Youngoides romeri and the origin of the Archosauriformes

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ABSTRACT—Prior workers reported that all specimens attributed to *Youngopsis* and *Youngoides* could not be distinguished from the holotype of *Youngina capensis*. Others considered all specimens attributed to *Proterosuchus*, *Chasmatosaurus,* and *Elaphrosuchus* conspecific. In both cases distinct skull shapes were attributed to taphonomic variations due to distortion pressure or allometric growth. Here a large phylogenetic analysis of the Amniota (401 taxa) tests those hypotheses. The resulting tree recovers a den of small *Youngina* specimens preceding the Protorosauria. Another specimen nests at the base of the Protorosauria. Six others nest between the Protorosauria and the Archosauriformes. The most derived of these bears a nascent antorbital fenestra. Two other putative *Youngina* specimens nest at unrelated nodes. In like fashion, the various specimens assigned to *Proterosuchus* are recovered in distinct clades. One leads to the Proterochampsidae, Parasuchia and Choristodera. The latter lost the antorbital fenestra. Another clade leads to all higher archosauriforms. The present analysis reveals an evolutionary sequence shedding new light on the origin and radiation of early archosauriforms. Taphonomic distortion pressure and allometry during ontogeny were less of a factor than previously assumed. The splitting of several specimens currently considered *Youngina* and *Proterosuchus* into distinct genera and species is supported here.

INTRODUCTION

The Archosauriformes is a widely recognized monophyletic clade that includes, by definition, the most recent common ancestor of Proterosuchidae, Erythrosuchidae,

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Proterochampsidae, and Archosauria (Gauthier, 1986). Later studies (e.g., Sereno, 1991; Parrish, 1993; Juul, 1994; Ezcurra, 2010; Nesbitt, 2011) have universally rooted their archosauriform clades on Proterosuchidae or *Proterosuchus*. There is general consensus regarding the composition of the Archosauriformes, except Peters (2000) removed the Pterosauria (also see Supp. Data).

With regard to archosauriform outgroups, in the pre-cladistic era Broom (1914, 1922, 1946) proposed a younginid origin. Like Broom, Romer (1967) considered younginids members of the Lepidosauria from which arose the archosauriforms (then called archosaurs or thecodonts). Reig (1967, 1970) wrote there is little doubt that archosauriforms and lepidosaurs had a common origin, or that archosauriforms were derived from early lepidosaurians. However, Reig (1967) ruled out younginid and millerettid origins for archosauriforms, stating that both groups are 'more advanced' than proterosuchians, which have a posteriorly shifted jaw joint (suspensorium) and lack a squamosal ledge (otic notch). After giving credit to von Huene (1911) and Rozhdestvenskii (1964) for their ideas on a synapsid origin for proterosuchians, Reig (1967, 1970) proposed a varanopid origin for proterosuchians, with a focus on *Varanodon agilis* (Olson 1965). It shares with proterosuchids a jaw joint far posterior to the occiput, lacks an otic notch, has a lateral temporal fenestra and has an antorbital fenestra. Related taxa, including *Ophiacodon* and *Varanops* (Supp. Data), have another trait found in proterosuchids, a mandibular fenestra. Post-cranial similarities were also noted (Reig, 1967), however the antorbital fenestra of *Varanodon agilis* remains an autapomorphy, with no second appearance in proximal sister taxa (Witmer, 1995; Supp. Data). Gow (1975) compared *Youngina* specimens to one another in a paper otherwise

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devoted to *Prolacerta* (Fig. 1), but did not see a relationship between these two genera. However, Gow (1975) did note similarities between *Prolacerta* and *Proterosuchus* (Fig. 1).

In the post-cladistic era Gauthier (1986) nested Prolacertiformes, Rhynchosauria, and Lepidosauromorpha as successively more distant outgroup taxa to the Archosauriformes. Evans (1988) nested *Megalancosaurus*, *Trilphosaurus* and the Thalattosauria as outgroups. Bickelmann et al. (2009), based on Müller (2003), recovered Rhynchosauria as the sister clade to the Archosauriformes. *Trilophosaurus*, *Prolacerta*, *Macrocnemus,* and *Tanystropheus* were successively more distant outgroups. *Youngina* nested six nodes further toward the base of the tree. Nesbitt (2011) rooted an archosauriform tree on *Mesosuchus* and *Prolacerta*. Ezcurra et al. (2014) nested the following as successively more distant outgroup taxa: *Prolacerta*, Rhynchosauria, *Trilophosaurus*, Protorosauria, Lepidosauriformes, Younginiformes, *Coelurosauravus,* and Araeoscelida.

The preceding list of prior studies shows both disparity and consensus with regard to archosauriform outgroup taxa. Unfortunately, there is a considerable morphological gap between the Rhynchosauria + *Trilophosaurus* and the Archosauriformes + *Prolacerta*. At present, no taxa with a suite of plesiomorphic traits morphologically unite the above taxa or fill this gap.

Youngina Specimens

Youngina studies had their genesis with the original descriptions of *Youngina capensis* by Broom (1914; AMNH 5661, Fig. 1). Later Broom (1921, 1922) described 'an imperfect

skeleton' (BPI 3859, Fig. 2) found eight yards from the holotype and assigned it to *Y. capensis*. Broom (1924) described postcrania, including the tarsus and metatarsals, from his 'third' specimen (TM 200). Olson (1936) described the palate and occiput of FMNH UC 1528 (Figs. 1, 3) and referred it to *Y. capensis*. Olson and Broom (1937) redescribed and renamed that specimen *Youngoides romeri*. Broom (1937) described the skull of *Youngopsis kitchingi* (TM 1490, Fig. 1). Broom and Robinson (1948) described two more skulls, *Youngopsis rubidgei* (RC 90, Fig. 1) and *Youngoides minor* (RC 91, Fig. 1).

Gow (1975) concluded that all known *Youngina*, *Youngopsis,* and *Youngoides* specimens could be referred to a single genus, *Youngina capensis*. Differences were ascribed to variations in taphonomic distortion (contra Watson, 1957). That assessment has been followed ever since.

Evans (1987) reported on the braincase of another *Youngina* specimen (TM 3603, Fig. 1). Smith and Evans (1996) described a den of six 'juveniles' (SAM K7710, Fig. 1). These were the first purported *Youngina* specimens with articulated post-crania. All prior specimens were from the Beaufort Group assigned to the *Dicynodon* (*Daptocephalus*) Assemblage Zone, uppermost Permian (Anderson and Cruickshank, 1978). The den was found in the lower Tropidostoma Assemblage Zone, two to three million years older.

More recently, Gardner et al. (2010) examined the holotype of *Youngina capensis* (AMNH 5561) with a high resolution X-ray computed tomography scanner and recovered braincase data. They were able to make comparisons with several amniote clades, not settling on one as a closest relative.

Youngina Systematic Relationships

In the pre-cladistic era, Romer (1945) erected the Younginiformes to include

Younginidae, Prolacertidae and Tangasauridae. At that time Younginidae included

Youngina, *Youngoides* and *Youngopsis* along with the lepidosauromorphs *Paliguana*,

Palaegama, *Saurosternon*, and other incomplete specimens, including *Galesphyrus*

(Carroll, 1976; Fig. 2). Later Romer (1966) removed Prolacertidae from Younginiformes.

Currie (1981, 1982) considered *Youngina* close to *Hovasaurus* (Piveteau, 1926; Currie,

1981)*, Kenyasaurus* (Harris and Carroll, 1977), and *Tangasaurus* (Haughton, 1924a;

Currie, 1982; Fig. 2).

Gauthier et al., (1988) erected the clade Lepidosauromorpha, for Lepidosauria and

all taxa sharing a more recent common ancestor with it than with Archosauria. That clade

originally contained the Younginiformes, but Laurin (1991) removed them. According to

Laurin (1991), Archosauromorpha + Lepidosauromorpha constitute the Sauria, and

Sauria + Younginiformes constitute the Neodiapsida.

More recently, Younginiformes was defined as the last common ancestor of

Acerosodontosaurus (Currie, 1980; Bickelmann et al., 2009; Fig. 2), *Hovasaurus*,

Youngina, and all its descendants (Benton, 1985; Evans, 1988; Gauthier et al., 1988a;

Laurin, 1991; Laurin and Reisz, 1995). Thus defined the clade Younginiformes retains

only *Youngina* and Tangasauridae from Romer (1945), according to Laurin and Reiz

(1995).

In the post-cladistic era, Evans (1988) nested *Youngina* between

Acerosodontosaurus and (*Thadeosaurus + Kenyasaurus*) and (*Tangasaurus +*

Hovasaurus) in a clade with *Palaegama* at its base. Laurin and Reisz (1995) nested

Younginiformes with Araeoscelida as basal branches of the Diapsida. Müller (2003)

nested *Youngina* six nodes from basalmost amniotes, between *Apsisaurus* and *Claudiosaurus*. Bickelmann et al. (2009) nested *Youngina* with an unresolved clade that included *Galesphyrus*, *Thadeosaurus* (Carroll, 1981; Fig. 2)*, Lanthanolania* (Modesto and Reisz, 2003) and *Kenyasaurus*, plus another clade that included *Tangasaurus*, *Hovasaurus* and *Acerosodontosaurus*. The authors suggested these taxa do not form a monophyletic relationship with each other to the exclusion of other diapsids. Rather, stem-diapsid relationships were unresolved.

Gardner et al. (2010) summarized the then current state of knowledge regarding *Youngina capensis* when they reported *Youngina* is often regarded as the 'archetypal' basal diapsid (Smith and Evans, 1996) or ancestral morphotype (Carroll, 1988). Gardner et al. (2010) nested *Youngina* within the Amniota and the Diapsida, basal to *Claudiosaurus*, Kuehneosauridae*, Coelurosauravus*, Ichthyopterygia + Thalattosauriformes, Archosauromorpha, Choristodera, Sauropterygia, Testudines and Squamata + *Sphenodon* in order if increasing phylogenetic distance. However, Gardner et al. (2010) also noted those relationships have been disputed (Currie 1981, 1982).

