

A survey of skeletal elements in the orbit of Pseudosuchia and the origin of the crocodylian palpebral

Sterling J. Nesbitt¹, Alan H. Turner² and Jonathan C. Weinbaum³

¹Burke Museum and Department of Biology, University of Washington, Seattle, WA 98195, USA.
Current address: Center for Integrative Research, The Field Museum, 1400 S. Lake Shore Drive,
Chicago, IL 60605-2496, USA.
Email: sjn@gmail.com

²Department of Anatomical Sciences, Stony Brook University, Stony Brook, NY 11794-8081, USA.

³Biology Department, Southern Connecticut State University, New Haven, CT 06515, USA.

ABSTRACT: Ossified skeletal elements within the orbit, such as scleral ossicles, palpebrals, supraorbitals and sesamoids, are widespread across Reptilia, including extant members of Crocodylia, Aves, Squamata and Chelonia. Extant crocodylians lack scleral ossicles, but have a unique palpebral that has recently been shown, through developmental studies, to be an osteoderm in the upper eyelid. Here, we examine the diversity and disparity of the crocodylian palpebral in extant members of Crocodylia and, through the fossil record, trace the origin and evolutionary history of the element throughout Pseudosuchia (all archosaurs more closely related to crocodylians than avians). We show that the crocodylian palpebral originated outside of Crocodylomorpha in early pseudosuchian groups (e.g. Aetosauria, Loricata) and that scleral ossicles are lost in nearly all groups of pseudosuchians, but appear in poposauroids, at least one early crocodylomorph, and some partially or fully marine Crocodyliformes (e.g. thalattosuchians). The morphology and number of palpebrals differs across Crocodyliformes; the presence of two palpebrals is plesiomorphic, but this is reduced to one by Crocodylia. We further recommend the restriction of the term palpebral to the structure in crocodylians and their homologues, but not to the structure in ornithischian dinosaurs.



KEY WORDS: *Aetosaurus ferratus*, Archosauria, Crocodylomorpha, evolution, novelty, *Postosuchus kirkpatricki*, *Saurosuchus galilei*, supraorbital

The vertebrate eye, a delicate soft tissue structure, in gnathostomes is protected by a number of different skeletal tissues (Ritchie 1968; Burrow *et al.* 2005; Franz-Odenaal & Vickaryous 2006). These skeletal tissues within the eye consist of two types of tissues, cartilage (e.g. scleral cartilage) and bone (e.g. scleral ossicles, os opticus) (Franz-Odenaal & Vickaryous 2006). Furthermore, skeletal tissues are found directly associated with the eye (e.g. within the eyelids). These tissues are usually composed of bony tissues that include, for example, palpebrals in reptiles, sesamoid-like elements found in some avians (e.g. owls), and neomorphic bones in reptiles (e.g. parafrenal bones in geckos, supraorbitals in falconiform birds) (Franz-Odenaal & Vickaryous 2006). This collection of skeletal tissues within or among the eye has been a focus of studies examining the development of the eye in extant gnathostomes (e.g. Coulombre 1965) and using the extant phylogenetic bracket (*sensu* Witmer 1995) to elucidate the evolution of skeletal features in the vertebrate eye (Burrow *et al.* 2005; Franz-Odenaal & Vickaryous 2006; Vickaryous & Sire 2009). To examine the origin of these features, we must turn to the fossil record. Unfortunately, the fossil record ordinarily only preserves bony elements of the orbit, as cartilage is only preserved in extraordinary cases (e.g. Dal Sasso & Maganuco 2011). Therefore, we are limited to hard parts in our understanding of the origin and evolution of skeletal elements associated with the eye.

With few exceptions, these bony elements are limited to palpebral bone(s), supraorbital(s) and scleral ossicles in a variety of extinct reptiles. Additionally, the morphology and presence of these elements have been used as behaviour indicators (e.g. the size of the sclerotic ring suggests diving depth in Ichthyosauria, Motani *et al.* 1999; Hall *et al.* 2011; Schmitz & Motani

2011). Scleral ossicles are found across the family tree of Reptilia and more distantly related clades within Vertebrata, suggesting that the presence of scleral ossicles is plesiomorphic for all of Reptilia (Fig. 1). Palpebrals or supraorbitals are found in a variety of reptiles including microsaur (Daly 1973), lizards (lacertids, scincoids, and anguimorph lizards; Estes *et al.* 1988), pterosaurs (Coombs 1972; Wang *et al.* 2007), ornithischian dinosaurs (Coombs 1972; Maidment & Porro 2010) and crocodylomorphs (including Crocodylia) and other pseudosuchians (Walker 1961; Desojo & Baez 2007; Schoch 2007; Weinbaum 2011). Although all of these elements in the dorsal portion of the orbit have been referred to as either palpebrals or supraorbitals, the homology of these structures among extinct groups with the structures in extant reptile clades remains untested. Furthermore, the terms palpebral and supraorbital have been used interchangeably (Romer 1956). For example, the orbital structure(s) in ornithischian dinosaurs have been called ‘palpebrals,’ (Romer 1956), but the homology of these structures with those of crocodylians is contentious; the structures in ornithischians could be neomorphic elements that are not homologous with palpebrals of crocodylians.

Recent developmental studies of crocodylian palpebrals (Vickaryous & Hall 2008) have made it possible to determine the origin of tissues that lead to the formation of palpebrals. Palpebral elements are part of the dermal skeletal system (i.e., metaplastic ossification, not preformed in cartilage) that develops within the upper eyelid, and this type of development is not the same as dermal elements of the skull (Vickaryous & Hall 2008). In crocodylians, the mode and pattern of skeletogenesis of the palpebral matches identically with that of postcranial osteoderms (Vickaryous & Hall 2008). Essentially, crocodylians

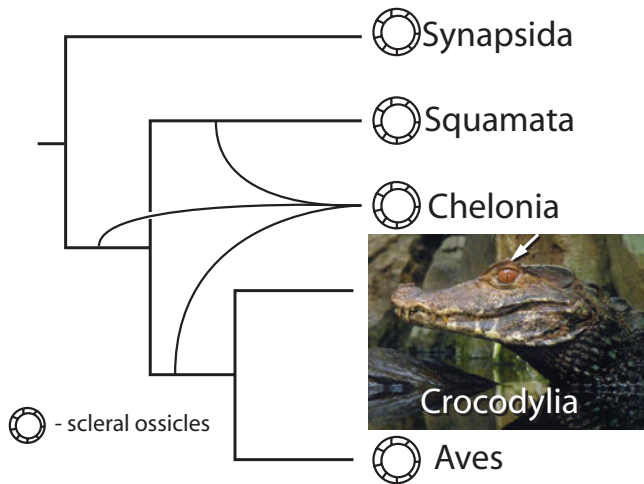


Figure 1 The distribution of bony skeletal elements in the orbits of extant amniotes. The possible relationships of Chelonia among amniotes includes a phylogenetic position as a non-saurian sauropsid, a lepidosauromorph and an archosauromorph. The presence of a sclerotic ring is plesiomorphic for Amniota and secondarily lost among the crocodylian-line archosaurs, as demonstrated by the crocodylian *Paleosuchus* located at the Shedd Aquarium in Chicago, IL. The white arrow highlights the palpebral above the eye.

have an osteoderm in the orbit. The development of the palpebrals of crocodylians may be understood, but the evolutionary history of the crocodylian palpebral has not been examined in detail.

Extant crocodylians, one of the two living groups of archosaurs, bear a distinct palpebral at the dorsal margin of their orbit and lack sclerotic ossicles. In contrast, avians, the other group of living archosaurs, lack palpebral elements and nearly all possess sclerotic ossicles, a plesiomorphic condition within Reptilia. Given this distribution of ossified elements in the orbits of crocodylians, the origin of the palpebral and the loss of the sclerotic ring must have occurred among taxa more closely related to crocodylians than to avians, or within the clade Pseudosuchia (= Crurotarsi of Sereno *et al.* 2005; = crocodylian-line archosaurs). In the present contribution, we survey the distribution and forms of skeletal elements in the orbit of crocodylians and among their closest relatives and discuss the origin of the palpebral and the loss of the sclerotic ossicles within Pseudosuchia (Fig. 1). After recent revisions of the anatomy of non-crocodylomorph pseudosuchians such as *Postosuchus kirkpatricki* (Weinbaum 2011) and *Aetosaurus ferratus* (Schoch 2007), it is clear that skeletal elements were present in or around the eye in close relatives of crocodylomorphs. These key pseudosuchian taxa have triggered the reevaluation of other closely related non-crocodylomorph pseudosuchians and illuminated the origins and early evolution of the skeletal elements in the orbit of pseudosuchians.

This study does observe the following limitations when examining skeletal elements in the orbit of extinct taxa. First, skeletal elements of the eye are prone to loss during the fossilisation process, given that most are not articulated to other hard parts. Given that the eye decomposes soon after death (Gordon & Shapiro 1975), the usually fragile skeletal elements become disassociated from the rest of the skeleton at a much faster rate than other hard tissues. Furthermore, once skeletal elements of the orbit are displaced from the orbital area, they become difficult to orient, articulate with other skeletal elements near or within the orbit, or even identify the bone in question as a skeletal element of the eye. Skeletal elements formed in the orbit of vertebrates also are thin, sometimes

poorly ossified structures prone to collection and preparation biases in vertebrate palaeontology. For example, delicate skeletal features of the orbit are easily removed if special care is not taken within the orbit of a fossil vertebrate.

Secondly, the identification of certain elements may be impossible without developmental sequences (e.g. Hall 2005; Vickaryous & Hall 2008). For example, the identification of a palpebral (osteoderm) versus a neomorphic circumorbital dermal bone may not be determinable from morphology, composition or position, without an understanding of the underlying development process in the taxon being examined (see Hall 2005).

Thirdly, the timing of ossification of the skeletal elements in the orbit during ontogeny may be variable across taxa, and determining the ontogenetic age of archosaurs outside of Aves and Crocodylia is problematic with our current interpretations of skeletal chronological correlates (Brochu 1996; Irmis 2007). For example, crocodylians only ossify osteoderms and the palpebral after the first year of life (Vickaryous & Hall 2008). So, the presence or absence of certain skeletal elements of the orbit may be related to ontogenetic stage of an individual. This is further exemplified by the apparent absence of a palpebral in the long snouted crocodylian *Gavialis* in adults, even though a palpebral is present in hatchlings (see below).

Clade names utilised in this contribution derive from Sereno *et al.* (2005) and recent revisions and additions from Nesbitt (2011).

Institutional abbreviations. AMNH, American Museum of Natural History, New York NY, USA; BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; CM, Carnegie Museum of Natural History, Pittsburgh PA, USA; DGM, Departamento de Produção Mineral, Rio de Janeiro, Brazil; FMNH, The Field Museum of Natural History, Chicago IL, USA; IGM, Mongolian Institute of Geology, Ulaanbaatar, Mongolia; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge MA, USA; MG, Museo Geológico, Lisbon, Portugal; MOZ, Museo Profesor J. Olsacher, Zapala, Argentina; MPMA, Monte Alto Museum of Paleontology, Monte Alto SP, Brazil; MTM, Hungary Natural History Museum, Budapest, Hungary; NHMUK, Natural History Museum, London, UK; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; PVL, Instituto Miguel Lillo, Tucuman, Argentina; PVSJ, Division of Paleontology of the Museo de Ciencias Naturales de la Universidad Nacional de San Juan, Argentina; SAM, South African Museum, Cape Town, South Africa; SMNH, Royal Saskatchewan Museum (formerly the Saskatchewan Museum of Natural History), Regina, Canada; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TMM, Vertebrate Paleontology Laboratory, Texas Natural Science Center, Austin TX, USA; TTU-P, Texas Tech University Museum, Lubbock TX, USA; UA, University of Antananarivo, Madagascar; UCMP, University of California Museum of Paleontology, Berkeley CA, USA; UH, Urweltmuseum Hauff, Holzmaden, Germany; UNC, University of North Carolina, Chapel Hill NC, USA; YPM, Yale Peabody Museum, New Haven CT, USA; ZPAL, Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, Poland.

