	Tinamiformes	Eudromia	elegans	NSMT AS1142	5	0.7	19	1.28
Aves	Aves	Sphenisciformes	Spheniscus	humboldti	NSMT AS1248	16	1.2	42	1.62
Aves	Aves	Accipitriformes	Terathopius	ecaudatus	NSMT AS1289	13	1.1	48	1.68
Aves	Aves	Piciformes	Ramphastos	tucanus	NSMT AS1310	8	0.9	43.5	1.64
Aves	Aves	Bucerotiformes	Penelopides	panini	NSMT AS1192	7	0.85	35	1.54
Aves	Aves	Psittaciformes	Agapornis	fischeri	NSMT AS1194	4	0.6	19	1.28
Aves	Aves	Bucerotiformes	Tockus	alboterminatus	NSMT AS1252	5	0.7	30	1.48
Aves	Aves	Anseriformes	Dendrocygna	viduata	NSMT AS1315	5.5	0.74	20	1.30
Aves	Aves	Bucerotiformes	Bycanistes	brevis	NSMT AS716	10	1	43	1.63
Aves	Aves	Anseriformes	Anser	anser	NSMT AS76	9	0.95	28	1.45
Aves	Aves	Anseriformes	Anser	indicus	NSMT AS36	10	1	30	1.48
Aves	Aves	Falconiformes	Falco	tinnunculus	NSMT AS1080	5.6	0.75	28	1.45
Aves	Aves	Procellariiformes	Puffinus	griseus	NSMT AS1230	6.2	0.79	32	1.51
Aves	Aves	Pelecaniformes	Scopus	umbretta	NSMT AS1332	7.6	0.88	24	1.38
Aves	Aves	Podicipediformes	Podiceps	griseus	NSMT AS1244	5	0.7	20	1.30
Aves	Aves	Gaviiformes	Gavia	arctica	NSMT AS1162	6.3	0.8	22	1.34
Aves	Aves	Accipitriformes	Pandion	haliaetus	NSMT AS1163	9.4	0.97	37	1.57
Aves	Aves	Passeriformes	Alauda	arvensis	NSMT AS1207	3.1	0.49	12	1.08
Aves	Aves	Anseriformes	Mergus	serrator	NSMT AS1110	6.3	0.8	26	1.41
Aves	Aves	Accipitriformes	Sarcoramphus	papa	YIO65369	11	1.04	52.5	1.72
Aves	Aves	Non-tinamid	Casuarius		AMNH 1736	29	1.46	79	1.90
Aves	Aves	Cariamiformes	Cariama	cristata	AMNH 1392	13	1.11	39	1.59
Aves	Aves	Apodiformes	Chaetura	pelagica	AMNH 3057	2	0.3	13	1.11
Aves	Aves	Galliformes	Alectura	lathamii	AMNH 1371	7.6	0.88	18.5	1.27
Aves	Aves	Caprimulgiformes	Steatornis	caripensis	AMNH 15015	10.5	1.02	33	1.52
Aves	Aves	Caprimulgiformes	Steatornis	caripensis	AMNH 22733	9.5	0.98	32	1.51
Aves	Aves	Caprimulgiformes	Podargus	strigoides	AMNH 30765	6.7	0.83	43	1.63
Aves	Aves	Caprimulgiformes	Podargus	strigoides	AMNH 2308	9.5	0.98	45	1.65
Aves	Aves	Caprimulgiformes	Podargus	strigoides	AMNH 12462	9.5	0.98	53	1.72
Aves	Aves	Caprimulgiformes	Podargus	strigoides	AMNH 4414	9	0.95	50	1.70
Aves	Aves	Caprimulgiformes	Caprimulgus	europaeus	AMNH 3389	5	0.7	25 (skull width)	1.40
Aves	Aves	Caprimulgiformes	Caprimulgus	macrurus	AMNH 29720	5.2	0.72	27 (skull width)	1.43

Aves	Aves	Apodiformes	Chaetura	pelagica	AMNH 17936	2.3	0.36	14.5 (skull width)	1.16
Aves	Aves	Columbimorpha	Columba	livia	AMNH 27126	4.5	0.65	17	1.23
Aves	Aves	Charadriiformes	Turnix	melanogaster	AMNH 13744	2.8	0.45	15	1.18
Aves	Aves	Charadriiformes	Turnix	varius	AMNH 1601	3	0.48	14	1.15
Aves	Aves	Columbimorpha	Pterocles	exustus	AMNH 2995	4	0.6	13	1.11
Aves	Aves	Columbimorpha	Pterocles	orientalis	AMNH 4073	4	0.6	18	1.26
Aves	Aves	Columbimorpha	Pterocles	quadricinctus	AMNH 2867	4	0.6	17 (skull width)	1.23