More recently, Reisz et al. (2011) nested *Youngina* with *Thadeosaurus* (within the Younginidae), derived from Tangasauridae (*Tangasaurus*, *Acerosodontosaurus,* and *Hovasaurus*) and basal to *Claudiosaurus*, Archosauromorpha, and Lepidosauromorpha (the latter two labeled, 'Sauria').

***Proterosuchus* Specimens**

Proterosuchus studies had their genesis with the original descriptions of *Proterosuchus fergusi* (Broom, 1903; SAM 591), followed by *Chasmatosaurus vanhoepeni* (Haughton,

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1924b; TM 201; Fig. 3), *Elaphrosuchus rubidgei* (Broom, 1946; RC59; Fig. 3) and

Chasmatosaurus alexandri (Hoffman, 1965; QR 1484/C. 3016; Fig. 3). Other more

complete specimens followed (listed in Welman, 1998; Fig. 3).

Proterosuchus Systematic Relationships

In the pre-cladistic era, Cruickshank (1972) referred all specimens of *Proterosuchus*,

Chasmatosaurus and *Elaphrosuchus* to the species *Proterosuchus fergusi* and

hypothesized the morphological differences could be the result of allometric growth.

In the cladistic era, Gauthier (1986) rooted his archosauriform tree with the

Proterosuchidae and included Prolacertiformes, Rhynchosauria, and Lepidosauromorpha

as successively distant outgroups. Juul (1994), Bennett (1996), Dilkes & Sues (2009),

Ezcurra et al. (2010) and Nesbitt (2011) continued that tradition. Evans (1988) nested her

clade 'Archosauria' as the sister to *Prolacerta*, *Protorosaurus*, *Boreopricea,*

Macrocnemus, *Cosesaurus*, *Tanystropheus* and *Tanytrachelos*. These were all derived

from a sister to *Megalancosaurus*, *Trilophosaurus*, Thalattosauria, Rhynchosauria,

Kuehneosauridae and Choristodera in order of increasing distance.

Müller et al. (2009) nested turtles as the proximal outgroup to the

Archosauriformes (represented by *Chasmatosaurus*), preceded by rhynchosaurs,

protorosaurs, *Macrocnemus, Tanystropheus* and the Choristodera.

Without employing phylogenetic analysis, Welman and Flemming (1993)

demonstrated with a statistical evaluation that a number of size-related differences quoted

by Cruickshank (1972) could not be used for this purpose. Later, an evaluation of size-

related and size-unrelated characters (Welman, 1998) determined the four species were

subjective synonyms and that the RC59 (*Elaphrosuchus*) specimen was the smallest member of the growth series. Following fieldwork, Welman (1998) reported that all four purported species were from the same Early Triassic strata, supporting the claim that they were all conspecific.

Likewise without publishing a phylogenetic analysis, Ezcurra et al. (2013) discussed proterosuchids and erythrosuchids, both in and out of South Africa, and provided a summary of their systematic history. They concluded the taxonomic contents and internal relationships of Proterosuchidae and Erythrosuchidae have not yet been tested thoroughly. Those relationships are tested here (Fig. 4, Supp. Data).

Institutional abbreviations

AMNH: American Museum of Natural History, New York, U.S.A.; **BSPHM**: Bayerische Staatssammlung für Paläontologie und historische Geologie, Münich, Germany; **BPI**: Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, South Africa; **CGH**: National Museum, Prague, Czechoslovakia; **DMSW**: D. M. S. Watson collection at the University Museum of Zoology at Cambridge, England (see UMZC); **FMNH UC**: Field Museum of Natural History, University of Chicago, U.S.A.; **G**: The Hancock Museum, Newcastle upon Tyne, England; **GMV**: Geological Museum of China, Beijing, China; **KUVP**: University of Kansas Museum of Natural History, Lawrence, U.S.A.; **MB.am**: Sammlung Lilienstern im Museum für Naturkunde der Humboldt Universität Berlin, Germany; **MP**: Mestké Museum Historicté, Pilzen, Czechoslovakia; **MPUM**: Museo Paleontologia Universita degli Studi di Milano, Italy; **NMS**: National Museums Scotland, Edinburgh Scotland; **PIMUZ**: Paläontologisches

Institut und Museum der Universität Zürich, Zürich, Switzerland; **PIN**: Palaeontological

Institute, Russian Academy of Sciences, Moscow, Russia; **PVL**: Paleontologia de

Vertebrados Lillo, Universidad Nacional de Tucuman, Tucuman, Argentina; **PVSJ**:

Museo do Ciencias Naturles, Universidad Nacional de San Juan, Juan Juan, Argentina;

RC: Rubidge Collection, Wellwood, Graaff Reinet, South Africa; **SMNS**: Staatliches

Museum für Naturkunde, Stuttgart, Germany; **TA**: Adpression code for Museum für

Naturkunde Chemnitz, Germany, U.S.A.; **TM**, Ditsong: National Museum of Natural

History (formerly Transvaal Museum), Pretoria, South Africa. **UMZC**: University

Museum of Zoology at Cambridge, England.

MATERIALS AND METHODS

Prior phylogenetic analyses that included *Youngina* (e.g. Gauthier, 1986; Evans, 1988;

Müller, 2003, and all trees based on it) analyzed sample taxa from a wide spectrum of

amniote clades. The present analysis (Supp. Data) of 401 specimen- to genus-based taxa

and 228 characters covers the same gamut. It also employs eight taxa attributed to

Youngina and seven taxa attributed to *Proterosuchus* for the first time. The great size of

the present study minimizes the effects of tradition and/or subjective decision-making

while creating a taxon inclusion set. It also provides a larger number of possible nesting

sites for all included taxa.

Due to the wide range and large size of the inclusion set, data were collected from

firsthand observation, digital photographs, and the literature. The taxon at the focus of

this report, *Youngoides romeri* (FMNH UC 1528), was examined firsthand. Taxa and

characters were compiled in MacClade 4.08 (Maddison and Maddison1990) then

imported into PAUP* 4.0b (Swofford 2002) and analyzed using parsimony analysis with

the heuristic search algorithm. All characters were treated as unordered and no character

weighting was used. Bootstrap support figures for 100 replicates were calculated for

overlapping subsets; then combined and documented in the tree (Fig. 4, Supp. Data).

The oldest known archosauriform, *Archosaurus* (Tatarinov 1960), was not tested

because it lacks a complete skull and substantial post-crania. For the same reason,

Sarmatosuchus, a specimen that Gower and Sennikov (1997) nested with *Fugusuchus*

(Fig. 3), was also excluded.

RESULTS

The present phylogenetic analysis of 401 taxa and 228 characters recovered three optimal

trees (Supp. Data) with a length of 6266 steps, a Consistency Index (CI) of .094, a

Retention Index (RI) of .749, a Rescaled Consistency Index (RC) of .070 and a

Homoplasy Index (HI) of .906. The homoplasy score was high due to the great propensity

of tested taxa to converge on traits and to the high number of taxa within the inclusion set.

Loss of resolution occurred at the node in which the skull only *Gualosuchus* nested with

the skull-less *Lagerpeton* (Fig. 4, Supp. Data). Otherwise smaller subsets recovered

single optimal trees with the same topology. Virtually all branches had high Bootstrap

scores (Fig. 4, Supp. Data). Lower scores were associated with incomplete taxa.

A subset of that large tree is presented here (Fig. 4). It includes the 54 taxa that

surround *Youngoides romeri* (FMNH UC 1528). This subset tree had a length of 805

steps, a Consistency Index (CI) of .383, a Retention Index (RI) of .721, a Rescaled

Consistency Index (RC) of .276 and a Homoplasy Index (HI) of .617. In this subset 33

characters are constant. Ten variable characters are parsimony uninformative. The

character: taxon ratio is 4.222 (or 3.49 based on the 185 informative characters).

The present phylogenetic analysis (Fig. 4, Supp. Data) produced a clear record of

the interrelationships between the various tested specimens of *Youngina* and

Proterosuchus, the majority of which were recovered in distinct clades. None had

identical scores.

The BPI 3859 specimen (Fig. 2) did not nest with the other *Youngina* specimens,

but with *Acerosodontosaurus,* between *Adelosaurus huxleyi* (Hancock and Howse, 1870;

Watson, 1914; Evans 1988) and *Thadeosaurus,* in a large clade that included the

Enaliosauria (ichthyosaurs and plesiosaurs according to Owen, 1839, Supp. Data). While

derived members were aquatic and had flippers, basal members, like the BPI 3859

specimen, retained traits similar to their long-legged, basal diapsid forebearers.

The oldest and smallest *Youngina* specimens, the den members of SAM K7710

(Fig. 1), were also the most primitive of tested *Youngina* specimens (Fig. 4). These were

derived from a sister to the basal diapsids, *Spinoaequalis schultzei* (deBraga and Reisz

1995; KUVP 12484, Figs. 1, 2) and *Galesphyrus. Spinoaequalis* precedes the SAM K

7710 specimen by 50 million years. The only known specimen of *Galesphyrus* was

nearly a contemporary of *Youngina*.

The BPI 375 specimen (Fig. 1) nested basal to the Protorosauria (=

Prolacertiformes), which divide into two clades (Fig. 4, Supp. Data). The first includes

Protorosaurus and *Prolacerta*. The second includes *Jaxtasuchus*, *Boreopricea* and

Pamelaria. Other protorosaurs, including *Malerisaurus* (Chatterjee, 1980) and

Czatkowiella (Borsuk−Biaynicka & Evans, 2009), were not tested. Several taxa related to

Macrocnemus and formerly considered 'prolacertiformes' (e.g. Evans, 1988) now nest

within a new lepidosaur clade between the Squamata and the Sphenodontia (Supp. Data).