1. Osseous skeletal element(s) in the orbit of pseudosuchians

1.1. Extant crocodylians

Crocodylians are the only extant group of reptiles to possess a palpebral and lack any scleral ossicles. With the exception of

Paleosuchus and *Osteolaemus*, all extant crocodylians possess a palpebral that is typically small and situated in the antero-medial corner of the orbit. The shape and thickness of the palpebral differs across Crocodylia, but generally consists of a sub-rounded element that is mediolaterally compressed. The dorsal surface is rugose, similar to that of the surrounding skull roof elements and osteoderms, and the ventral surface is almost smooth. The palpebral rests upon a facet on the orbital edge of the prefrontal and may or may not contact the frontal along its medial margin. The prefrontal and the palpebral articulate by connective tissue. The shape of the palpebral is variable among crocodylians, but is usually amygdaloidal with the long axis aligned anteroposteriorly (Fig. 2). Furthermore, the size and shape of palpebrals can vary within a species (e.g. *Alligator mississippiensis*), or even an individual (Fig. 2C). The palpebral in most crocodylians does not reach the posterior or lateral margins of the orbit.

The palpebral in extant crocodylians forms from a single ossification centre, except in *Paleosuchus* and *Osteolaemus*. In these taxa, the single palpebral is formed from either two or three ossifications (*Osteolaemus tetraspis*; Figs 2E, 3), or three ossifications (*Paleosuchus*; Fig. 2D). Nearly all specimens of *Osteolaemus tetraspis* possess a single palpebral consisting of two ossifications (Christopher Brochu, pers. comm. 2012), but the specimen presented in Figure 3 possesses a single palpebral composed of three ossifications. In *Osteolaemus tetraspis* and *Paleosuchus*, the palpebral is a single structure, in contrast with the two distinct palpebrals in some extinct pseudosuchians (see below).

Paleosuchus and *Osteolaemus* also show the most deviation in palpebral morphology from the typical crocodylian palpebral, as exemplified by *Alligator mississippiensis* (Fig. 2C). The two species of *Paleosuchus* have large palpebrals that traverse most of the dorsal aspect of the orbit (Fig. 2D, B). The palpebral reaches or nearly reaches the postorbital (but does not have a facet on the bone) and overhangs the dorsolateral portion of the orbit. The medial margin of the palpebral tightly follows the lateral edge of the frontal, but does not share a cranial suture with the bone. In *Paleosuchus trigonatus*, the palpebral is often elevated above the dorsal surface of the skull table. *Osteolaemus tetraspis* also has an enlarged palpebral relative to other crocodylians, but not to the extent present in the two *Paleosuchus* species. The palpebral of *Osteolaemus* does not reach the postorbital and the medial margin does not parallel the frontal (Fig. 2E). In general form and location, the palpebral of *Osteolaemus* is very similar to the anterior palpebral in most fossil crocodyliforms.

1.2. *Postosuchus* and other raiisuchids (*sensu* Nesbitt 2011)

In 1985, Chatterjee described one of the most complete “rauisuchian” (rauisuchid of Nesbitt 2011) archosaurs to date, *Postosuchus kirkpatricki* from the Late Triassic of the Dockum Group of Texas. The well-preserved, nearly complete skull (TTU-P 9000) possesses an unusual triangular bone lying dorsal to the orbit that Chatterjee (1985) interpreted as a prefrontal. This interpretation was followed by Long & Murry (1995) and Peyer *et al.* (2008) for *Postosuchus alisonae*. However, in a revised description of the skull of TTU-P 9000, Weinbaum (2011) identified a small, but complete prefrontal incorporated into the dermatocranium, suggesting that the triangular “prefrontal” observed by Chatterjee (1985) had been misinterpreted. Given the revised interpretation of the prefrontal (*sensu* Weinbaum, 2011) and the unorthodox topological relationship of the putative “prefrontal” *sensu* Chatterjee (1985), a reassessment of the homology of this latter element is given here. We, following Weinbaum (2011), hypothesise that this

element represents a palpebral that was firmly attached to the surrounding skull roof elements in *P. kirkpatricki*. Our interpretation is consistent with the morphology of palpebrals of crocodylomorphs, the spatial associations (connectivity) of the surrounding bones, and the development of the palpebral in *Alligator* (see Vickaryous & Hall 2008). Furthermore, the reinterpretation of the bone in *P. kirkpatricki* has also led to a reinterpretation of similar elements in other raiisuchids and closely related taxa (e.g. *Batrachotomus* and *Saurosuchus*).

The external surface of the palpebral of *Postosuchus kirkpatricki* (TTU-P 9000, 9002, Fig. 4G, H, I) is ornamented with an irregular pattern of striations and interwoven bone fibres penetrated by numerous small foramina – a pattern typical of osteoderms of pseudosuchians and other archosaurs (Hill 2005). The irregular ornamentation of the palpebral of *P. kirkpatricki* contrasts with the relatively smooth unornamented bone texture of the adjacent frontal, postorbital and lacrimal of the same specimen (TTU-P 9000). The dorsal surface is slightly convex, whereas the ventral surface is slightly concave and smooth.

The morphology and position of the palpebral of *P. kirkpatricki* is generally similar to the palpebral of the closely related (from Nesbitt 2011) early crocodylomorph *Hesperosuchus agilis* (CM 29894). In *Hesperosuchus*, one large, circular palpebral dominates the space at the dorsal margin of the orbit (Clark *et al.* 2000; Fig. 9a). Even though the palpebral of *P. kirkpatricki* is triangular in overall shape, a seemingly homologous circular structure delimited by a roughened boundary occupies the middle portion of the element in ventral view (Fig. 4H; see Nesbitt 2011, fig. 25d) and this smooth portion of the element is an extension of the orbital fossa on the ventral surface of the frontal. The distinct circular structure in the centre of the osteoderm, visible on both the dorsal and ventral surfaces, is concave ventrally, convex dorsally, and the ventral surface has less sculpturing than the dorsal surface (see Nesbitt 2011, fig. 25). Compared to the size of the orbit, the relative size of the circular structure within the palpebral is similar to the size of the palpebral of the early crocodylomorph *Hesperosuchus* (CM 29894; see below). Thus, we hypothesise it may be a homologous structure. In *Hesperosuchus*, the palpebral is composed of a single ossification that spans the dorsal margin of the orbit, but it remains unclear how many ossifications compose the palpebral of *P. kirkpatricki*, as there are no clear sutures within the triangular element.

Unlike those of extant crocodylians and *Hesperosuchus agilis* (CM 29894), the palpebral of *P. kirkpatricki* is fully integrated into the supraorbital region in the largest specimens (e.g. TTU-P 9000). In *P. kirkpatricki* the palpebral bridges this region and attaches to the frontal medially, the postorbital and postfrontal posteromedially, and the prefrontal and lacrimal anteromedially, obscuring the dorsal portion of the orbit from dorsal view. Interdigitating sutures similar to those among skull elements join the palpebral and the circumorbital skull elements. These sutures illustrate that the palpebral and surrounding bones were tightly integrated. The disarticulated palpebral of a specimen referred to *P. kirkpatricki* (UCMP 140035) by Long & Murry (1995) shows that the sutural surface is speckled with pits and spires of bone, thus indicating that the interdigitating suture is present throughout the dorsoventral length of the element. In this regard, the shape and connectivity of the palpebral of *P. kirkpatricki* is most similar to the extant crocodylian species *Paleosuchus trigonatus* (FMNH 81980) and *Paleosuchus palpebrosus* (FMNH 69871), in comparison with that of *Hesperosuchus agilis* (CM 29894). In *Paleosuchus* (Fig. 2D), the palpebral traverses the dorsal portion of the orbit and contacts the circumorbital elements. The greatest difference between the palpebrals of *P. kirkpatricki* and *Paleosuchus* is that in the latter taxon, the body of the palpebrals retain some of

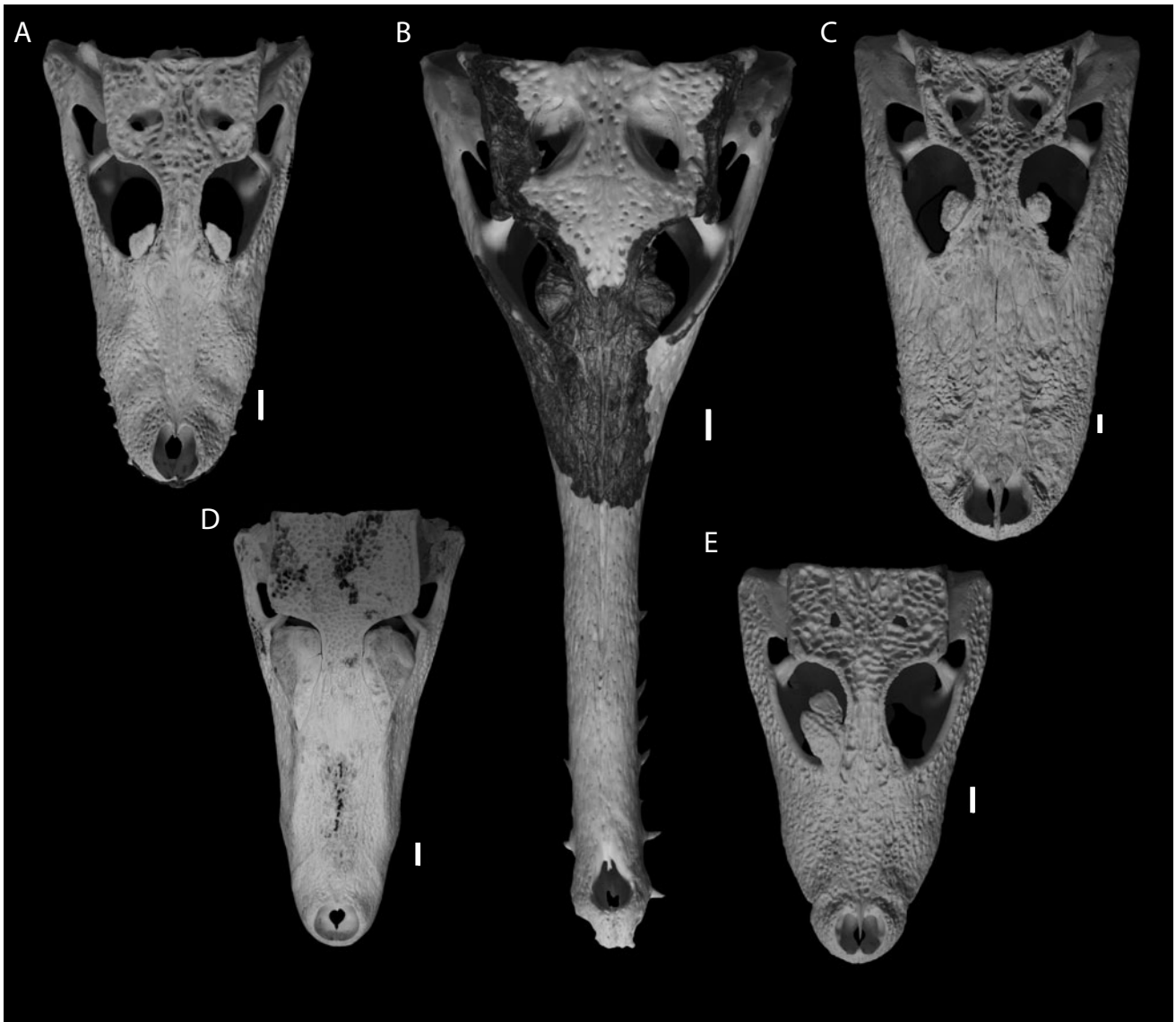


Figure 2 Extant crocodylians with articulated palpebral(s) in dorsal view: (A) *Caiman crocodylus yacare* (TMM M-7365) with a palpebral composed of a single ossification; (B) *Tomistoma schlegelii* (TMM M-6432) with a palpebral still embedded in dried skin (black); (C) *Alligator mississippiensis* (TMM M-7487) with a palpebral element composed of a single ossification; (D) *Paleosuchus palpebrosus* (YPM R11407) with palpebrals composed of three ossification centers forming a single element; (E) *Osteolaemus tetraspis* (TMM M-6774) with palpebrals composed of two ossifications (the left element has been removed). Scale bars = 1 cm.

the dorsoventral arching common to many crocodyliform palpebrals (Fig. 2).