Aves	Aves	Charadriiformes	Haematopus	ostralegus	AMNH 25251	7	0.85	22	1.34
Aves	Aves	Non-tinamid	Struthio	camelus	AMNH 2732	23	1.36	89.5 (skull width)	1.95
Aves	Aves	Non-tinamid	Rhea	americana	AMNH 4692	19.5	1.29	64	1.81
Aves	Aves	Non-tinamid	Rhea	sp.	AMNH 14820	11	1.04	59	1.77
Aves	Aves	Non-tinamid	Struthio	camelus	AMNH 1501	34.5	1.54	87	1.94
Aves	Aves	Non-tinamid	Struthio	camelus	AMNH 4261	33	1.52	88	1.94
Aves	Aves	Non-tinamid	Struthio	camelus	AMNH 3644	30	1.48	93 (skull width)	1.97
Aves	Aves	Tinamidae	Nothoprocta	ornata	AMNH 6498	6	0.78	26 (skul width)	1.73
Aves	Aves	Tinamidae	Nothoprocta	ornata	AMNH 6502	7	0.85	26	1.41
Aves	Aves	Tinamidae	Nothura	maculosa	AMNH 10804	5	0.7	20.5	1.31
Aves	Aves	Tinamidae	Eudromia	elegans	AMNH 11436	4.7	0.67	20	1.30
Aves	Aves	Non-tinamid	Dromaius	novahollandiae	AMNH 2647	18	1.26	59	1.77
Aves	Aves	Non-tinamid	Rhea		AMNH 2357	11	1.04	42	1.62
Aves	Aves	Pelecaniformes	Platalea	flavipes	AMNH 4964	11	1.04	29	1.46
Aves	Aves	Pelecaniformes	Platalea	leucorodia	AMNH 2631	10	1	26	1.41
Aves	Aves	Pelecaniformes	Leptoptilos	crumerifer	AMNH 5862	18	1.26	77	1.89
Aves	Aves	Galliformes	Penelope	superciliaris	AMNH 1262	9	0.95	25	1.40
Aves	Aves	Galliformes	Ortalis	motmot	AMNH 18140	10.5	1.02	24	1.38
Aves	Aves	Galliformes	Meleagris	ocellata	AMNH 11530	10	1	38	1.58
Aves	Aves	Passeriformes	Tyrannus	tyrannus	AMNH 26582	4	0.6	15.5	1.19
Aves	Aves	Passeriformes	Cardinalis	cardinalis	AMNH 29230	3.67	0.56	19	1.28
Aves	Aves	Passeriformes	Cardinalis	cardinalis	AMNH 26676	3.38	0.53	18	1.26
Aves	Aves	Passeriformes	Cardinalis	cardinalis	AMNH 26587	3.02	0.48	18	1.26
Aves	Aves	Passeriformes	Cardinalis	cardinalis	AMNH 32252	2.68	0.43	17.5	1.24
Aves	Aves	Psittaciformes	Nestor	meridionalis	AMNH 27323	7.5	0.88	35.5	1.55
Aves	Aves	Psittaciformes	Psittaculirostris	salvadorii	AMNH 27273	4.8	0.68	22	1.34
Aves	Aves	Gruiformes	Grus	grus	AMNH 23	13	1.11	26	1.41
Aves	Aves	Gruiformes	Balearica	regulorum	AMNH 12828	13	1.11	42	1.62
Aves	Aves	Gruiformes	Psophia	crepitans	AMNH 2356	6.5	0.813	24	1.38
Aves	Aves		Jacana	jacana	AMNH 29190	4	0.6	8	0.90
Aves	Aves	Psittaciformes	Thectocercus (Psittacara)	acuticaudatas	AMNH 6907	6.2	0.79	30.5	1.48

Aves	Aves	Passeriformes	Columba	livia	AMNH 16525	3.91	0.59	15.43	1.19
Aves	Aves	Passeriformes	Columba	livia	AMNH 12109	4.04	0.61	18.68	1.27
Aves	Aves	Passeriformes	Columba	livia	AMNH 20017	3.77	0.58	15.01	1.18
Aves	Aves	Psittaciformes	Nymphicus	hollandicus	AMNH 12897	4.71	0.67	20.02	1.30
Aves	Aves	Piciformes	Capito	niger	AMNH 18160	4.12	0.61	19.43	1.29
Aves	Aves	Psittaciformes	Eclectus	roratus	AMNH 11620	8.82	0.95	36.44	1.56
Aves	Aves	Passeriformes	Climacteris	rufus	AMNH 29996	2.71	0.43	8.9	0.95
Aves	Aves	Strigiformes	Tyto	alba	AMNH 21944	10.48	1.02	31.46	1.50
Aves	Aves	Bucerotiformes	Phoeniculus	purpureus	AMNH 2513	4.93	0.69	20.43	1.31
Aves	Aves		Phaethon	lepturus	AMNH 31223	6.59	0.82	32.72	1.51