A series of six *Youngina* specimens nested between the Protorosauria and the

Archosauriformes in this order: (1) TM 3603; (2) RC 90; (3) RC 91; (4) TM 1490; (5)

AMNH 5561; and (6) FMNH UC 1528 (Fig. 4). The last of these had a nascent antorbital

fenestra (Fig. 5). The RC 90 specimen was not included on figure 4 because it is

represented by so few visible character traits, all based on a sketch by Watson (1957), but

it is included on the large amniote tree (Supp. Data). A shift of RC 90 to either one of its

proximal sisters, TM 3603 or RC 91, adds one step.

The smallest and basalmost *Proterosuchus*, the BPI/1/4016 specimen (Figs. 1, 3),

is derived from a sister to the FMNH UC 1528 specimen of *Youngina.* A list of

transitional traits and autapomorphies (see below) indicates the BPI/1/4016 specimen is

not a juvenile of a larger proterosuchid. Two clades arise from this node.

The first clade derived from a sister to the BPI/1/4016 specimen includes the

larger, narrow-skulled proterosuchids, RC96 and NMQR 1484. Three large, wide-skulled

proterosuchids (TM 201, SAM PK 11208 and QR 880/C. 500; Figs. 3, 4, 6) follow. More

derived taxa include the smaller *Elaphrosuchus* (Figs. 3, 6), the larger SAM PK K10603

(Fig. 6), and the much smaller BPI 2871 specimen (Figs. 1, 3, 6), which Gow (1975)

ascribed to *Youngina*. It has no antorbital fenestra.

A sister to the BPI 2871 specimen gave rise to *Doswellia* and the Choristodera

(Fig. 6) on one branch. These taxa likewise do not preserve an antorbital fenestra. If an

antorbital fenestra is present on *Doswellia* it is a vestige. The other branch includes *Diandongosuchus*, *Teraterpeton*, the Phytosauria, and the Proterochampsidae (Fig. 6).

Thus *Elaphrosuchus* was not a primitive taxon, nor a juvenile, but a derived taxon demonstrating the first stages of phylogenetic miniaturization that reached its nadir with the tiny BPI 2871 specimen. Thereafter several clades were larger. However, *Cteniogenys* (Fig. 6), a basal choristodere, remained tiny, nesting at the base of a clade of other small choristoderes.

The second clade derived from a sister to the small BPI/1/4016 proterosuchid includes the smaller taxa, *Euparkeria* and *Osmolskina,* splitting at the first dichotomy (Fig. 4, Supp. Data). The next dichotomy splits the Rauisuchidae + Ornithosuchidae from the Erythrosuchidae, including *Fugusuchus*, *Revueltosaurus* and *Tasmaniosaurus* at its base. The basalmost rauisuchid, *Venjukovia*, was also basal to the Archosauria and several intervening clades (Supp. Data).

Despite the many convergent traits, proterosuchids did not nest with *Varanodon agilis* (contra Reig, 1967, 1970). Shifting all the Archosauriformes to *Varanodon* adds 53 steps to the most parsimonious tree. However, the Diapsida, as recovered here (Supp. Data) was derived from basalmost synapsids.

Deleting all archosauriforms nests the *Youngina* series between *Adelosaurus* and *Acerosodontosaurus* + the BPI 3859 specimen. Basal archosauriforms (proterosuchids) are required to restore the topology of the complete tree. This is so because neither *Galesphyrus* nor *Adelosaurus* preserve skulls. Most *Youngina* specimens are skull only taxa, and all tested proterosuchids include skull material.

Other Phylogenetic Results

The present analysis does not support the nesting of rhynchosaurs (including

Mesosuchus) basal to the Archosauriformes (contra Gauthier, 1986, and all trees based on

it). Given additional nesting opportunities (Supp. Data) rhynchosaurs and trilophosaurs

nest as the most derived of the Sphenodontia. *Sapheosaurus* and *Priosphenodon* are

transitional taxa. Shifting *Mesosuchus* and the rhynchosaurs to the base of the

Archosauriformes adds 31 steps to the most parsimonious tree.

　　　The present analysis does not support the nesting of turtles (Testudines) as the

proximal outgroup to the Archosauriformes (contra Müller et al., 2009). Turtles nest

more parsimoniously with *Stephanospondylus* and the Pareiasauria (Supp. Data). Shifting

turtles to the base of the Archosauriformes adds 55 steps to the most parsimonious tree.

　　　Several taxa once considered prolacertiformes, including *Macrocnemus* and

Tanystropheus (Evans, 1988; Peters, 2000; Müller et al., 2009), now nest within a novel

clade of lepidosaurs between the Squamata and the Sphenodontia (Supp. Data).

Pterosaurs often nested by default with basal archosaurs or archosauriformes (e.g.,

Gauthier, 1986; Müller, et al., 2009; Nesbitt, 2011), but here they nest in this new clade

of lepidosaurs. The taxa that phylogenetically precede the Pterosauria, including

Cosesaurus, *Sharoviptery, Longisquama*, and all their ancestors, document the long

sought gradual accumulation of pterosaurian traits, confirming the results of Peters

(2000).

　　　The present analysis does not support the nesting of the drepanosaur,

Megalancosaurus, as the proximal outgroup to the Archosauriformes (contra Evans,

1988). *Vallesaurus,* the only tested drepanosaur, also nests within the new clade of lepidosaurs (Supp. Data).

Lagerpeton (Romer, 1971; Nesbitt, et al., 2009; Nesbitt, 2011) does not nest with basal dinosauromorphs, but with *Gualosuchus* and *Tropidosuchus* in the Proterochampsidae. Shifting *Lagerpeton* to the basal dinosauromorphs adds 14 steps.

Despite herbivorous teeth and a reduced antorbital fenestra with expanded fossa converging with aetosaurs (contra Nesbit, 2011), *Revueltosaurus* nests here (Fig. 4) with *Fugusuchus* and *Tasmaniosaurus*. In the present tree, shifting *Reveultosaurus* to the aetosaurs adds 30 steps.

Vancleavea (Nesbitt et al., 2009; Nesbitt, 2011) does not nest within the Archosauriformes, but with *Helveticosaurus* in the Thalattosauriformes. Nesbitt (2011) included no thalattosaurs in his phylogenetic analysis. In the present tree, shifting *Vancleavea* to the Erythrosuchidae adds 63 steps.

Spinoaequalis (de Braga and Reisz, 1995) was nested within the Araeoscelidae. Here (Supp. Data) it nests outside that clade, the most basal taxon of all other diapsids (sans Lepidosauriformes). Several other novel nestings of various taxa are also recovered here (Supp. Data).

DISCUSSION

The present study includes the first phylogenetic analysis to employ several specimens attributed to *Youngina* and *Proterosuchus*. The results (Fig. 4, Supp. Data) do not support prior studies (Gow, 1974; Evans, 1987; Smith and Evans, 1996; Gardner, et al., 2010)

that considered all specimens currently attributed to *Youngina capensis* conspecific. In similar fashion, the present analysis does not support prior studies (Cruickshank, 1972; Welman, 1998; Ezcurra et al., 2010) that considered all specimens currently attributed to *Proterosuchus* conspecific. Rather each specimen nests separately in the present analysis, some with autapomorphies. No two scores were identical. Their specific differences (detailed below) are not those expected from taphonomic distortion or allometry during ontogeny. Rather those traits provide a gradual accumulation of derived traits across each series.

The present results support a younginid origin for the Archosauriformes and provide new insight into the early radiation of basal Archosauriformes. Here (Supp. Data) the origin of the Archosauriformes can be traced back to basal diapsids, basal archosauromorphs, basal amniotes, and basal tetrapods. Here (Figs. 1-6), one can trace origin and phylogenetic enlargement of the prominent hook snout of large proterosuchids as well as the later reduction in smaller, more derived taxa under the hypothesis of phylogenetic paedomorphosis and miniaturization (Hanken and Wake, 1993). The antorbital fenestra was also lost in the tiny BPI 2871 specimen and its phylogenetic descendants, the Choristodera. The antorbital fenestra was retained or regained in *Diandongosuchus*, *Teraterpeton*, the Phytosauria and the Proterochampsidae.

Only two sets of *Proterosuchus* specimens nest with close, possibly conspecific counterparts (but see below). Thus, most *Youngina* and *Proterosuchus* specimens should retain their original nomenclature while others require new generic and/or specific names.

Prior Phylogenetic Analyses with *Youngina*

The Müller (2003), Bickelmann et al. (2009) and Gardner et al. (2010) trees recovered some odd mismatches that should have alerted them to problems. For instance, the rib-gliders, *Coelurosauravus* and the Kuehneosauridae, nested between the aquatic *Claudiosaurus* and the aquatic Ichthyopterygia + Thalattosauriformes. Testudines nested between Sauropterygia and Lepidosauria (*Sphenodon* + Squamata). In those studies at certain nodes sister taxa do not resemble one another, nor do their phylogenetic series document a gradual accumulation of derived traits. The use of suprageneric taxa is a major part of the problem. In the present analysis (Fig. 4, Supp. Data) no suprageneric taxa were used. Here the morphological gaps between sister taxa have been minimized and a gradual accumulation of derived traits can be traced for every taxon and every lineage.

A Gradual Accumulation of Traits in the Lineage of *Youngina*

Here (Fig. 4, Supp. Data), in phylogenetic order are the taxa in the direct lineage of *Youngina capensis*, *Youngoides romeri* and the Archosauriformes. These characters document the gradual accumulation of derived traits used and recovered in the present study. Autapomorphies and notes are also reported. The first taxon in the *Youngina* series, SAM K 7710, is distinct from its phylogenetic predecessor, the basal diapsid *Spinoaequalis* (Fig. 2) in the following traits.