The degree of integration of the palpebral with the surrounding skull elements may be controlled ontogenetically. The largest specimen of *P. kirkpatricki* (TTU-P 9000) has a palpebral that has a contact surface for the pre- and postfrontals, frontal, lacrimal and postorbital. In addition, the similarly sized, isolated palpebral mentioned above (UCMP 140035), bears sutural surfaces on all sides of the element save the lateral edge, thus demonstrating that the holotype and UCMP 140035 had a fully integrated palpebral at death. However, in smaller individuals of *P. kirkpatricki*, the palpebral is not fully integrated into all the dorsal circumorbital elements. For example, the paratype of *P. kirkpatricki* (TTU-P9002) is about 75% the size of the holotype and the palpebral is firmly attached to the frontal and the postfrontal, but has little contact with the postorbital. Furthermore, even though the lacrimal and the prefrontal are not completely preserved, the anteromedial edge of the palpebral is largely rounded and does not exhibit an obvious contact surface with either element. Additionally, a similarly sized frontal–postfrontal (UCMP 27480) of a referred specimen of *P. kirkpatricki*

shows a sutural contact for the attachment of the palpebral on the lateral side of the frontal, but not on the lateral side of the postfrontal. This pattern of the development of more sutural contacts between the palpebral and surrounding bones in larger individuals is consistent with an ontogenetic trajectory but, at this point, little data is supporting this notion and, additionally, little is known about individual variation in *P. kirkpatricki*.

Among other rauisuchids, similar elements to what we interpret as a palpebral were found disassociated from the skulls in the holotypes of *Postosuchus alisonae* (UNC 15575) and *Polonosuchus silesiacus* (ZPAL Ab III 563). Originally, Peyer *et al.* (2008) interpreted the element in *Postosuchus alisonae* as a frontal, whereas Sulej (2005) interpreted the element as a prefrontal, following Chatterjee (1985) for *Postosuchus kirkpatricki*. However, the elements in both *Postosuchus alisonae* and *Polonosuchus silesiacus* share a nearly identical morphology to that of the palpebral of *Postosuchus kirkpatricki* (TTU-P 9000); all are concave ventrally and convex dorsally, have a triangular shape in dorsal view, a rugose external surface, and articulation surfaces for skull elements on the anteromedial and posteromedial sides (Fig. 4). Therefore, we reinterpret these elements as

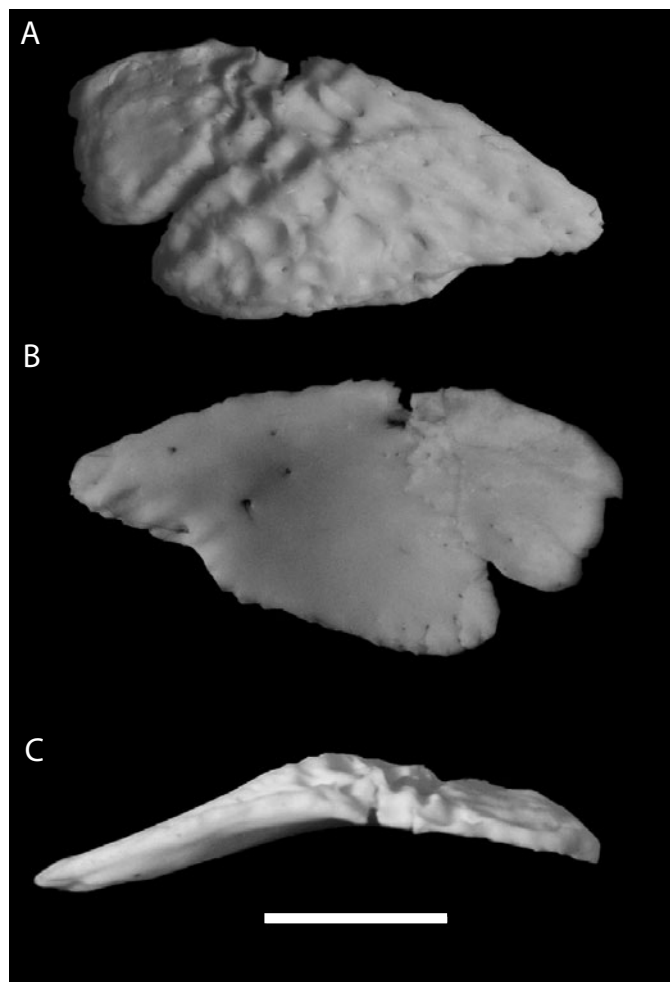


Figure 3 The right palpebral of *Osteolaemus tetraspis* (TMM M-6774) in dorsal (A), ventral (B), and lateral (C) views. Scale bar = 1 cm.

homologous with the palpebral of *Postosuchus kirkpatricki*. The palpebrals of *Postosuchus alisonae* and *Polonosuchus silesiacus* do show variation from each other and with *Postosuchus kirkpatricki*. For example the palpebral of *Polonosuchus silesiacus* is dorsally arched at its centre relative to the other taxa, and the palpebral of *Postosuchus alisonae* has relatively deeper sculpturing on the lateral edge of the ventral surface compared to the other taxa (Fig. 4). Furthermore, in both *Postosuchus alisonae* and *Polonosuchus silesiacus*, the circular element in the middle of the palpebral described above for *Postosuchus kirkpatricki* is more prominent and distinct relative to the surrounding portions of the element.

Batrachotomus kupferzellensis, a loricatan pseudosuchian just outside Rausuchidae and Crocodylomorpha, is represented by at least three partial, well preserved skeletons including mostly disarticulated skull material (Gower 1999, 2002; Gower & Schoch 2009). A separate palpebral has not been identified among the remains of *B. kupferzellensis*; however, a prefrontal–postfrontal–frontal complex of a paratype of *B. kupferzellensis* (SMNS 80260) preserves evidence of the attachment of the palpebral similar to that on the holotype of *Postosuchus kirkpatricki* (TTU-P 9000), suggesting that *B. kupferzellensis* likely had a palpebral attached to the dorsal circumorbital bones. The complete frontal with articulated pre- and postfrontals (Fig. 5) bears a dorsoventrally thick lateral margin that consists of small spires of bone and pits, like that of the medial articulation surface of the isolated palpebral of *P. kirkpatricki* (UCMP 140035) and the exposed lateral margin of the frontal, postfrontal and prefrontal of *P. kirkpatricki* (TTU-P 9000). The

frontal of *B. kupferzellensis*, like that of *P. kirkpatricki*, has little contribution to the orbit, unlike that of paracrocodylomorphs such as *Arizonasaurus babbitti* (Nesbitt 2005). Additionally, the lateral margin of the frontal and postfrontal is straight antero-laterally and the lateral margin of the prefrontal is straight postero-laterally (Fig. 5), a pattern present in *P. kirkpatricki* (TTU-P 9002). These straight lateral margins of *B. kupferzellensis* and the morphology of the lateral surfaces are consistent with an articulation surface for a palpebral, as in rausuchids.

1.3. *Saurosuchus galilei*

Saurosuchus galilei is a large (~6 m) early loricatan from the late Carnian Ischigualasto Formation of Argentina (Reig 1959; Sill 1974; Alcober 2000; Trotteyn *et al.* 2011). The taxon is known from a variety of specimens, including a partial skull (PVL 2062 holotype) and a nearly complete, well-preserved skull (PVSJ 32). Both skulls bear a unique dorsal margin of the orbit and seemingly unique arrangement of circumorbital elements that was discussed by both Sill (1974) and Alcober (2000) in their diagnoses of the species. Sill (1974) termed the unusual dorsal margin of the orbit as the “orbital arch” and considered that the frontal composed the entire “orbital arch”. Furthermore, Sill (1974) concluded that the pre- and postfrontals were small relative to the frontal. In the description of PVSJ 32, Alcober (2000) paid particular attention to skull roof elements, but largely followed the interpretation of Sill (1974) in identifying the frontal as the thick element overhanging the dorsal margin of the orbit. Three (numbers 7–9) of the seven autapomorphies of *Saurosuchus galilei* identified by Alcober (2000) pertain to the features of the frontal and the arrangement of the frontal to other skull roof elements. In Alcober’s (2000) interpretation, the frontal of *S. galilei* forms the thick lateral margin of the orbit, excludes the postfrontal from the orbital margin, contacts the postorbital, and has a unique posterolateral projection.

Here, we reinterpret the element at the dorsal portion of the orbit as a palpebral, largely following the re-interpretation of and arguments given for *Postosuchus kirkpatricki* and closely related taxa (Fig. 6). The separate ossification is almost fully integrated into the skull roof, even more so than in *P. kirkpatricki*. Like that of *P. kirkpatricki* (TTU-P 9000) and crocodyliforms, a rugose surface with small foramina characterises the dorsal surface of the palpebral element of *S. galilei*. This ornamentation, similar to osteoderms in the trunk region (Trotteyn *et al.* 2011), is distinct relative to the rest of the skull table and is utilised to determine the extent of the palpebral, given that sutures on the dorsal surface of the skull roof cannot be readily traced. We outline the extent of the palpebral where the ornamentation of the palpebral meets the less rugose, nearly foramina-free smooth ornamentation of the frontal, prefrontal and postfrontal (Fig. 6). The partially visible sutures present on the ventral surface of skull roof elements (Fig. 6) further support our interpretation of the extent of the palpebral in dorsal view.

The palpebral of *S. galilei* is triangular, like that of *P. kirkpatricki* (TTU-P 9000), but is concave laterally instead of anteroposteriorly straight. The thickened lateral margin of the palpebral arcs dorsally, as does the middle portion, thus resulting in an expansion dorsal to all other skull roof elements. The concave lateral margin is also thickened relative to the other portions of the palpebral. These features of *S. galilei* differ from *P. kirkpatricki* (TTU-P 9000), in which the lateral margin of the palpebral is nearly straight and similar in thickness to the middle portion. Only one ossification appears to compose the palpebral of *S. galilei*, although sutures are difficult to observe on both the dorsal and ventral sides.

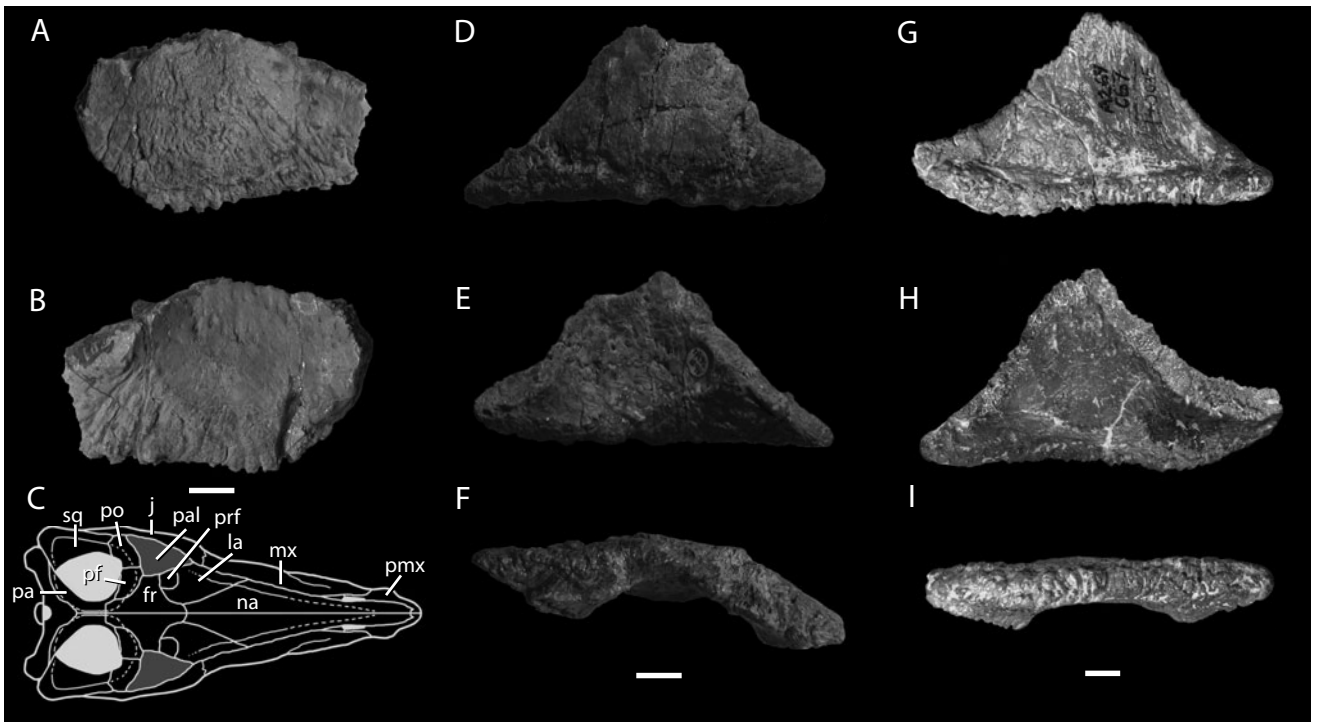


Figure 4 Palpebrals of members of Rausuchidae (*sensu* Nesbitt 2011): (A–B) the right palpebral element of *Postosuchus alisonae* (UNC 15575) in dorsal (A) and ventral (B) views; (C) a reconstruction of the dorsal view of the skull of *Postosuchus* to illustrate the position and connectivity of the palpebral of rausuchids; (D–F) the left palpebral of *Polonosuchus silestiacus* (ZPAL Ab III/563) in dorsal (D), ventral (E) and lateral (F) views; (G–I) the left palpebral of *Postosuchus* (UCMP 140035) in dorsal (G), ventral (H) and lateral (I) views. Scale bars = 1 cm. Arrow indicates the anterior direction. Abbreviations: fr = frontal; j = jugal; la = lacrimal; mx = maxilla; na = nasal; pa = parietal; pal = palpebral; pf = postfrontal; pmx = premaxilla; po = postorbital; prf = prefrontal; sq = squamosal.