Aves	Aves	Pelecaniformes	Pelecanus	philippensis	AMNH 6030	12.93	1.11	65.92 (skull width)	1.82
Aves	Aves	Pelecaniformes	Pelecanus	occidentalis	AMNH 21610	13.34	1.13	58	1.76
Aves	Aves	Psittaciformes	Psittacus	erithacus	AMNH 12777	7.59	0.88	25.24	1.40
Aves	Aves	Psittaciformes	Barnardius	zonarius	AMNH 2564	6.4	0.81	25.43	1.41
Aves	Aves	Charadriiformes	Tringa	flavipes	AMNH 27688	4	0.6	10	1.00
Aves	Aves	Anseriformes	Presbyornis	sp.	USNM PAL299846	5.5	0.74	16	1.20
Dinosauria	Pinacosaurus	Ornithischia	Pinacosaurus	grangeri	IGM 100/3186	64.7	1.81	100	2.00
Crocodylia	Crocodylia		Tomistoma	schlegelii (left)	AMNH 113078	27	1.43	182	2.26
Crocodylia	Crocodylia	Crocodylidae	Paleosuchus	palpebrosus	AMNH 137161	6	0.78	51	1.71
Crocodylia	Crocodylia	Alligatoridae	Alligator	mississippiensis	AMNH R67134	4.5	0.65	31	1.49
Crocodylia	Crocodylia	Alligatoridae	Alligator	mississippiensis	AMNH 46842	33	1.52	178 (estimated)	2.25
Testudines	quiet turtles	Chelidae	Chelus	fimbriata	AMNH R70638	7	0.85	80	1.90
Testudines	quiet turtles	Chelidae	Chelus	fimbriata	AMNH R43305	8	0.9	79	1.90
Testudines	quiet turtles	Cheloniidae	Chelonia	mydas	AMNH R46848	11	1.04	58	1.76
Testudines	quiet turtles	Cheloniidae	Caretta	caretta	AMNH R118692	15	1.18	102	2.01
Testudines	quiet turtles	Chelydridae	Chelydra	serpentina	AMNH R69737	8	0.9	56	1.75
Testudines	quiet turtles	Chelydridae	Chelydra	serpentina	AMNH R43300	10	1	72	1.86
Testudines	quiet turtles	Chelydridae	Chelydra	serpentina	AMNH R69735	6	0.78	41	1.61
Testudines	quiet turtles	Kinosternidae	Kinosternon	sonoriense	AMNH R69759	3.3	0.52	24	1.38
Testudines	quiet turtles	Kinosternidae	Kinosternon	sonoriense	AMNH R73821	2.5	0.4	19	1.28
Testudines	quiet turtles	Pelomedusidae	Podocnemis	vogli	AMNH R62586	5	0.7	33	1.52
Testudines	quiet turtles	Pelomedusidae	Podocnemis	expansa	AMNH R46250	14	1.15	76	1.88
Testudines	quiet turtles	Kinosternidae	Sternotherus	carinatus	AMNH R69744	3.5	0.54	23.5	1.37
Testudines	quiet turtles	Kinosternidae	Sternotherus	carinatus	AMNH R69745	3.5	0.54	25	1.40
Testudines	vocal turtles	Emydidae	Chrysemys	picta	AMNH R69894	2.5	0.4	14	1.15
Testudines	vocal turtles	Emydidae	Chrysemys	picta	AMNH R69895	3	0.48	16	1.20
Testudines	vocal turtles	Emydidae	Clemmys	guttata	AMNH R69800	3	0.48	12	1.08
Testudines	vocal turtles	Emydidae	Clemmys	insculpta	AMNH R75106	4.5	0.65	26	1.41

Testudines	vocal turtles	Emydidae	Clemmys	muhlebergii	AMNH R69794	2	0.3	13	1.11
Testudines	vocal turtles	Emydidae	Clemmys	insculpta	AMNH R123188	3	0.48	20	1.30
Testudines	vocal turtles	Emydidae	Emydoidea	blandingii	AMNH R73809	4.4	0.64	25	1.40
Testudines	vocal turtles	Emydidae	Deirochelys	reticularia	AMNH R95924	3	0.48	19	1.28
Testudines	vocal turtles	Emydidae	Graptemys	geographica	AMNH R69921	3	0.48	13	1.11