***Youngina?* SAM K 7710**—(1) Skull table (cranium) convex; (2) ventral naris chiefly premaxilla; (3) lateral rostral shape concave; (4) premaxilla ascending process beyond naris; (5) lacrimal does not contact naris; (6) naris opening dorsolateral; (7) posterolateral

premaxilla present, narrower than naris; (8) maxilla taller than 0.4x orbit height; (9) quadrate vertical; (10) occiput shape, ovate; (11) mandible depth posterior to coronoid even; (12) presacrals, 25 or fewer; (13) second sacral rib bifurcate; (14) distal chevron wider than proximal; (15) caudal anterior transverse processes (ribs) not bent posteriorly; (16) cleithrum absent; (17) mineralized sternum or sternae present; (18) ilium anterior process small; (19) fibula trochanter is a long, low ridge; (20) fibula is appressed to tibia or nearly so; (21) metatarsal five hooked, not straight, and proximally it is the widest metatarsal.

Notes: Known from a den of five, these SAM K 7710 specimens were considered immature (Smith and Evans, 1996) based on their small size and the following traits: (1) the roofing bones are unsculptured; (2) the paired frontals and parietals are joined by simple sutures; (3) the postorbital bar is slender; (4) the eyes and parietal foramen are proportionately large; (5) the sternal plates are weakly ossified and remain paired; (6) the pubis and ischium are separated by a weakly ossified area; (7) the obturator foramen is open posteriorly; (8) the ends of the long bones lack well-formed joint surfaces; (9) the carpals and tarsals appear incompletely preserved; and (10) there is no trace of a notch on the calcaneum or astragalus for a perforating artery. The small size is shared with its phylogenetic predecessors, *Spinoaequalis*, along with the following traits: 1, 2, 4–10. The more derived BPI 375 specimen (Fig. 1), at twice the size of SAM K 7710, also shares traits 1–4. Smith and Evans (1996) also noted a lack of ossified dermal bones, as seen in the outlier BPI 3859 specimen, but that specimen with that autapomorphy no longer nests in the *Youngina* series. Evans (1988) considered the closely related *Adelosaurus*

immature. De Braga and Reisz (1995) considered the closely related *Spinoaequali*s immature. Taxa at this node appear to share 'immature' traits that belong to adults.

Youngina? **BPI 375**—(1) Snout constricted in dorsal view; (2) nasals narrow toward naris; (3) major axis of naris horizontal to 30º (based on phylogenetic bracketing); (5) frontal/nasal angle zigzags; (6) jugal depth not gracile. Notes: While in the lineage of Young*ina capensis*, this specimen also nests at the base of the clade, Protorosauria. Characters associated with protorosaurs only (to the exclusion of proximal younginids) follow.

Youngina? **BPI 375 + Protorosauria**—(1); maxilla ventrally concave; (2) quadrate posteriorly concave; (3) quadratojugal reduced to quadrate ramus; (4) quadrate lateral coverage minimal; (5) opisthotic connected to quadrate; (6) lower temporal arch incomplete.

Youngina? **TM 3603**—(1) Skull width 2x height; (2) skull table flat; (3) postfrontal contacts upper temporal fenestra; (4) suborbital jugal shorter than posterior jugal process; (5) jugal extends nearly to posterior medial parietal rim; (6) squamosal large, supratemporal long; (7) occiput shape converging dorsally; (8) basipterygoid process not prominent. Autapomorphies: (1) Postorbital contacts supratemporal. Notes: Autapormorphies not in the present character list (Supp. Data) include: (1) deep maxilla ventral to jugal; (2) anteriorly-oriented orbits and a narrow rostrum (based on cheek

angles); (3) postorbital dorsally placed resulting in much smaller upper temporal fenestrae.

***Youngopsis rubidgei* RC 90**—(1) Naris elongated 2x height; (2) squamosal descending angle obtuse. Autapomorphies: (1) Frontal enters upper temporal fenestra.

***Youngoides minor* RC91**—(1) Snout not constricted; (2) nasals longer than frontals; (3) quadrate leans anteriorly; (4) splenial visible in lateral view; (5) mandibular fenestra present; (6) mandible ventral shape straight, then convex. Autapomorphies: (1) Lateral rostral shape straight. Notes: This specimen is poorly preserved.

***Youngopsis kitchingi* TM 1490 (1937)**—(1) Major axis of naris > 30º; (2) naris opening anterolateral; (3) prefrontal contacts maxilla; (4) paroccipital angle > 40º. Autapomorphies: (1) Premaxilla tooth number < 4. Notes: This is the largest specimen prior to *Proterosuchus*. It had proportionately larger and fewer teeth.

***Youngina capensis* AMNH 5561**—(1) Premaxilla oriented down; (2) possible antorbital fenestra without maxilla fossa; (3) orbit smaller than postorbital skull; (4) temporal ledge created by squamosal; (5) supraoccipital not broader than exoccipitals. Autapomorphies: (1) Maxilla ventrally concave; (2) maxillary teeth not 2x deeper than long. Notes: This is the holotype of *Youngina capensis*. The rostrum has been taphonomically damaged, but a nascent antorbital fenestra appears to be present, leaving a narrow ascending process of the maxilla and a lacrimal fossa.

***Youngoides romeri* FMNH UC 1528**—(1) Skull table convex; (2) maxilla ventrally convex; (3) tiny pineal foramen less than one fifth of parietal length; (4) frontal length/width < 4:1; (5) squamosal and quadratojugal barely indented with nascent semicircle shape; (6) opisthotic connected to quadrate; (7) ectopterygoid shape, pterygoid process wider; (8) mandible tip rises; (9) mandible depth posterior to dentary, deeper anteriorly. Notes: This specimen has more numerous and smaller teeth. The temporal region is more robust. A nascent antorbital fenestra is present (Fig. 5).

***Youngina?* BPI 3859**—The following traits set the BPI 3859 specimen (Broom 1921, 1922, and attributed by all other workers to *Youngina*) apart from the lineage of *Youngina capensis* and nest it with *Adelosaurus* and *Acerosodontosaurus*: (1) orbit does not enter anterior half of skull; (2) postorbital does not contact parietal; (3) jugal shape, longer anterior to postorbital process*; (3) parietal strongly constricted; (4) jugal does not extend to medioposterior parietal rim*; (5) jugal gracile* (*only shared with SAM K 7710 specimens).

As most *Youngina* specimens lack postcrania, the incomplete postcrania of the BPI 3859 specimen can be compared only to the SAM K 7710 specimen: (1) Mid-cervical vertebra length shorter than mid-dorsal; (2) second sacaral rib not bifurcate; (3) second caudal transverse process longer than centrum width; (3) scapulocoracoid fused; (4) ulna not longer than 3x radius + ulna width; (5) ilium anterior process small; (6) ilium not longer than tall; (7) acetabulum ventrally open. Notes: More traits may be added to this list whenever new, more complete specimens are described. Sister taxa to the BPI

3859 specimen (Supp. Data) do not have a 'hooked' fifth metatarsal or one with an

expanded proximal rim similar to that of *Prolacerta*, *Proteroschus* or Broom's (1924)

'third specimen' (TM 200). In like fashion, sister taxa of the BPI 3859 specimen have a

pedal 5.1 that extends beyond metatarsal 4. The SAM K 7710 specimen, protorosaurs and

proterosuchids do not have this trait.

A Gradual Accumulation of Traits in the Lineage of *Proterosuchus*

Cruickshank (1972), Wellman (1975) and Ezcurra et al. (2010) agreed that all specimens

referred to *Elaphrosuchus* and *Chasmatosaurus* were conspecific with *Proterosuchus*

fergusi. However, the present phylogenetic analysis does not support that hypothesis.

Here (Fig. 4, Supp. Data), in phylogenetic order, are the taxa in the lineage of

Proterosuchus documenting the gradual accumulation of derived traits recovered in the

present study. Autapomorphies and notes are included. The first taxon, the BPI/1/4016

specimen, is distinct from its phylogenetic predecessor, *Youngoides romeri* (FMNH UC

1528, Figs. 1, 3).

***Proterosuchus?* BPI/1/4016**—(1) Skull width < 2x height; (2) lateral rostral shape

smooth, convex; (3) naris not larger than antorbital fenestra; (4) orbit does not enter

anterior half of skull; (5) prefrontal does not contact maxilla; (6) quadratojugal acutely

angled; (7) occiput anterior to jaw joint; (8) premaxilla tooth number > 4. Notes: Twice

as large as the FMNH UC 1528 specimen, yet half the size of its successors, the

BPI/1/4016 specimen was not a juvenile, but a transitional taxon. Compared to the

FMNH UC 1528 specimen of *Youngoides romeri*, the BPI/1/4016 specimen has a larger

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antorbital fenestra, a longer rostrum and a drooping premaxilla, though not as large, long and drooping as in more derived proterosuchids.

Proterosuchus? **NMQR 1484/C**—(1) only rostrum elongated (more so here than in preceding taxa); (2) premaxilla/maxilla notch > 45º; (3) orbit not larger than lateral temporal fenestra; (4) frontals without posterior processes; (5) postparietals appear on dorsal plane; (6) tabulars absent/fused; (7) squamosal descends at right angle; (8) quadrate posteriorly concave; (9) quadrate lateral coverage minimal; (10) internal nares, medial, vomer narrow; (11) interpterygoid vacuity with parallel medial rims; (12) vomer-maxilla contact; (13) in lateral view pterygoid transverse process visible below jaw line; (14) coronoid process absent. Autapomorphies: (1) Naris opening anterior; (2) orbit taller than wide; (3) ventral mandible, two-tier convex.