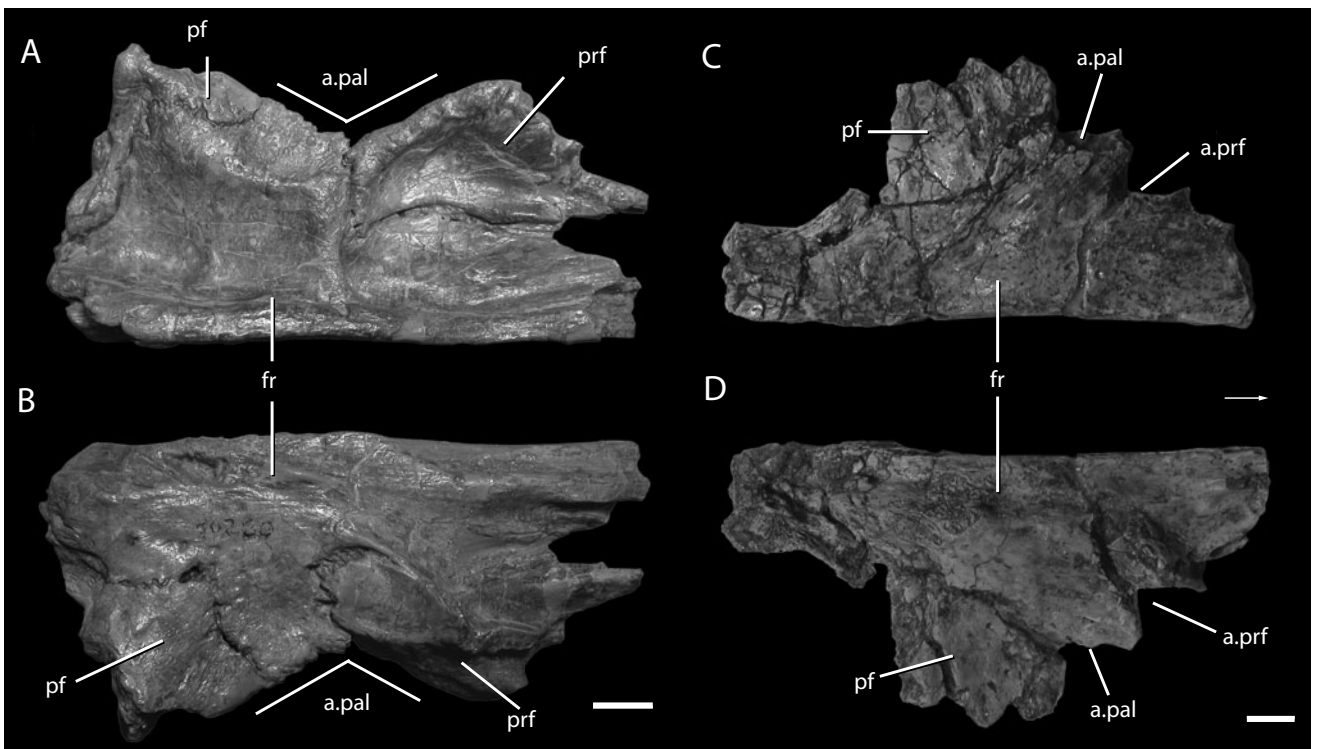


Figure 5 The frontals of the non-crocodylomorph loricatans *Batrachotomus kupferzellensis* and *Postosuchus kirkpatricki*: (A–B) the prefrontal, postfrontal and frontal of *Batrachotomus kupferzellensis* (SMNS 90260) in dorsal (A) and ventral (B) views; (C–D) the frontal and postfrontal of the holotype of *Postosuchus kirkpatricki* (TTU-P 9000) in dorsal (C) and ventral (D) views. The similarities between the lateral margins of the frontals and the arrangement of the pre- and postfrontals of *Postosuchus* and *Batrachotomus* suggest that *Batrachotomus* may have also had a palpebral integrated into the skull roof. Scale bars = 1 cm. Arrow indicates the anterior direction. Abbreviations: a. = articulates with; fr = frontal; pal = palpebral; pf = postfrontal; prf = prefrontal.

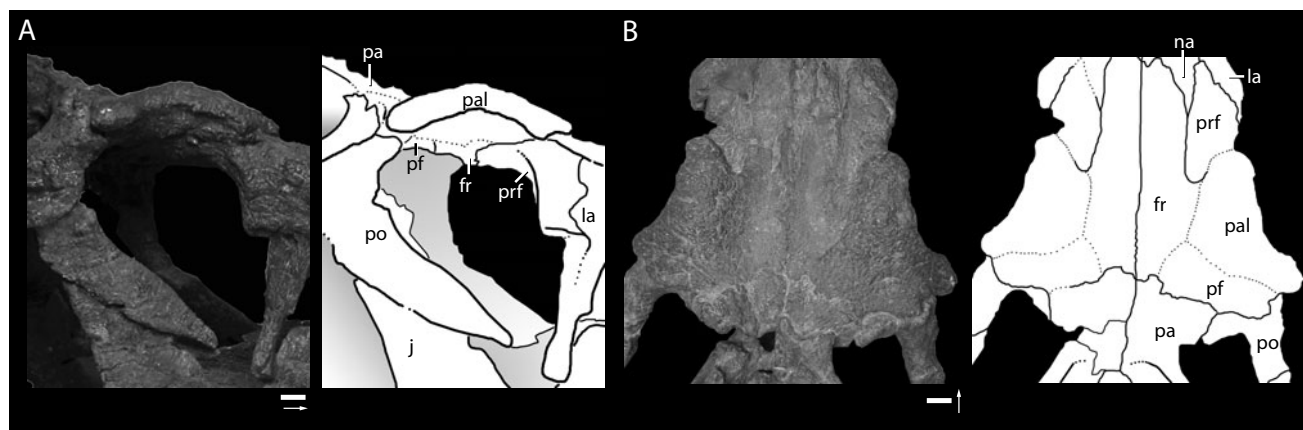


Figure 6 The palpebrals of *Saurosuchus galilei* following our reinterpretation of the identification of the skull roof elements: the right orbit of *Saurosuchus galilei* (PVSJ 32) in lateral view (A) and a dorsal view (B) of the skull roof elements. Scale bars = 1 cm. Arrow indicates the anterior direction. Abbreviations: fr = frontal; j = jugal; la = lacrimal; na = nasal; pa = parietal; pal = palpebral; pf = postfrontal; po = postorbital; prf = prefrontal.

The palpebral of *S. galilei* articulates with the frontal medially, the prefrontal anteromedially, the postfrontal posteromedially, and likely the postorbital posterolaterally. The anterior end of the palpebral terminates in a rounded boss, displaced dorsal to the articulation with the prefrontal. A tongue of the prefrontal lies on the ventromedial surface of the palpebral and, dorsally, the lateral side of the frontal and the anteromedial side of the palpebral constrict the posterior process of the prefrontal. The frontal–palpebral articulation of *S. galilei* is similar to that of *P. kirkpatricki* (TTU-P 9000) in which the lateral edge of the frontal is constricted by the prefrontal anteriorly and the postfrontal posteriorly. The lateral edge of the frontal appears to be curving dorsally where the two elements meet. Posteriorly, the palpebral and the postfrontal meet in a mediolaterally oriented contact. Posterolaterally, the palpebral terminates in a rounded, ventrally directed point, just lateral and anterior to its contact with the postorbital. The exact sutural surface between the palpebral and surrounding elements cannot be determined.

The palpebral of *S. galilei* is unique among loricatans in that the element is completely integrated into the skull roof, with the obliteration of most sutures, and in the dorsal arcing of the element, the thickness of the element, and the presence of an anterolateral boss that lies dorsal to the prefrontal. Without the integrated palpebral, the arrangement of the prefrontal, frontal and the postfrontal would be similar to that of other pseudosuchians, where all three elements form a portion of the orbit. Therefore, of the original autapomorphies cited by Alcober (2000) that concerned the lateral margin of the orbit, autapomorphies eight and nine (Alcober 2000, p. 304) pertain to the palpebral and not the frontal.

1.4. Poposauroida

Recent contributions on the relationships of the traditionally termed group “rauisuchians,” (including rauisuchids, and/or poposaurs) have identified a distinct and morphologically diverse group of pseudosuchians now referred to as poposauroids (Gower 2000; Nesbitt 2003, 2005, 2007, 2011; Weinbaum & Hungerbühler 2007; Brusatte *et al.* 2010; Butler *et al.* 2011). This varied group of largely osteoderm-free pseudosuchians includes the sail-backed ctenosauriscids (Nesbitt 2003; Butler *et al.* 2011), the poorly understood taxon *Poposaurus gracilis* (Mehl 1915; Colbert 1961; Weinbaum & Hungerbühler 2007; Gauthier *et al.* 2011; Schachner *et al.* 2011), the sail-backed and edentulous *Lotosaurus edentus* (Zhang 1975) and the bipedal and edentulous shuvosaurids (Nesbitt & Norell 2006;

Nesbitt 2007). Only recently has there been unequivocal cranial material assigned to any poposauroid taxa (Nesbitt 2003, 2007; Li *et al.* 2006; Gauthier *et al.* 2011) and of these specimens, the skulls of the shuvosaurid *Effigia okeeffeae* (Nesbitt & Norell 2006) and the early poposauroid *Qianosuchus mixtus* (Li *et al.* 2006) bear skeletal elements in the orbit.

The large orbits of both specimens of *E. okeeffeae* (Fig. 7B; AMNH FR 30587 and 30589) have a partially preserved sclerotic ring composed of thin osseous plates (Nesbitt 2007). Each scleral ossicle has a low keel and the shape of the ossicles varies from oval in AMNH FR 30587 to rectangular in AMNH FR 30589. The portion of the sclerotic ring of AMNH FR 30589 that remains in life position, and the width of each scleral ossicle, indicates that the ring has only a slightly smaller radius than that of the orbit and the ring itself occupied much of the orbit. Likewise, the paratype skull of *Q. mixtus* (Fig. 7A; IVPP V14300) preserves a sclerotic ring in the right orbit (Li *et al.* 2006). The sclerotic ring is fully preserved and remains in life position. The sclerotic ring consists of an unknown number of scleral ossicles, but has a similar width and ratio of the radius of the sclerotic ring relative to that of the radius of the orbit as *E. okeeffeae*.