Testudines	vocal turtles	Emydidae	Graptemys	geographica	AMNH R7002	3	0.48	30.5	1.48
Testudines	vocal turtles	Emydidae	Emys	orbicularis	AMNH R73604	3	0.48	15	1.18
Testudines	vocal turtles	Emydidae	Malaclemys	terrapin	AMNH R69928	4.8	0.68	23.5	1.37
Testudines	vocal turtles	Emydidae	Malaclemys	terrapin	AMNH R69927	3	0.48	18	1.26
Testudines	vocal turtles	Emydidae	Pseudemys	peninsularis	AMNH R69899	4	0.6	26	1.41
Testudines	vocal turtles	Emydidae	Pseudemys	concinna	AMNH R69908	4	0.6	28	1.45
Testudines	vocal turtles	Emydidae	Pseudemys	concinna	AMNH R69907	5	0.7	30 (skull width)	1.48
Testudines	vocal turtles	Emydidae	Pseudemys	peninsularis	AMNH R69900	5.5	0.74	31	1.49
Testudines	vocal turtles	Emydidae	Terrapene	carolina	AMNH R43297	3.5	0.54	19.5	1.29
Testudines	vocal turtles	Emydidae	Terrapene	carolina	AMNH R69786	4.5	0.65	16	1.20
Testudines	vocal turtles	Emydidae	Terrapene	ornata	AMNH R69772	3.6	0.56	13	1.11
Testudines	vocal turtles	Testudinidae	Kinixys	erosa	AMNH R7210	6	0.78	28	1.45
Testudines	vocal turtles	Trionychidae	Apalone	ferox	AMNH R5932	13.5	1.13	61	1.79
Testudines	vocal turtles	Trionychidae	Apalone	spinifera	AMNH R69931	7.8	0.89	29	1.46
Testudines	vocal turtles	Testudinidae	Gopherus	berlandieri	AMNH R73817	5.5	0.74	24	1.38
Testudines	vocal turtles	Testudinidae	Gopherus	polyphemus	AMNH R73815	9	0.95	41	1.61
Testudines	vocal turtles	Testudinidae	Geochelone	pardalis	AMNH R32885	17	1.23	61	1.79
Testudines	vocal turtles	Testudinidae	Geochelone	carbonaria	AMNH R62585	7.5	0.88	32	1.51
Squamata	Squamata	Cordylidae	Cordylus	giganteus	AMNH 62940	4	0.6	35	1.54
Squamata	Squamata	Agamidae	Hydrosaurus	amboinensis	AMNH R140825	5	0.7	27	1.43
Squamata	Squamata	Eublepharidae	Eublepharis	macularius	AMNH 89838	4	0.6	19	1.28
Squamata	Squamata	Eublepharidae	Eublepharis	macularius	AMNH 89837	4	0.6	24	1.38
Squamata	Squamata	Cordylidae	Cordylus	giganteus	AMNH R154707	3	0.48	27	1.43
Squamata	Squamata	Gekkonidae	Gekko	gecko	AMNH R154719	8	0.9	29	1.46
Squamata	Squamata	Varanidae	Varanus	komodoensis	AMNH 37913	9	0.95	100	2.00
Squamata	Squamata	Varanidae	Varanus	salvadorii	AMNH R59873	10	1	57	1.76
Squamata	Squamata	Iguanidae	Iguana	sp.	AMNH 32377	8	0.9	70	1.85
Squamata	Squamata	Iguanidae	Sauromalus	ater	AMNH 75096	3	0.48	25	1.40
Squamata	Squamata	Varanidae	Varanus	niloticus	AMNH R140805	5	0.7	24	1.38
Squamata	Squamata	Colubridae	Masticophis	flagellum	AMNH 87381	3	0.48	16	1.20
Squamata	Squamata	Colubridae	Rhinocheilus	lecontei	AMNH R140797	2	0.3	9	0.95
Squamata	Squamata	Pythonidae	Morelia	viridis	AMNH R140838	3.5	0.54	20	1.30
Squamata	Squamata	Viperidae	Bitis	nasicornis	AMNH R46395	5.5	0.74	38	1.58

Squamata	Squamata	Pythonidae	Python	reticulatus	AMNH R142608	4	0.6	18	1.26
Squamata	Squamata	Boidae	Corallus	caninus	AMNH R155264	4	0.6	28	1.45
Squamata	Squamata	Colubridae	Masticophis	flagellum	AMNH R140781	3.5	0.54	17	1.23