Proterosuchus? **RC96**—As above, with the following autapomorphies: (1) posterolateral process of premaxilla not narrower than naris; (2) maxilla ventrally straight; (3) jugal quadratojugal process descends. Notes: The NMQR 1484/C and RC96 specimens nest together. The latter is larger than the former and has a larger premaxilla. The orbit is taller and more upright. The jugal, quadratojugal, postorbital and squamosal are more robust. More teeth tip the mandible, extending onto the anterior rim, and the mandibular fenestra is smaller. Several of these differences are likely phylogenetic as small taxa evolve into larger taxa, but could be ontogenetic.

Chasmatosaurus? **SAM PK 11208**—(1) Skull width > 2x height; (2) skull table flat; (3) quadrate posterior concave; (4) squamosal-quadratojugal nascent V-shape (convergent with euparkeriids and ornithosuchids); (5) ectopterygoid pterygoid and cheek process subequal; (6) mandible shape posterior to coronoid, mid-rise. Autapomorphies shared with QR 880/C.500, not TM 201: (1) ventral aspect of premaxilla a third or greater; (2) maxilla-orbit contact; (3) squamosal descends at an obtuse angle without a temporal ledge; (4) opisthotics rise with posttemporal fenestra; Notes: data from the TM 201 specimen (Fig. 3) are based on a simple line drawing in lateral view in Broili and Schröder 1934, so comparative details are not included in this section but may be gleaned from the supplementary data.

Chasmatosaurus vanhoepeni **QR 880/C.500**—As above, with the following autapomorphies: (1) posterolateral process of premaxilla not narrower than naris. Notes: The SAM PK 11208 and QR 880/C.500 specimens nest together. The latter has a less vertical premaxilla, a more gracile upper temporal arch and a more acute quadratojugal with a more posterior jaw joint. The mandible lacks a mandibular fenestra. These traits could distinguish one species from another or may represent individual variation.

Elaphrosuchus **RC59**—(1) Both rostrum and mandible elongate; (2) posterolateral premaxilla not narrower than naris; (3) orbit 2x longer than tall; (4) pineal foramen at least one-fifth of the parietal length; (5) mandible ventrally straight. Notes: The RC59 pineal foramen is represented by a triangular, rather than a circular opening, and other bits of cranial bone are likewise missing. The phylogenetic proximity of the BPI 2871

specimen, which has an large pineal foramen, supports the presence of a pineal foramen in this sister taxon, but another, less damaged specimen is needed for confirmation.

Proterosuchus? **SAM PK K10603**—(1) List traits, compare above and below.

Youngina? **BPI 2871**—1) Dorsal nasal shape, parallel sides; 2) premaxilla/maxilla notch less than 25º; (3) major axis of naris horizontal to 30º; (4) naris opening dorsal; (5) naris displaced from snout tip; (6) antorbital fenestra absent; (7) naris larger than antorbital fenestra; (8) frontal length: height ratio, not less than 4:1. Autapomorphies: (1) Lateral rostral shape, concave (also in *Cteniogenys* and in other taxa with elongate rostra and elevated orbits); (2) posterolateral premaxilla absent. Note: the loss of the antorbital fenestra here is extended to the Choristodera, but not to other, more derived clades, including the Phytosauria and the Proterochampsidae.

The Origin of the Archosauriform Antorbital Fenestra

The present analysis (Supp. Data) documents the origin of an antorbital fenestra at least four times within the Amniota: (1) Chroniosuchidae (*Chroniosaurus*); (2) Fenestrasauria (*Cosesaurus*); (3) Protorosauria (*Pamelaria* + *Jaxtasuchus*); and 4) Archosauriformes (FMNH UC 1528 + *Proterosuchus* and more derived taxa). A possible fifth instance in *Varanodon agilis* (discussed above) may be an artifact of preservation.

The antorbital fenestra is secondarily lost in the BPI 2871 specimen attributed to *Youngina* (Gow, 1975; Figs, 1, 3, 6) and descendants among the Choristodera. The

antorbital fenestra is either retained or regained in the Proterochampsidae, where it remains small, and in a related taxon, *Teraterpeton*, (Fig. 6), where it is larger.

The proximity of *Youngoides romeri* (FMNH UC 1528) to basal proterosuchids with a prominent antorbital fenestra prompted an examination of the specimen. Here (Fig. 5) one can observe the genesis of an antorbital fenestra similar in morphology to that of basal proterosuchids, like BPI/1/4016, but much smaller. The tiny antorbital fenestra is dorsally sheltered by the laterally expanded lacrimal with fossa, and bordered below by the maxilla without a fossa.

Published photographs (Gardner et al., 2010) of the damaged rostrum of AMNH 5661 show at least a weakness in the bones surrounding what would someday be the antorbital fenestra in archosauriformes. This opening is posterior to an undamaged maxillary ascending process and an overarching lacrimal with fossa.

The Origin of the Proterosuchid Drooping Premaxilla

Youngina was not formerly associated with *Proterosuchus* in phylogenetic analyses. Now that *Youngina* and *Youngoides* nest in series ancestral to *Proterosuchus* (Fig. 4, Supp. Data) some thought may be give to the absence of the majority of the premaxilla in *Youngina* (AMNH 5661) and *Youngoides* (FMNH UC 1528). Gow (1975) considered these taxa to have 'terminal' nares, but no sister taxa have similar nares. If the largely missing premaxilla in *Youngina* and *Youngoides* were a nascent version of the drooping premaxilla seen in basal *Proterosuchus* (BPI/1/4016), it would not have been protected by the presence of the anterior dentary whenever the mouth was closed, as it is in the TM 1490 specimen (Fig. 1). Moreover, the premaxillae of *Youngina* and *Youngoides* were

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angled down at their damaged bases. In life if the premaxillae extended slightly beyond

the mandible (restored in gray, Fig. 1), that would have put them at greater risk of

breakage during burial.

Composition of the Younginiformes

The clade 'Younginiformes' was defined by Laurin and Reisz (1995) as the last common

ancestor of *Acerosodontosaurus, Hovasaurus*, and *Youngina*, and all its descendants.

Here (Supp. Data) that last common ancestor was a sister to *Spinoaequalis*. Thus the

Younginiformes remains a monophyletic clade with an expanded membership including

the Enaliosauria, Protorosauria, Archosauriformes and several basal diapsids, including

the Tangasauridae and *Galesphyrus*.

The BPI 3859 specimen previously attributed to *Youngina* does indeed nest with

Acerosodontosaurus, Thadeosaurus, Galesphyrus, *Hovasaurus*, and *Tangasaurus* (Currie

1981, 1982, Bickelmann et al., 2009), but that series is distinct and separate from the

Youngina series. New clade names will have to be proposed for both the terrestrial and

marine lineages of the Younginformes.

Miscellaneous

Some of the earlier confusion regarding the phylogenetic placement of *Youngina* (when

all specimens were considered conspecific) may be ascribed to creating a chimaera of the

best-preserved character traits from portions of several specimens (Broom 1924, Gow

1975). The present study shows that creating a chimaera is a practice to be avoided, if

possible. Here (Figs. 1-6) only individual specimens are employed. Most are far from complete specimens.

Bickelmann et al. (2009) reported that the purported quadratojual of *Acerosodontosaurus* (Fig. 2) was actually a piece of rib. In the present study the phylogenetic results are the same whether the lower temporal bar was complete or not. Sister taxa, including the BPI 3859 specimen ascribed to *Youngina*, have a tiny quadratojugal and a gracile jugal, so *Acerosodontosaurus* could have had a tiny quadratojugal, perhaps not preserved or unrecognized at present.

Palaegama, *Lanthanolania*, *Coelurosauravus* and the Kuehneosauridae nest together in a monophyletic basal lepidosauriform clade (Supp. Data, contra Evans, 1988; Bickelemann et al., 2009), not at discreet nodes widely separated from one another.

Based on phylogenetic bracketing (Fig. 4, Supp. Data), in *Champsosaurus* (Fig. 6) the median bone dorsoposterior to the naris is actually the ascending process of a three-part premaxilla, not a pair of fused nasals. Thus the prefrontals were fused to the nasals, which explains the oddity of purported prefrontals located in the traditional location of the nasals.

In the present amniote tree (Supp. Data) the first dichotomy splits the Archosauromorpha from the Lepidosauromorpha using definitions proposed by Gauthier (1986). This tree topology is a profound departure from traditional trees built upon far fewer taxa and often suprageneric taxa that too often did not provide for every lineage a gradual accumulation of derived traits.

CONCLUSION

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The present study is the first to include multiple specimens of *Youngina* and *Proterosuchus* in phylogenetic analysis. Both were found to include several genera and species that nested at distinct nodes and in series. In the *Youngina* series several specimens document the gradual accumulation of derived traits leading to the origin of the Archosauriformes. In the *Proterosuchus* series several specimens document the gradual accumulation of derived traits leading to all higher archosauriforms. Here (Supp. Data) the origin of the Archosauriformes can be traced back to basal diapsids, basal archosauromorphs, basal amniotes, and basal tetrapods. The holotypes of *Youngina capensis* and *Youngoides romeri* were derived from basal diapsids including *Spinoaequalis* and a series of more primitive younginids. A sister to *Youngina* and *Youngoides* ultimately gave rise to proterosuchids (basal archosauriforms). Rather than representing an ontogenetic series, the several specimens that prior workers lumped under *Proterosuchus* also form a phylogenetic series with narrow-skulled forms leading toward erythrosuchids and rauisuchids. Wide-skull forms phylogenetically preceded proterochampsids and phytosaurs. The archosauriform antorbital fenestra and drooping premaxilla had their genesis in the proximal outgroup taxon, *Youngoides romeri* (FMNH UC 1528). The antorbital fenestra is lost in a clade of derived archosauriforms including the tiny BPI 2871 specimen and the Choristodera.