E. okeeffeae and *Q. mixtus* represent the only poposauroids with well-preserved skulls and each preserve a sclerotic ring. Furthermore, no palpebral-like elements are present in any poposauroid. Although *E. okeeffeae* and nearly all other poposauroids lack osteoderms (Nesbitt 2003, 2005, 2007, 2011), small osteoderms are present along the vertebral column of *Q. mixtus* (Li *et al.* 2006).

1.5. Aetosauria

Aetosaurs were a group of herbivorous or omnivorous pseudosuchians, covered in a dense carapace composed of osteoderms, that had a global distribution during the Late Triassic (e.g. Long & Ballew 1985; Heckert & Lucas 2000; Small 1998). Aetosaurs are one of a few groups of pseudosuchian archosaurs that are currently known to possess skeletal elements within the orbit. The element(s) have been referred to supraorbitals (Walker 1961) and palpebrals (Schoch 2007) for *Aetosaurus ferratus* and a palpebral/supraorbital in *Neo-aetosauroides engaeus* (Desojo & Baez 2007). Furthermore, a new, undescribed “*Aetosaurus*-like” taxon from the Chinle Formation of Colorado also possesses structures like those of *Aetosaurus ferratus* (B. Small, pers. comm. to JCW 2011). Thus far, aetosaurs have not been found to possess any scleral ossicles.

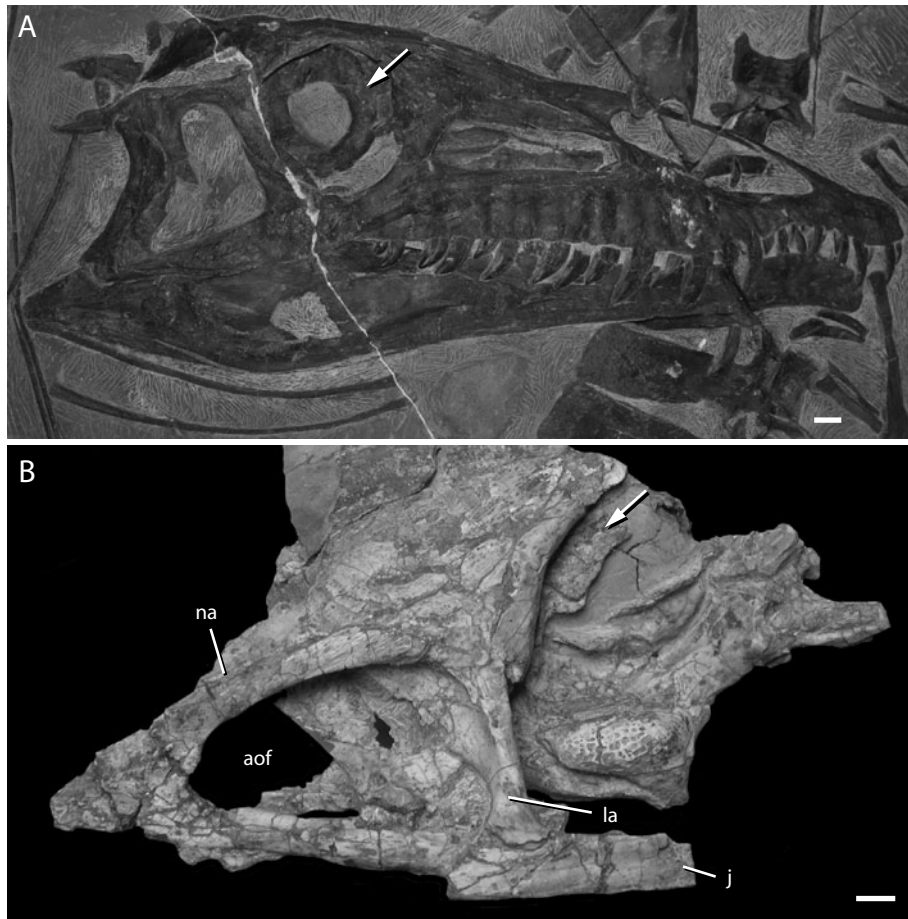


Figure 7 Sclerotic rings in the orbits of poposauroids: a complete sclerotic ring in the paratype of *Qianosuchus mixtus* (IVPP V 14300) (A) compared with the partial sclerotic ring in the left orbit of the paratype of *Effigia okeeffeae* (AMNH FR 30589) (B). Scale bars = 1 cm. White arrows highlight the skeletal elements in the orbit. Abbreviations: aof = antorbital fenestra; j = jugal; la = lacrimal; na = nasal.

Aetosaurus ferratus is represented by at least 22 nearly complete specimens, including intact skulls and orbital regions (Fraas 1877; Walker 1961; Schoch 2007). The skeletal elements in the orbit were first identified by Walker (1961) and then further described by Schoch (2007). Here, we supplement their descriptions. In *A. ferratus* (Fig. 8), three small, bony elements lie at the dorsal portion of the orbit and stretch from just posterior to the prefrontal to just anterior of the postfrontal and postorbital in an anteroposteriorly oriented row (Walker 1961; Schoch 2007). In most cases (see below), the three elements articulate with each other at interdigitating sutures, but do not have a contact with the dermal bones of the skull. The elements are mediolaterally thin and bear a rugose pattern on the lateral side, like that of the sculpturing of the external surface of the skull table. Additionally, the centre of each element has a weakly developed anteroposterior trending ridge. These elements likely represent palpebrals homologous with those of crocodylians, but the identification of these elements remains uncertain (see below).

The skeletal elements in the orbit of *A. ferratus* show variation in the following ways: (1) connectivity with each other; (2) relative sizes of the elements; and (3) possibly the number of elements. In some specimens (e.g. SMNS 5770 S-18), the elements meet each other at interdigitating contacts, whereas in other specimens (e.g. SMNS 5770 S-7, S-16) the elements fail to meet. The three elements of *Aetosaurus* are relatively close in size; however, the anteriormost element is 10–20% longer than the middle and posterior element in several specimens (e.g. SMNS 5770 S-16, S-18). The size of the anteriormost element of *Aetosaurus* is variable; the anterior element is never

more than approximately one and a half times the length of the other palpebral elements combined. The number of skeletal elements in the orbit of *A. ferratus* varies from one (SMNS 5770 S-8) to two (SMNS 5770 S-16) or three (SMNS 5770 S-18, S-7). The number of elements can differ in each orbit in the same individual. For example, in SMNS 5770 S-18, there are two elements in the right orbit, whereas there are three elements in the left orbit (see Schoch 2007, fig. 7). Nevertheless, it is not clear if the number of elements in the orbit represents variation within *A. ferratus*, or if it is a product of slight disarticulation and loss, the absence of complete preparation, or the removal during preparation. Given that all are about the same size and thus ontogenetic stage, this variation in the aforementioned features may represent variation with a single population.

A single skeletal orbital element was recently described for *Neoaetosauroides engaeus* (Desojo & Baez 2007) on both sides of PVL 5698. The element consists of a rounded, osseous element in the dorsal portion of the orbit near the prefrontal. The skeletal element within the orbit does not contact the prefrontal or any other skull roof element (Desojo & Baez 2007). The bone may be homologous to the anteriormost palpebral within the orbit of *Aetosaurus*, but the homology within Aetosauria is unclear. Details of the thickness and surface sculpturing cannot be determined as the result of poor preservation.

As hypothesised by Schoch (2007) in his thorough review of *A. ferratus*, the elements within the orbit are unlikely to be components of the sclerotic ring because of the presence of sutures between the elements instead of a simple overlap and the morphology of the anterior element, which is elongate and tapers to a point anteriorly. Furthermore, in all specimens

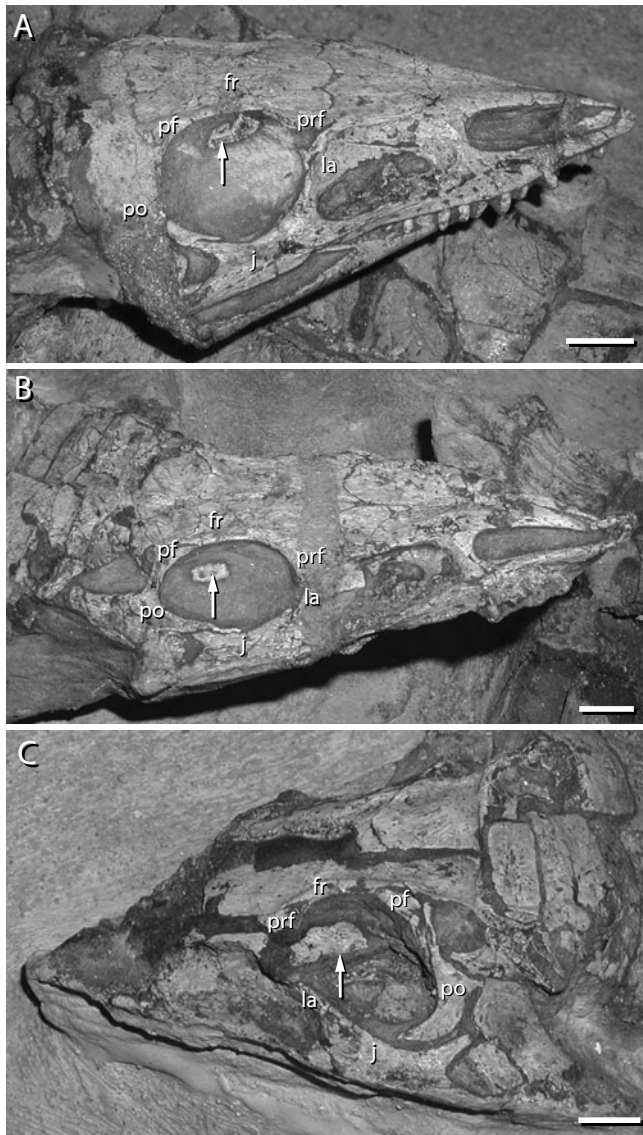


Figure 8 Skulls of *Aetosaurus ferratus* (SMNS 5770) with skeletal elements in the orbit: *Aetosaurus ferratus* number XVI (A) in right lateral view, VIII (B) in right lateral view, and I (C) in left dorsolateral view. The skulls in (A) and (C) preserve two elements in the dorsal portion of the orbit whereas (B) preserves only one element. Schoch (2007) reported that *Aetosaurus ferratus* had up to three elements in the dorsal portion of the orbit. Scale bars = 1 cm. White arrows highlight the skeletal elements in the orbit. Abbreviations: fr = frontal; j = jugal; la = lacrimal; pf = postfrontal; po = postorbital; prf = prefrontal.

the elements fail to form a ring, as they do in all well preserved taxa with scleral ossicles. Therefore, it appears that no member of Aetosauria possess sclerotic ossicles. The assignment of the elements in the orbit of aetosaurs to a palpebral (homologous with those of crocodylians) or supraorbital bones (neomorphic bones with a similar developmental history of dermal bones) remains unclear. On one hand, the elements appear to have formed in the upper eyelid, as evidenced by the dorsal position within the orbit, which is similar to extant crocodylians. Moreover, the upper eyelid appears to have been completely mobile, given that the ossicles are not articulating with other skull bones. The external texture is similar to those of osteoderms and may have shared a similar developmental history, and the interconnection of the elements is similar to that of *Osteolaemus* (Fig. 2). On the other hand, the number of elements, shape of those elements, and lack of contact with the prefrontal is different from those of early lorica-

tans and early crocodylomorphs. With that said, we currently interpret these elements as palpebrals, but with the differences between crocodylomorphs and aetosaurs noted (see discussion).

1.6. Extinct crocodylomorphs

Early crocodylomorphs from either the Triassic or the Jurassic remain rare components of faunal assemblages. Skulls of crocodylomorphs have been particularly difficult to study, given the fragmentary condition (e.g. *Hesperosuchus agilis*, AMNH FR 6758) or poor preservation (*Terrestriusuchus gracilis*, Crush 1984). Fortunately, a series of recent discoveries of well-preserved skulls of early crocodylomorphs have revolutionised our understanding of crocodylomorph systematics and our understanding of their palaeobiology (Clark *et al.* 2000, 2004; Clark & Sues 2002; Sues *et al.* 2003). A specimen referred to *Hesperosuchus agilis* (CM 29894) preserves the earliest record of an unequivocal palpebral among crocodylomorphs (Clark *et al.* 2000). The single, sub-circular element lies in the dorsal portion of both orbits (Clark *et al.* 2000). The edges of the palpebral (Fig. 9A) are slightly serrated, consisting of small bone spicules radiating from the centre. The surface of the palpebral consists of small grooves and ridges similar to the ornamentation of osteoderms on the neck and back of the same specimen. The dorsal surface of the palpebral is convex dorsally. Within the orbit, the palpebral extends laterally beyond the orbital margin and lies just ventral to lateral margin of the frontal, without contacting the bone. Additionally, the palpebral covers much of the dorsal margin of the orbit. Of the known Triassic crocodylomorphs, CM 29894 is the only specimen with a palpebral preserved in the orbit. A closely related taxon, *Dromicosuchus grallator* (Sues *et al.* 2003) is known from a complete skull and partial skeleton, but there does not appear to be any palpebral.