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FIGURE CAPTIONS

Figure 1. The lineage of *Youngina* to scale. Specimens are known chiefly from skulls and

are shown in roughly phylogenetic order (Fig. 4). The basal diapsid, *Spinoaequalis,* is the

outgroup taxon, followed by a single SAM K 7710 specimen from the den fossil. The

BPI 375 specimen is more derived and basal to the Protorosauria, represented here by

two specimens of *Prolacerta*. A series of six *Youngina, Youngoides*, and *Youngopsis*

specimens leads to the base of the Archosauriformes in this order: TM3603, RC90.

RC91, TM 1490, AMNH 5561 and FMNH UC 1528. The basalmost archosauriform

tested here is the small proterosuchid, BPI/1/4016. The BPI 2871 and BPI 3859

specimens (both boxed) nest elsewhere (see Figs. 2, 3 and 6). Scale bar equals 5 cm.

[full page image]

Figure 2. Taxa related to the BPI 3859 specimen to scale. Distinct from the lineage of

Youngina, the BPI 3859 specimen was derived from a sister to *Adelosaurus* and was a

sister to *Acerosodontosaurus*. The *in situ* skull of the BPI 3859 specimen is

dorsoventrally crushed. Here the skull roof is restored to a higher position. A gray

addition to the broken ilium restores that bone to a shape in keeping with sister taxa.

Dorsal osteoderms are autapomorphies, not found in sister taxa or younginids. The

nearest taxa with dorsal osteoderms are *Heleosaurus* and *Jaxtasaurus,* several nodes distant in both cases. Note the tall narrow vertebrae of the BPI 3859 specimen in contrast to the low, wide vertebrae of the the SAM K 7710 specimen. Also shown are *Spinoaequalis*, the SAM K 7710 specimen and the *Youngina* holotype, AMNH 5661. Scale bar equals 10 cm.

[two column image]

Figure 3. Basal archosauriform skulls to scale. The FMNH UC 1528 specimen of *Youngoides romeri* is the outgroup taxon. The BPI/1/4016 specimen is the basalmost proterosuchid (archosauriform) followed by the NMQR 1484/C and RC96 specimens. Derived from this clade are *Euparkeria*, *Osmolskina*, *Revueltosaurus*, *Fugusuchus*, *Tasmaniosaurus* and *Garjainia*. The TM 201, SAM-PK-11208 and NMQR 880/C specimens represent another clade of proterosuchids. These are basal to *Elaphrosuchus* and the tiny BPI 2871 specimen. These in turn give rise to the Proterochampsidae and other clades (Fig. 6). Scale bar equals 30 cm.

[full page image]

Figure 4. The base of the Archosauriformes. This subset of the large amniote tree (Supp. Data) focuses on the origin and radiation of basal archosauriforms. Bootstrap scores are shown. Former *Youngina* specimens are in bold type. The results of the present analysis support the splitting of these specimens into distinct genera and species.

[one column image]

Figure 5. Anterolateral view of *Youngoides romeri*, FMNH UC 1528. Arrow points to the nascent antorbital fenestra in this proximal outgroup taxon to the Archosauriformes. Scale bar equals 3 cm.

[one column image]

Figure 6. The proterochampsid/phytosaur/choristodere clade of the basal Archosauriformes to scale. This unnamed clade arises from the wide-skulled proterosuchids (Fig. 2) with the smaller *Elaphrosuchus* and the much smaller BPI 2871 specimen at its base. The latter has no antorbital fenestra or hooked snout, here a derived trait. Subsequent clades include *Doswellia* plus the Choristodera, represented by *Champsosaurus* and *Cteniogenys*. The Proterochampsidae is represented here by *Chanaresuchus*. The Phytosauria is represented here by *Parasuchus*. A new unnamed clade includes *Diandongosuchus* and *Teraterpeton*. Scale bar equals 30 cm.
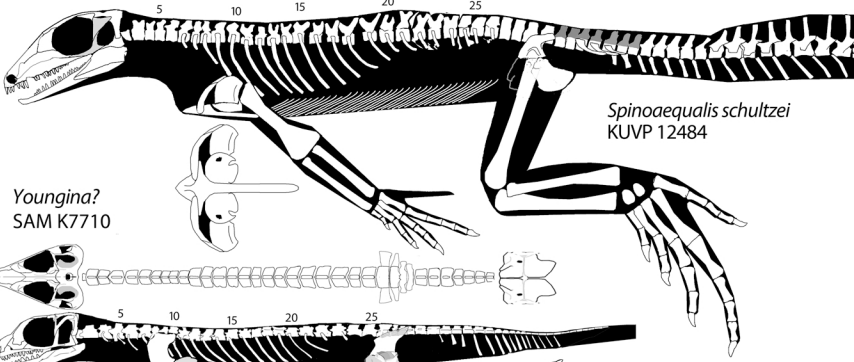
[full page image]

Spinoaequalis schultzei
KUVP 12484
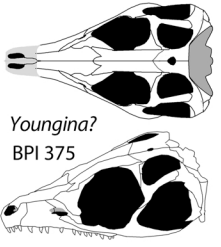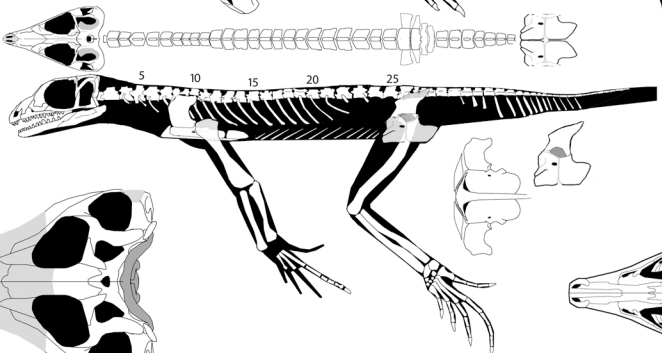
Youngina?
SAM K7710
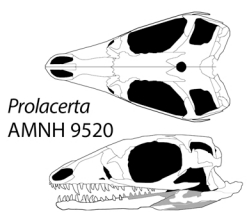
Youngina?
BPI 375

Prolacerta
AMNH 9520
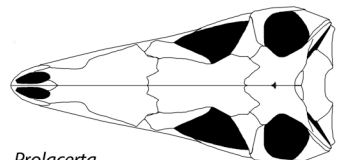
Prolacerta
BPI/1/471
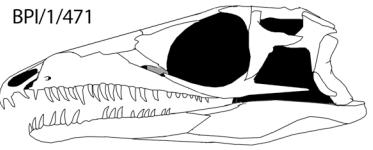
Youngina?
TM 3603
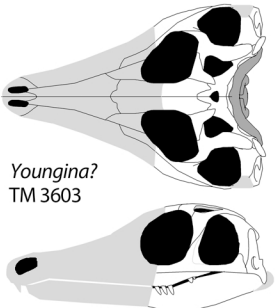
Youngopsis rubidgei
RC 90
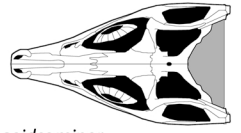
Youngoides minor
RC91
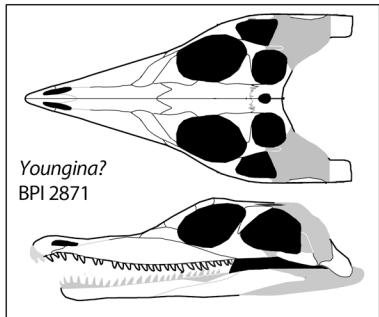
Youngina?
BPI 2871
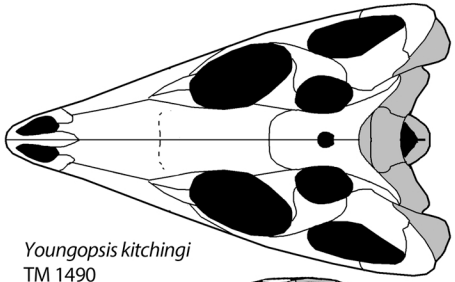
Youngina?
BPI 3859

Youngopsis kitchingi
TM 1490

Youngina capensis
AMNH 5561

0 1   5cm
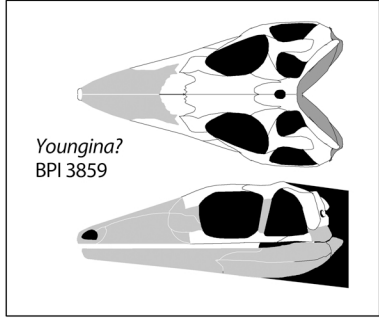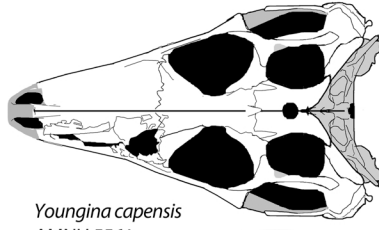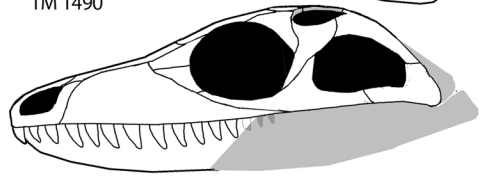
Proterosuchus?
BPI/1/4016

Youngoides romeri
FMNH UC 1528
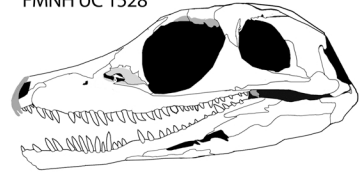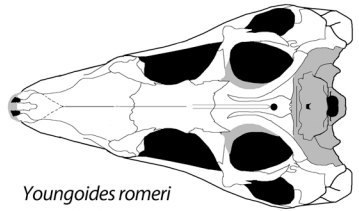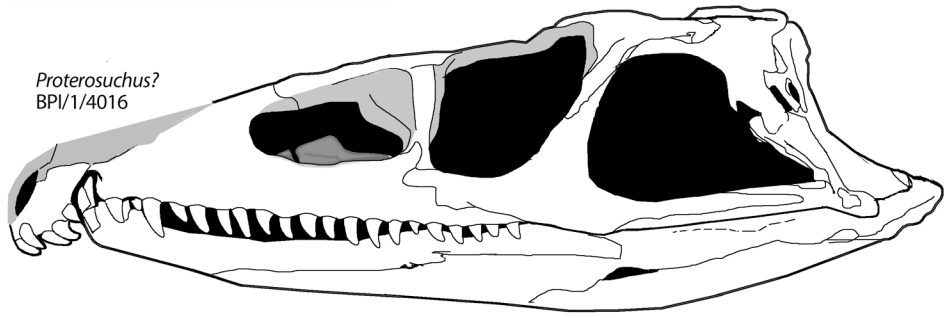
Spinoaequalis schultzei
KUVP 12484
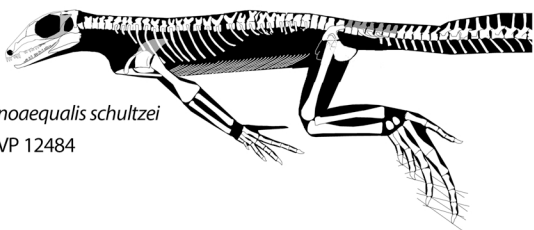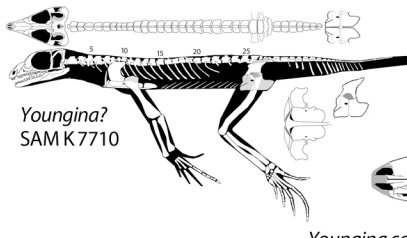
Youngina?
SAM K 7710

Youngina capensis
AMNH 5561
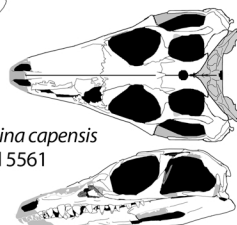
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SAM 2758
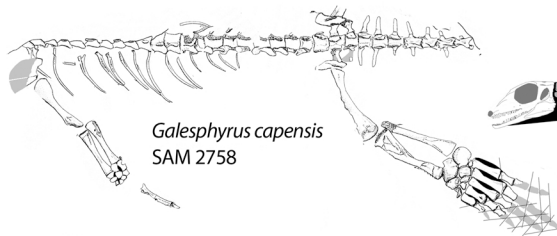
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G.26.49
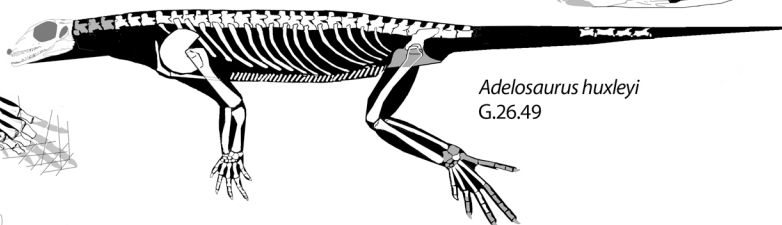
Youngina?
BPI 3859

Acerosodontosaurus piveteaui
MNHN 1908-32-57
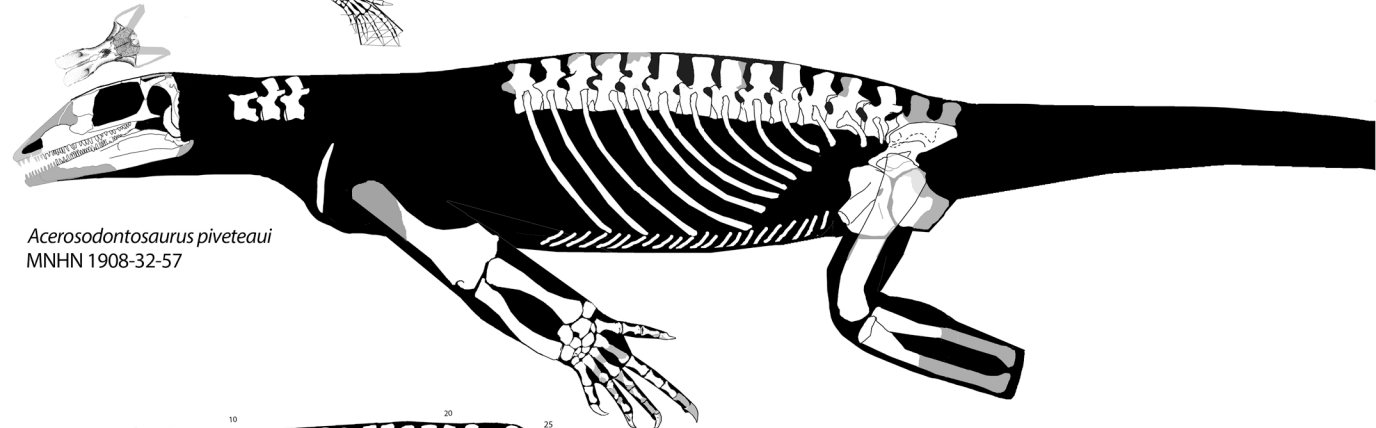
Thadeosaurus colcanapi

0 1   10cm
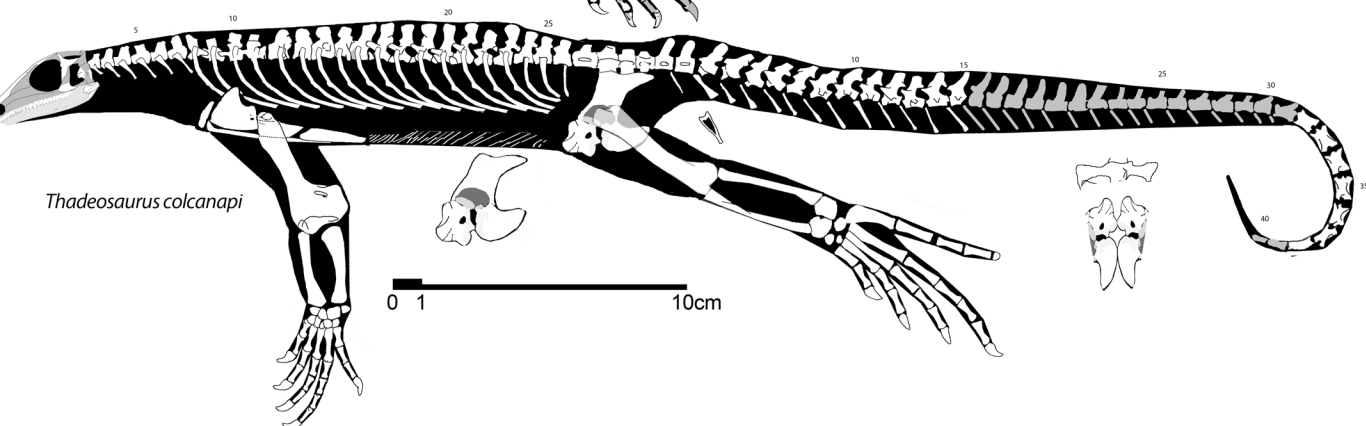
Proterosuchus sp.
BPI/1/4016

Youngoides romeri
FMNH UC 1528

Revueltosaurus

Tasmaniosaurus

Euparkeria
SAM-PK-5867

Osmolskina

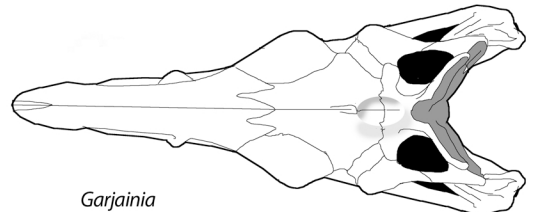*Chasmatosaurus alexandri*
NMQR 1484/C
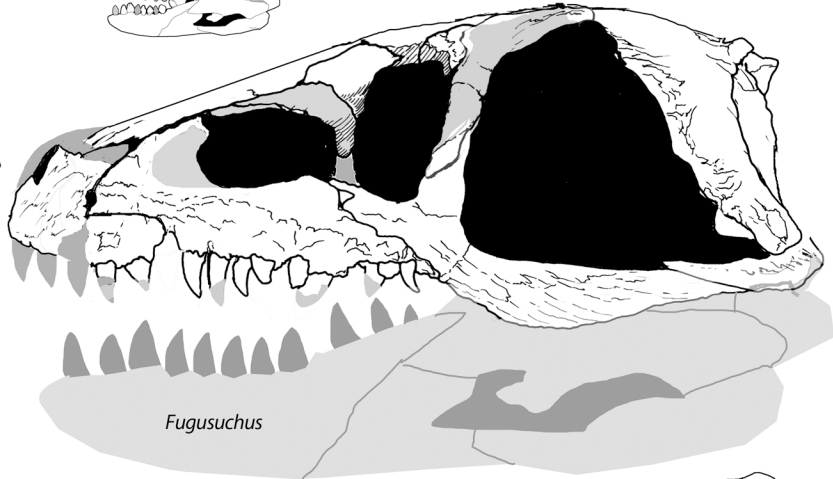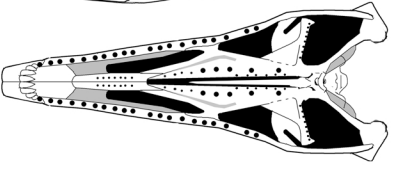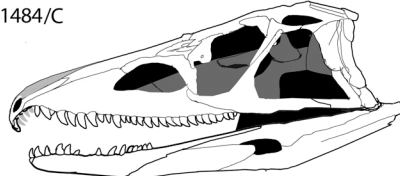
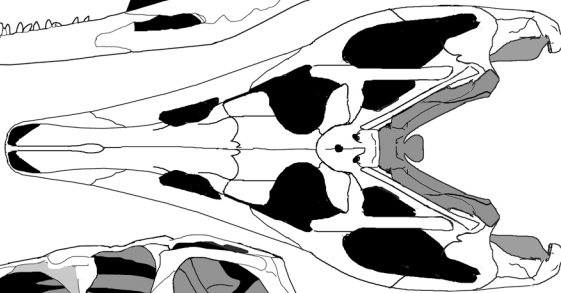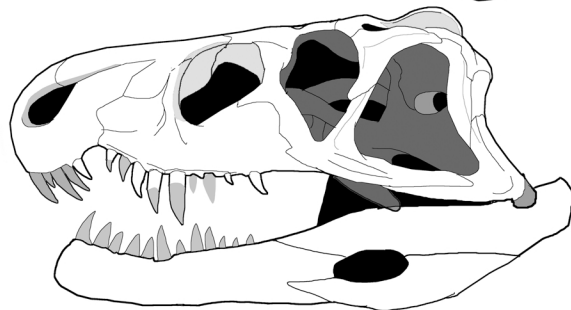*Fugusuchus*