Terrestriusuchus gracilis is an uncharacteristically gracile crocodylomorph from the Triassic–Jurassic fissure fills of the UK, known from partially articulated and disarticulated remains (Crush 1984). Of the skeletal material preserved, only the posterior half of one skull remains in articulation (Fig. 9B; NHMUK R7591b). The skull is crushed ventrolaterally, but still preserves an intact posterior, ventral and partial dorsal orbital margin. A partial sclerotic ring lies within the dorsal portion of the orbit of the *T. gracilis*. A minimum of five rectangular sclerotic ossicles composes the partial ring. The thin ossicles are slightly concave along the long axis of the elements, but it is not clear if this concavity is the result of crushing. Unfortunately, part of the dorsal and the entire anterior portions of the orbit are incompletely preserved, so it is not clear if a palpebral was also present.

Junggarsuchus sloani (Fig. 9C), a close relative of Crocodyliformes, (Clark *et al.* 2004) was found also to have a palpebral composed of one ossification in near life position. Generally, the palpebral is similar to that of CM 29894 in size, surface features and location in the orbit. The palpebral is distinctly concave ventrally and has a smooth lateral margin. The contact with elements of the skull roof is not clear. The anterior portion of the palpebral appears not to touch the prefrontal and the medial edge of the palpebral appears to be partially attached to the lateral side of the frontal. A sutural contact between the elements is not present. During preparation of the orbit, a series of sclerotic ossicles preserved in partial sclerotic ring were discovered in the right orbit (J. Clark pers. comm. 2012). The sclerotic ossicles are longer than tall and the proportions are similar to those of *Terrestriusuchus gracilis*. *Junggarsuchus sloani* represents the only confirmed pseudosuchian with both a sclerotic ring and a palpebral.

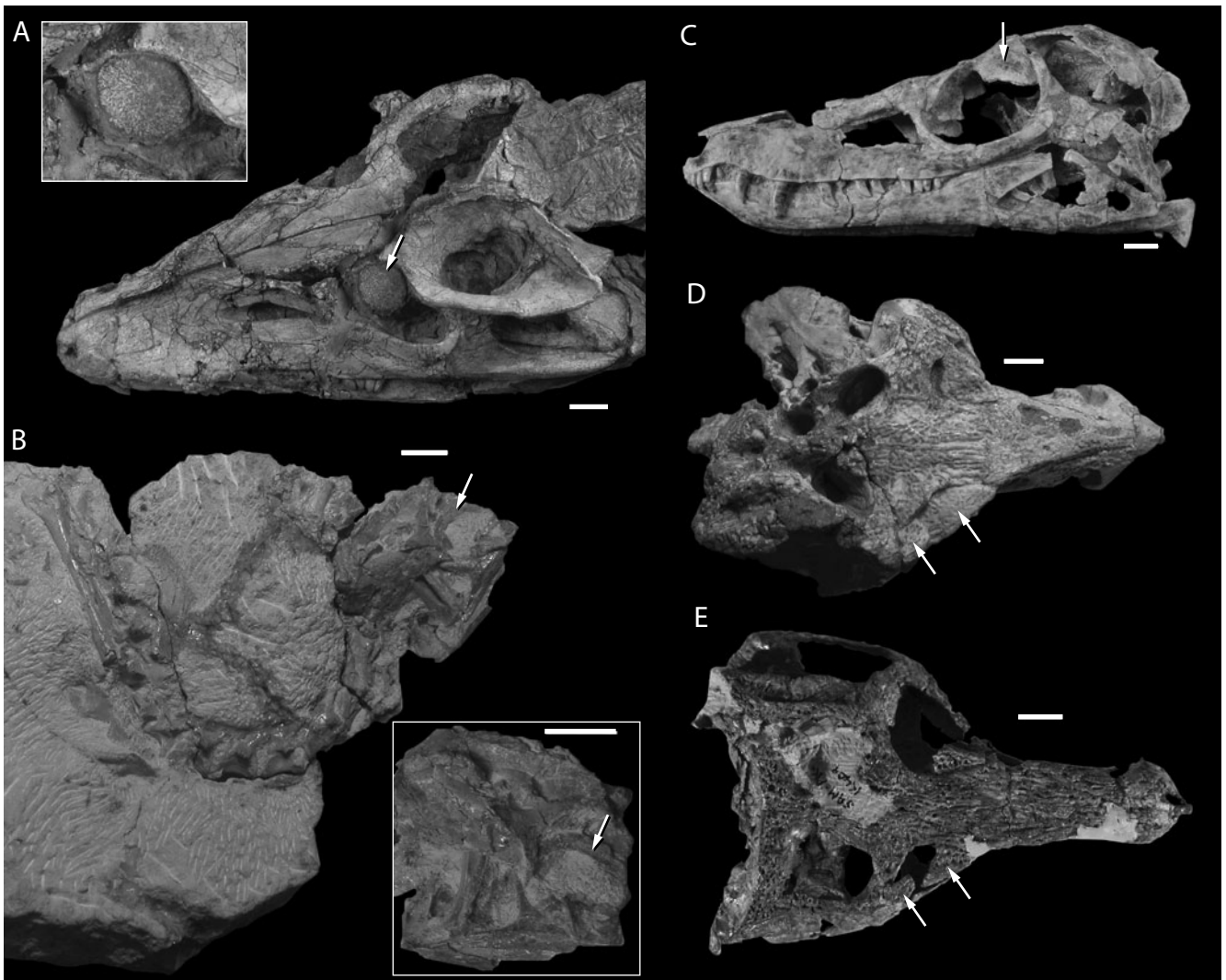


Figure 9 Skeletal elements in the orbits of early crocodylomorphs: (A) a skull referred to *Hesperosuchus agilis* by Clark *et al.* (2000) in dorsolateral view, with a close up (inset) of the palpebral in articulation; (B) partial skull and articulated skeleton of *Terrestriusuchus gracilis* (NHMUK R7591 b) in right lateral view with a close up (inset) of the partially preserved sclerotic ring in articulation; (C) the skull of *Junggarsuchus sloani* (IVPP V 14010) in left lateral view with a single palpebral; (D) a nearly complete skull of *Protosuchus richardsoni* (MCZ 6727) in dorsal view exhibiting two large palpebrals; (E) the holotype skull of *Orthosuchus strombergi* (SAM-K-409) in dorsal view, bearing two palpebrals. Scale bars = 1 cm. White arrows highlight the skeletal elements in the orbit.

Palpebrals are likely plesiomorphic for Crocodyliformes, given their presence in a number of crocodylomorph outgroups (as discussed above) and in the most plesiomorphic members of the clade (e.g. protosuchids, gobiosuchids, shartegosuchids), according to our understanding of crocodylomorph relationships (e.g. Clark 1986; Brochu 2001; Pol *et al.* 2009). A major shift in number and morphology of the palpebrals occurs at Crocodyliformes relative to their proximal outgroups. Instead of a single rounded palpebral, two large similarly sized palpebrals occupy much of the area dorsal to the orbital cavity.

Protosuchus richardsoni (Fig. 9C), one of the earliest diverging taxa in Crocodyliformes, is known from a number of partial to complete skeletons from the Early Jurassic Moenave Formation of Arizona (Brown 1933; Colbert & Mook 1951; Crompton & Smith 1980). Although not described by Colbert and Mook (1951), two palpebrals are present at the dorsal portion of orbit in the holotype (AMNH FARB 3024). An anterior palpebral articulates with the dorsal surface of the prefrontal, whereas a more posterior palpebral articulates with the dorsal surface of the postorbital. A gap is present between the two palpebrals and between the palpebrals and the lateral margin of the orbit (Colbert & Mook 1951, plate 12). A

better-preserved specimen of *Protosuchus richardsoni* (MCZ 5727) exhibits a similar pattern (Fig. 9C) as the holotype. However, in MCZ 6727, the palpebrals meet and nearly hide the orbit in dorsal view. In MCZ 6727, the palpebrals contact the prefrontal, frontal and the postorbital, but do not suture to those elements. The anterior palpebral is triangular in dorsal view where it tapers to acute angles anteriorly and laterally. The posterior palpebral meets the anterior palpebral in a slightly interdigitating suture, like that of *Osteolaemus* (Fig. 2) and *Simosuchus clarki* (UA 8679). This contact is more well developed on the right side compared to the left, where a medial gap still persists between the two elements. The much smaller posterior palpebral is sub-rounded and occupies the posterior third of the dorsal margin of the orbit. Both palpebrals are slightly convex in dorsal view, appear to be concave in ventral view, and are uniformly thick throughout the length of the elements. The dorsal ornamentation of the palpebrals consists of small grooves and ridges, an identical ornamentation to the rest of the skull roof elements.

The palpebrals of *Protosuchus richardsoni* are typical for other protosuchids (e.g. Fig. 9D, *Orthosuchus strombergi*, SAM-K-409) and many other crocodyliforms (e.g. Fig. 10A, *Sichuanosuchus shushanensis*, IVPP V10594; Fig. 10B *Zosuchus*



Figure 10 (A–E) Extinct crocodyliforms with articulated palpebral(s) in dorsal view: (A) *Sichuanosuchus shushanensis* (IVPP V10594); (B) *Zosuchus davidsoni* (IGM 100/1305); (C) *Zaraasuchus shepardii* (IGM 100/1321); (D) *Nominosuchus matutinus* (PIN 4147-3); (E) *Baurusuchus salgadoensis* (MPMA 62-0001-02). (F) The thalattosuchian *Dakosaurus andiniensis* (MOZ 6146P) in right lateral view, illustrating the presence of a complete sclerotic ring and the absence of a palpebral. Scale bars = 1 cm (A–D); 5 cm (E–F). White arrows highlight the skeletal elements in the orbit.

davidsoni, IGM 100/1305; *Stegomosuchus longipes*, Walker 1968). However, a number of other early crocodyliforms deviate from this pattern. The Late Cretaceous gobiosuchid *Zaraasuchus shepardii* (Fig. 10C; Pol & Norell 2004; IGM 100/1321) has anterior and posterior palpebrals that tightly suture to each other and to the margins of the prefrontal, frontal and post-orbital. Along the lateral margin of the orbit, the posterior palpebral sends a small anterior projection to lap against the anterior palpebral, as well as a posterior projection that tracks along much of the anterolateral margin of the postorbital. This degree of palpebral development is most similar to what is seen on the right side of the MCZ 6727 specimen of *Protosuchus richardsoni*, suggesting that multiple levels of variation (i.e., individual, ontogenetic and/or phylogenetic) may exist in the palpebrals of early crocodyliforms.

Most mesoeucrocodylians share a similar palpebral morphology to early crocodyliforms, in that there are two palpebrals in the orbit and the anterior palpebral is dominant. Palpebral variation among mesoeucrocodylians typically takes three forms:

presence or absence of palpebrals; whether or not the anterior palpebral contacts the posterior one; and whether the anterior palpebral tracks along the orbital margin, or if the medial margin is posteriorly concave, thereby creating a fenestra dorsal to the orbit (see Sertich 2011).

The shartegosuchid *Fruitachampsia callisoni* from the Upper Jurassic Morrison Formation (Clark 2012) has a proportionally large anterior palpebral with a greatly concave medial margin forming the stereotypical “comma” shape common to many mesoeucrocodylian crocodyliforms. This anterior palpebral shape results in a fenestra dorsal to the orbit formed by the gap between the frontal and the anterior palpebral. The posterior palpebral is very small and does not contact the anterior palpebral in *Fruitachampsia*. The early mesoeucrocodylian (and probably notosuchian) taxa *Araripesuchus tsangatsangana*, *A. gomesii*, *A. patagonicus*, *Malawisuchus mwakasyungutiensis* and *Pakasuchus kapilimai* have a similar “comma”-shaped anterior palpebral. In these, as in *Fruitachampsia*, the posterior palpebral is small and does not contact the anterior palpebral.

Asian shartegosuchids, an enigmatic clade of crocodyliforms near the origin of Mesoeucrocodylia (Fiorelli & Calvo 2007), may have only a single large anterior palpebral. The holotype of *Shartegosuchus asperopalatum* (PIN 4171/2) has two preserved in left orbit, but it is not clear if they are both from left side. The *Nominosuchus matutinus* holotype (PIN 4147-3) is one of the better preserved specimens, and no posterior palpebral is evident in this individual. The anterior palpebral is proportionally large, being wider than the interorbital width of the frontal. The palpebral is semicircular in dorsal view, with a straight margin facing laterally and a curved medial margin abutting the lateral surface of the frontal for most of its length. However, the entire medial palpebral margin is not sutured to the frontal; this leaves a gap between the frontal and palpebral, approximately halfway along the interorbital region, and a large posterior gap between the palpebral and postorbital. The orbit in the holotype of *Adzhosuchus fuscus* (PIN 4174-5) is less well preserved compared to *Nominosuchus* (PIN 4147-3), but it still preserves a single large palpebral that has been displaced ventrally into the orbit. No indication of a posterior palpebral is present. It is possible that the posterior palpebrals in these taxa were very small (as in *Fruitachampsia*) and/or poorly attached to the postorbital and therefore simply failed to be preserved with the specimens.

In a number of advanced mesoeucrocodylians and notosuchians, the palpebral rests adjacent to the frontal margin for the entire (or nearly the entire) medial margin of the palpebral. This results in little or no fenestra dorsal to the orbit. However, not all taxa that have a close correspondence between the medial palpebral margin and the lateral frontal margin have palpebrals that are tightly integrated or sutured to the orbital margin. For example, the notosuchians *Simosuchus clarki* (UA 8679) and *Armadillosuchus arrudai* (Marinho & Carvalho 2009) have a large anterior palpebral that closely follows the orbital margin, but these palpebrals are not tightly sutured to the margin and are easily dissociated during preparation. Likewise, *Sebecus icaeorhinus* (AMNH FR 3160) has an anterior element that closely corresponds to the dorso-lateral portion of the orbit (Simpson 1937; Brown & Schlaikjer 1940; Colbert 1946). However, these anterior palpebrals are not tightly integrated to the margin and were discovered separated from the orbital margin.

Other advanced mesoeucrocodylians have highly integrated anterior palpebrals that shared tight sutures to the prefrontal and frontal. These taxa include the baurusuchids *Baurusuchus salgadoensis* (Carvalho *et al.* 2005) and *Stratiotosuchus maxhechti* (DGM 1477-R) as well as the peirosaurids *Uberabasuchus terrificus* (Carvalho *et al.* 2004), *Montealtosuchus arrudacamposi* (Carvalho *et al.* 2007), and *Lomasuchus palpebrosus* (Gasparini *et al.* 1991). Additionally, the peirosaurids have close contact between the anterior and posterior palpebrals and no indication of a dorsal fenestra. In *Baurusuchus* and *Stratiotosuchus*, the anterior and posterior palpebral also contact each other, but in *Baurusuchus* there remains a small dorsal fenestra above the orbit.

Absence of palpebrals is difficult to assess with fossilised specimens (see above) and this is especially problematic given that, for many mesoeucrocodylians, the palpebral would have been a loose element within the eyelid, and therefore easy to lose once the skin and connective tissue rotted. A number of early mesoeucrocodylians and eusuchians do not preserve palpebrals but, based on the presence of palpebral facets on the prefrontal and postorbital, it seems likely that the elements were present during life. These taxa include *Araripesuchus wegeneri* (Sereno & Larsson 2009), *Kaprosuchus saharicus* (Sereno & Larsson 2009), *Mahajangasuchus insignis* (Turner & Buckley 2008), *Anatosuchus minor* (Sereno & Larsson 2009), *Hamadasu-*

chus rebouli (Larsson & Sues 2007), *Mariliasuchus amarali* (Zaher *et al.* 2006; Andrade & Bertini 2008), *Shamosuchus djadochtaensis* (Pol *et al.* 2009), *Yacarerani boliviensis* (Novas *et al.* 2009) and *Adamantinasuchus navae* (Nobre & Carvalho 2006).

Thalattosuchians and pholidosaurids are two groups of crocodyliforms that do appear to genuinely lack palpebrals. This is supported by the absence of the element in numerous complete and exceptionally well-preserved individuals (e.g. *Geosaurus giganteus*, NHMUK 37020; *Pelagosaurus*, BSPG 1973 VII 592; *Cricosaurus suevicus*, SMNS 90513). Interestingly, thalattosuchians and some pholidosaurids are the only groups of crocodyliforms that preserve sclerotic rings in a number of its constituent species (e.g. *Dakosaurus andiniensis*, Pol & Gasparini 2009). Within Thalattosuchia, a number of specimens of *Pelagosaurus* (UH 1, BSPG 1973 VII 592; BSPG 1925 I 34), as well as *Geosaurus giganteus* (NHMUK 37020), *Cricosaurus suevicus* (SMNS 90513) and *Dakosaurus andiniensis* (Pol & Gasparini 2009), have sclerotic rings that are indistinguishable from other clades with the same structure (e.g. Ichthyosauria, Aves). Furthermore, Wu *et al.* (2001) reported scleral ossicles in the orbit of the pholidosaurid *Terminonaris robustus* (SMNH P2411.1), whereas there have been no other reports of sclerotic rings in any other pholidosaurid. All of the taxa within Thalattosuchia and Pholidosauridae with sclerotic rings have been found in marine sediments, ranging from the Early Jurassic through the Late Cretaceous (Buffetaut 1982). Additionally, these forms have been considered partially or fully marine, with adaptations for a full aquatic lifestyle (e.g. salt glands, Fernandez & Gasparini 2008; flipper-like forelimbs and hypocercal caudal region (Gasparini *et al.* 2006) and the sclerotic rings may have helped to stabilise the eye under pressure (Curtis & Miller 1938).

Among most other neosuchians, there is an apparent trend in palpebral reduction. *Alligatorum meyeri*, *Theriosuchus pusillus* and *Goniopholis simus* have only one palpebral in each orbit, but the element remains relatively large. An undescribed early neosuchian from the Cloverly Formation (MCZ 4453) preserves both a large anterior palpebral and a much smaller posterior palpebral that is similar to most other crocodyliforms in both shape and relationship to the orbital margin. Conversely, *Goniopholis simus* strongly integrates a single palpebral into the orbital margin (Andrade & Hornung 2011). In these specimens of *G. simus*, the palpebral is tightly integrated into the periorbital region, coossifying with the lacrimal, prefrontal, frontal and postorbital (Andrade & Hornung 2011). The ornamentation is continuous between the cranial bones and the palpebral, which can make distinguishing the medial border of the palpebral difficult or impossible. Among other goniopholidids, definitive palpebrals are known in *Goniopholis baryglyphaeus* (MG 2014) and *Nannosuchus gracilidens* (NHMUK 48217).

Among successive outgroups of Eusuchia, palpebrals are less commonly associated with specimens, but a depression for the articulation of the element persists on the orbital margin of the prefrontal (e.g. *Shamosuchus djadochtaensis* IGM 100/1195), as with extant crocodylians such as *Alligator mississippiensis*. Hylaeochampsid eusuchians such as *Hylaeochampsia vectiana* (NHMUK R177) and *Iharkutosuchus makadii* (MTM 2006.53.1) do not preserve palpebral ossifications, but it is not clear if these taxa lack palpebrals or if they were lost after death. By the crown-group, taxa that possess a palpebral show that it is very weakly integrated into the orbital margin and are typically small (see discussion of extant crocodylians above). Fossil evidence for palpebrals is rare among extinct members of Crocodylia, but the extinct taxa with palpebrals have a similar morphology and a similar attachment location as those of extant members of Crocodylia. Thus the range of morphology among

Table 1 Distribution of osseous skeletal elements in the orbit of pseudosuchians clades.

Clade	exemplar taxa	palpebral present	integration?	scleral ossicles
Phytosauria*		no	–	no
Ornithosuchidae		no	–	no
Aetosauria		yes	no	no
Poposauridae	<i>Qianosuchus</i>	no	–	yes
	<i>Effigia okeeffeae</i>	no	–	yes
non-crocodylomorph Loricata#	<i>Batrachotomus</i>	likely	likely	no?
	<i>Saurosuchus</i>	yes	yes	no?
Rauisuchidae	<i>Postosuchus</i>	yes	yes	no?
Non-crocodylomorph crocodyliforms	<i>Hesperosuchus agilis</i>	yes	no	no
	<i>Terrestriusuchus</i>	?	?	yes
	<i>Junggarsuchus</i>	yes	no	yes
Protosuchia		yes	~	no
Thalattosauria		no	–	yes
Crocodylia		yes	in some	no

* Most archosaur phylogenies (Sereni 1991; Juul 1994; Brusatte *et al.* 2010) have found Phytosauria as the basal-most pseudosuchian group, but recently Nesbitt (2011) found them as the sister-taxon to Archosauria.

does not include Rauisuchidae.

extant members of Crocodylia encompasses the morphology of extinct members of Crocodylia with few exceptions. Interestingly, there is no evidence for palpebral ossifications in the exquisitely preserved early globidontans such as *Brachychampsia* and *Stangerochampsia* although *Borealosuchus formidabilis*, *Alligator mcgrewi*, and *Procaimanoidea* have small palpebrals (Schmidt 1941). Therefore, it is possible that the absence of palpebrals in even the best preserved fossil crocodylians may still be the result of a preservational bias against small loosely attached dermal elements.

2. Discussion

2.1. The origin of the palpebral among pseudosuchians

Our description of the morphology, position and connectivity of the crocodylian palpebral, reinforced with recent work on the development of the element (Vickaryous & Hall 2008), strongly suggests that the osseous elements dorsal to the orbit in extinct crocodylomorphs are homologous to those of living crocodylians (Table 1). Furthermore, these same similarities between Crocodylia and extinct Crocodylomorpha are also present in the closest relatives of crocodylomorphs, the non-crocodylomorph pseudosuchians, suggesting that osseous elements in non-crocodylomorph pseudosuchians and the palpebral of Crocodylia are also homologous. Therefore, palpebrals are not restricted to Crocodylomorpha, but are also present in their closest relatives. Yet, the origin of the palpebral is difficult to understand, given the discontinuous distribution among early pseudosuchian groups and the questionable homology of the elements in aetosaurs. Osseous elements in the dorsal portion of the orbit have not been identified in stem archosaurs (e.g. *Euparkeria capensis*, Ewer 1965; *Vancleavea campi*, Nesbitt *et al.* 2009), in any early bird-line archosaur (= Ornithodira, = Avemetatarsalia), phytosaurs, or in the early diverging pseudosuchian members such as Ornithosuchidae or *Gracilisuchus stipanicicorum* (Romer 1972). At least some members of Aetosauria do possess palpebrals (see description above), but the homology of these elements remain unclear. The palpebrals of crocodylomorphs and aetosaurs share many similarities, but there are differences as well. The three ossified elements in *Aetosaurus ferratus* are likely ossified from the eyelid, given the position in the orbit as in Crocodylia. The external morphology is similar to that of osteoderms like those of crocodylomorphs. However, there are no crocodylomorphs with three independent palpebral elements (the palpebral of *Osteolaemus*

is composed of two or three ossifications, but the separate ossifications still form a single palpebral). This may not be a problem, given that all of the *Aetosaurus* specimens are juveniles (Schoch 2007), and that later in ontogeny the three elements may form a single palpebral. The immaturity of the skeleton of *Aetosaurus* may also explain why the three elements have little to no contact with the circumorbital bones of the skull. Moreover, in the larger specimens of *Aetosaurus*, it appears that the palpebrals are touching the prefrontal, as in all other pseudosuchians with preserved palpebrals. Because of these similarities, we argue that these elements in aetosaurs represent homologous elements with Crocodylia.