Proterosuchus sp.
RC 96

Chasmatosaurus vanhoepeni
TM 201
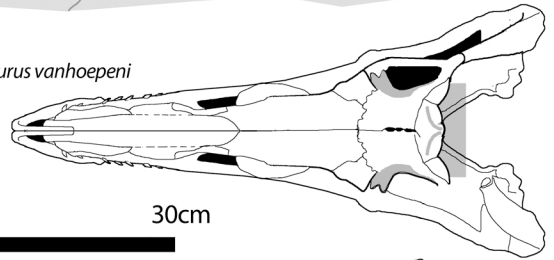
0   5   10   30cm

Chasmatosaurus
SAM-PK-11208
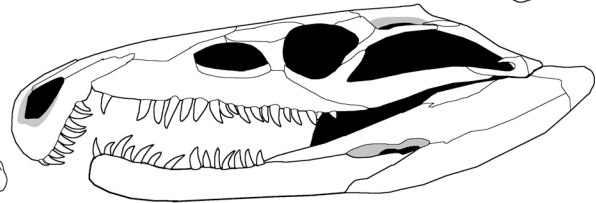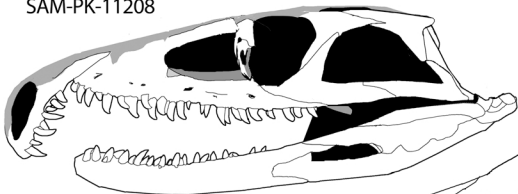
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NMQR 880/C
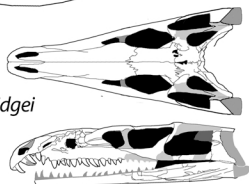
Garjainia
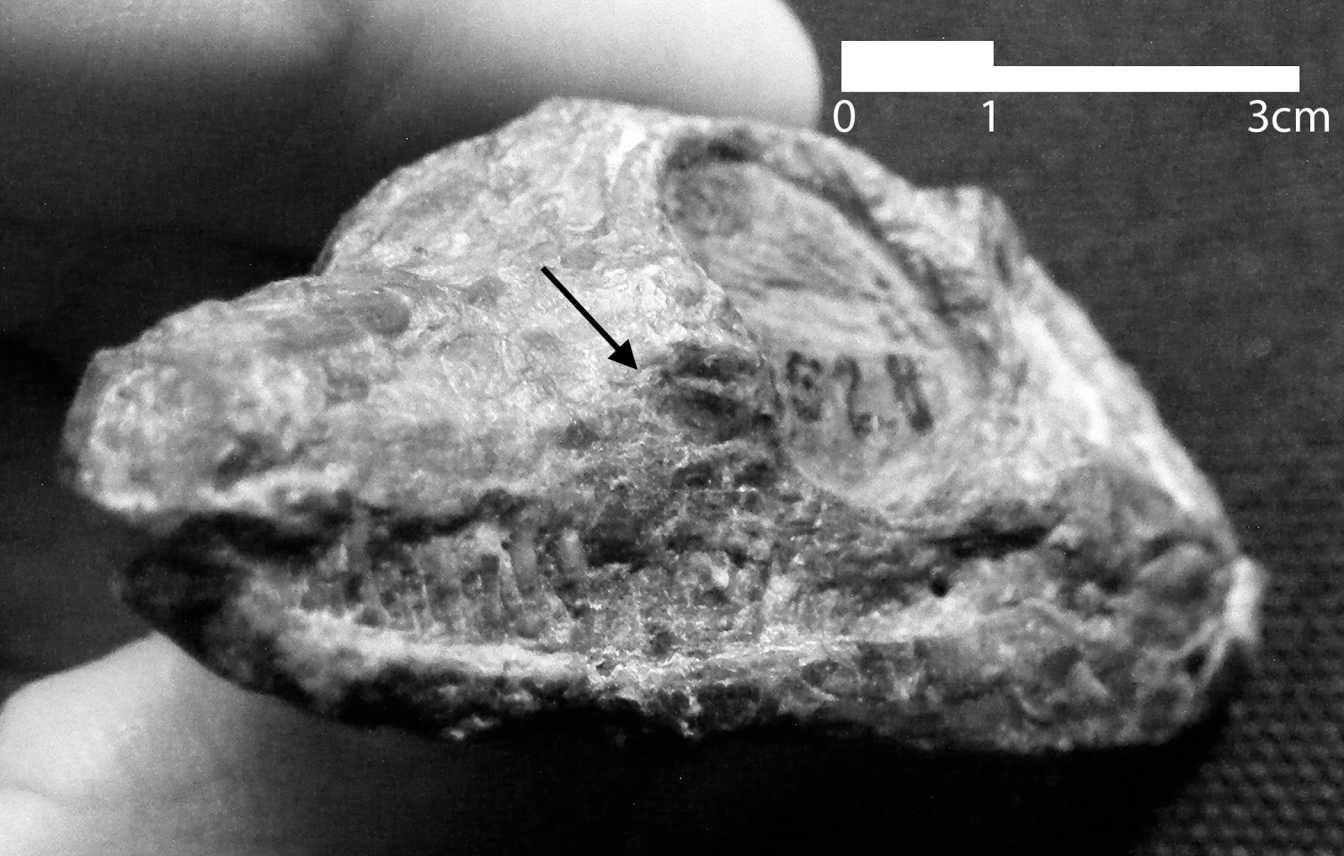
Youngina?
BPI 2871

Elaphrosaurus rubidgei
RC 59
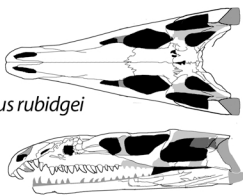
Heleosaurus
Mycterosaurus FMNH UC169
Nikkasaurus
Mesenosaurus PIN 158/1
Niaftasuchus
81
99
81
94
79

Anningia
Archaeovenator
Orovenator
Pyozia
88
89
95

Broomia
Milleropsis BPI-720
Erpetonyx
100
89

98
87

Ascendonanus MNC-TA0924

97
87

Eudibamus
Aphelosaurus
Petrolacosaurus
Araeoscelis
100
100
92

Spinoaequalis
Galesphyrus
Youngina BPI 3859
Acerosodontosaurus
Thadeosaurus
Tangasaurus
Hovasaurus
Claudiosaurus
Adelosaurus
Atopodentatus
Sinosaurosphargis
Largocephalosaurus
Omphalosaurus
Anarosaurus
Enaliosauria

85
94
72
85
83
90
100
98
100
72
100
84
89
72
75

Youngina SAM K7710
Youngina BPI 375
Prolacerta AMNH 9502
Ixalerpeton
Czatkowiella
Malerisaurus
Prolacerta BPI 1/471
Ozimek
Protorosaurus NHMW 1943I4*
Boreopricea
Jaxtasuchus
Protorosaurus NMK S 180
Protorosaurus WMsN P47361
Pamelaria

88
68
80
82
71
88
53
<50
57
84
<50
96

Youngina TM 3603
Youngopsis rubidgei RC90
Youngopsis kitchingi TM1490
Youngoides RC91
Youngina AMNH 5561
Youngoides UC1528

100
74
87
82
89
95

Proterosuchus BPI 1 4016
Chasmatosaurus QR 880C.500
Chasmatosaurus SAM PK 11208
Chasmatosaurus TM 201
Proterosuchus RC96
Chasmatosaurus NMQR 1484
Teyujagua
Elaphrosuchus RC59

87
100
91
75
71
95

Proterosuchus SAMPKK10603
Doswellia
Youngina BPI 2871
Elachistosuchus
Tchoiria
Ikechosaurus
Champsosaurus
Simoedosaurus
Cteniogenys
Philydrosaurus
Lazarussuchus
Hyphalosaurus
Monjurosuchus GMV216
Monjurosuchus NMM3671

93
97
86
98
94
97
100
88
99
97
94
64
100
91

Diandongosuchus
Teraterpeton
Mesorhinosuchus
Paleorhinus
Parasuchus
Chanaresuchus
Proterochampsa PVSJ 77
Proterochampsa PVSJ606
Pseudochampsa PVSJ 567
Gualosuchus
Cerritosaurus
Tropidosuchus PVL 4601
Tropidosuchus PVL 4602
Lagerpeton

93
96
91
100
81
57
92
83
90
88
94
95
95

89
87

95

Euparkeria SAM PK K6047A
Euparkeria SAM PK K5867
Osmolskina
Tasmaniosaurus
Revueltosaurus
Fugusuchus
Garjainia
Erythrosuchus
Luperosuchus
Shansisuchus

82
94
99
97
97
99
91

Riojasuchus
Ornithosuchus

100

Higher Archosauriformes

94
96
100

Elaphrosaurus rubidgei
RC 59

Proterosuchus?
SAM-PK-K10603

Doswellia

0 5 10 30cm

Youngina?
BPI 2871

Diandongosuchus

Chanaresuchus

Cteniogenys

Champsosaurus

Teraterpeton

Parasuchus