The other group (depending on the hypothesis of relationships, see Fig. 11A) is the “rauisuchians” of Brusatte *et al.* (2010), or the non-crocodylomorph loricatans of Nesbitt (2011). The three taxa with confirmed palpebrals, *Saurosuchus*, *Polonosuchus* and *Postosuchus*, share a general external morphology, position and connectivity with early crocodylomorphs such as *Hesperosuchus*. However, the non-crocodylomorph loricatan taxa have a unique articulation with the circumorbital bones not sampled in Crocodylomorpha, in which there is a cranial-like, interdigitating suture between the palpebral and the circumorbital bones.

From these data, it is likely that the palpebral evolved in close relatives of Crocodylomorpha. The differences among the palpebral in early pseudosuchian groups such as Aetosauria and “rauisuchians” and crocodylomorphs may have been the result of early experimentation with a novel element before it became somewhat more standardised in basal Crocodylomorpha and Crocodyliformes. The palpebral was present by the Late Triassic in aetosaurs and “rauisuchians” and, given phylogenetic estimates of Pseudosuchia, the feature was likely present in the last common ancestor of aetosaurs and crocodylomorphs at the end of the Early Triassic (Butler *et al.* 2011; Nesbitt 2011; Nesbitt *et al.* 2011). Furthermore, the palpebral may also be useful for determining relationships in early Archosauria. Nesbitt (2011) employed three characters that focused on the palpebral, one character examining the presence or absence of the palpebral (character 147), one character addressing the size of the elements (character 148), and one character addressing the connectivity of the elements with the circumorbital bones (character 149). Even though we do not have the ability to examine developmental sequences in extinct pseudosuchians, the origin of the palpebral attests to the importance

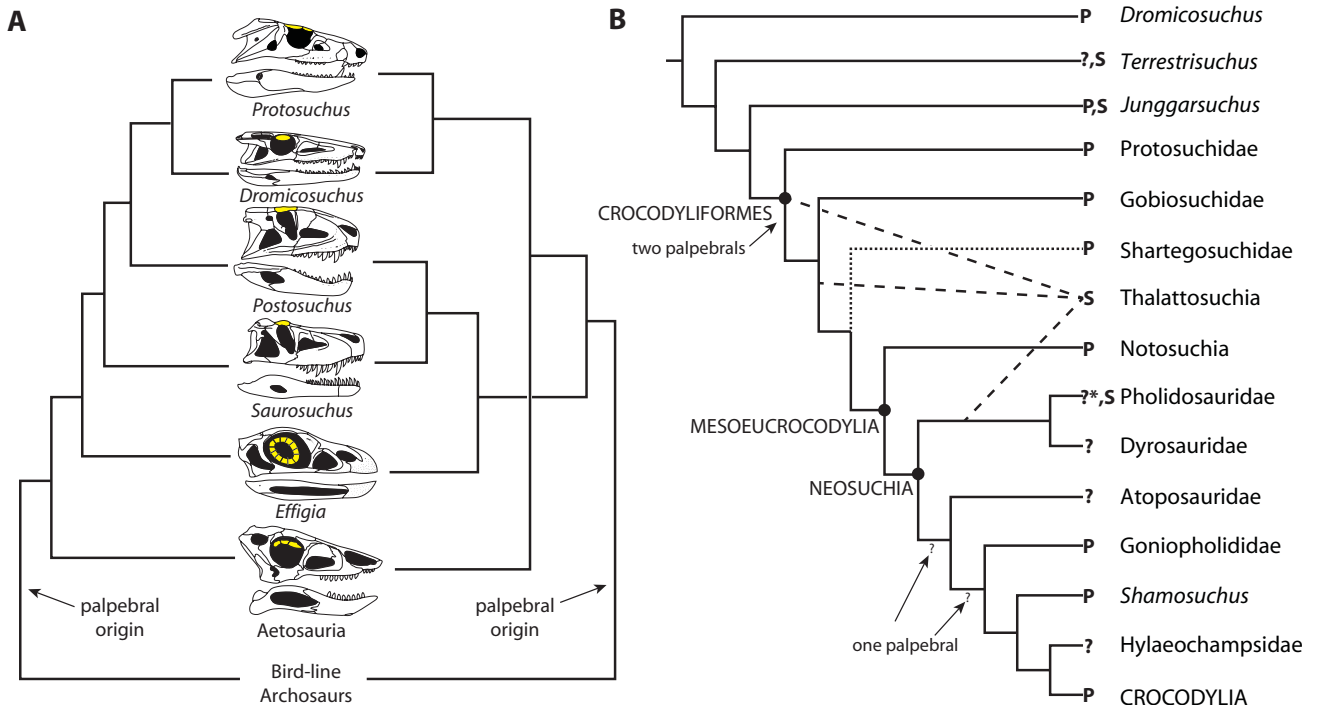


Figure 11 (A) The evolution of skeletal elements in the orbit of early pseudosuchians, based on the relationships of Nesbitt (2011) (left) and Brusatte *et al.* (2010) (right). Skeletal elements in the orbit are highlighted in yellow/gray. (B) The evolution of skeletal elements in the orbit of Crocodyliformes, based on the relationships of Clark *et al.* 2004, Pol *et al.* (2009), Turner & Sertich (2010) and Pritchard *et al.* (in press). The distribution of scleral ossicles and the palpebral among pseudosuchians is complicated, even when considering skeletal elements are lost easily in taphonomic processes. Abbreviations: ? = unknown condition; ?* = likely a genuine absence; P = palpebral; S = scleral ossicles / sclerotic ring. The dotted lines represent uncertainty in phylogenetic position.

of the fossil record when examining seemingly novel features in living groups of vertebrates.

2.2. The evolution of osseous skeletal elements in the orbit of pseudosuchians

The evolution of scleral ossicles and the palpebral within Pseudosuchia is complicated and likely intertwined throughout the evolutionary history of the group. For example, there is only one example of a pseudosuchian, *Junggarsuchus sloani*, bearing both a palpebral and scleral ossicles, whereas most pseudosuchians lack scleral ossicles. Both the palpebral and scleral ossicles are lost or “gained” throughout the history of Pseudosuchia.

The palpebral originated outside Crocodylomorpha and is not a crocodylian invention. Clearly, the palpebral is plesiomorphic for Crocodylomorpha, given the distribution of the element within Pseudosuchia (Fig. 11A). The general morphology (osteoderm-like, concave ventrally-convex dorsally), position within the orbit (in the upper eyelid), and the attachment location (prefrontal) of the palpebral is rather conservative across Pseudosuchia, whereas the number of total palpebral elements, size of the palpebral and the integration with circumorbital bones varies across Crocodylomorpha. In the earliest forms, a large single palpebral occupies the dorsal portion of the orbit, and this condition appears to be inherited from their closest relatives in Loricata. At the taxonomic level of Crocodyliformes, two palpebrals, an anterior and posterior element, are present and occupy most of the dorsal portion of the orbit. Most members of Crocodyliformes outside the Crocodylia retain two palpebral elements, whereas all members of Crocodylia only bear one element (Fig. 11B). The single palpebral in Crocodylia is hypothesised to be homologous to the anterior palpebral of non-crocodylian crocodyliforms, given the similarities in size and attachment position.

Although the position of the palpebral is conserved in crocodyliforms, the degree of integration with the skull roof varies across Crocodylomorpha. The integration of the palpebral with the circumorbital bones within Crocodylomorpha is not to the same degree as in non-crocodylomorph loricatans (i.e., a cranial suture is present), but several crocodyliforms such as *Sebecus*, *Simosuchus*, and the crocodylians, *Paleosuchus* and *Osteolaemus* show high degrees of integration. Furthermore, taxa with better integrated palpebral with the circumorbital bones have large palpebrals that span the entire dorsal margin of orbit. Interestingly, the extinct (e.g. *Simosuchus*, Georgi & Krause 2010; Sertich & Groenke 2010) and extant (*Osteolaemus*, Kofron 1992) taxa with this arrangement of palpebrals have been inferred to have a more terrestrial ecology than their more aquatic cousins.

No member of Crocodylia possess scleral ossicles. Nevertheless, scleral ossicles are present in early pseudosuchians and even within Crocodylomorpha. Therefore, the evolution of scleral ossicles within the orbit of pseudosuchians is complicated. The only non-crocodylomorph pseudosuchian clade to possess scleral ossicles is the highly disparate poposauroids. Interestingly, the earliest diverging member of this clade (Nesbitt 2011), *Qianosuchus*, has been hypothesised to have a marine ecology (Li *et al.* 2006). However, other members of this clade, the shuvosaurids, also have scleral ossicles, but are inferred to be a terrestrial clade without clear aquatic adaptations (Nesbitt & Norell 2006; Nesbitt 2007). Among non-crocodyliform crocodylomorphs, *Terrestrisuchus* and *Junggarsuchus* are the only members to possess a sclerotic ring. *Terrestrisuchus* lacks any clear aquatic adaptations in the skeleton and is from a terrestrial assemblage (Whiteside & Marshall 2008). Within Crocodyliformes, sclerotic rings are present, but are restricted to a number of closely related marine forms (e.g. *Dakosaurus andiniensis* (Gasparini *et al.* 2006), *Geosaurus giganteus* and *Cricosaurus suevicus*). No other crocodyliforms possess a sclerotic ring.

Scleral ossicles are rare among pseudosuchians, but in most cases are restricted to marine forms (e.g. *Qianosuchus* and *Thalattosuchia*) and may have helped stabilise the eye under pressure (Curtis & Miller 1938). Yet, scleral ossicles are present in a few non-marine taxa (e.g. *Terrestriusuchus* and *Shuvosauridae*) and are present in many non-marine amniotes. Given the distribution of these features among pseudosuchians (Fig. 11), it appears that multiple gains of scleral ossicles were occurring throughout pseudosuchian evolution. Interpreting the absence of scleral ossicles as multiple independent losses in the numerous lineages without them is a considerably less parsimonious scenario. Yet, the morphology, composition and location within the orbit of scleral ossicles in pseudosuchians are indistinguishable from those of other amniote taxa that retain the feature. Therefore, we conclude that scleral ossicles were likely lost early in pseudosuchian history, possibly near the origin of the clade. However, members of *Pseudosuchia* retained the ability to develop scleral ossicles. It is not clear if members of *Crocodylia* still retain this ability to develop scleral ossicles.

2.3. Further considerations of skeletal elements in the orbit and the use of the anatomical term palpebral

The term “palpebral” has previously been applied to any bony element in the dorsal portion of the orbit in members of *Reptilia* including: squamates, crocodylians, pterosaurs, birds and ornithischian dinosaurs (Romer 1956; Coombs 1972; Lee 1997; Clark *et al.* 2000; Mayr 2005; Wang *et al.* 2007; Maidment & Porro 2010). The use of the same term to describe somewhat similar features across a broad range of taxa implies homology, but the homology of these features has never been explicitly tested. Furthermore, a number of proposed synonyms are used interchangeably with palpebral, including the terms “supraorbital,” and “supraciliary,” for any element in the dorsal portion of the eye. Given recent breakthroughs in understanding the palpebral of crocodylians (Vickaryous & Hall 2008), it is clear that not all osseous elements in the dorsal portion of the orbit develop the same way. For example, the palpebral of crocodylians forms from metaplastic ossification, like that of osteoderms (Vickaryous & Hall 2008), but this is different from the formation of supraorbitals in osteichthyan fishes, where the bones form from a cartilaginous precursor (Hall 2005). Although examining the development of the skull bones of an extinct taxon is impossible, we can utilise Patterson’s (1982) requirements for homology (similarity and congruence tests) to clarify the term palpebral. We propose restricting the term “palpebral” to the element that develops in a similar fashion to that of an osteoderm and resides in the upper eyelid (as in crocodylians). This is a considerably more refined definition of palpebral, but is similar to the original definition proposed by Peters (1964). Furthermore, it is our view that the terms “supraorbital,” and “supraciliary” should also be restricted to a particular group.

With this restricted definition of palpebral, it is clear that the term palpebral should not be applied to the structures across the orbits of ornithischians. In a comprehensive contribution examining the homology of the ornithischian “palpebral” across the entire clade, Maidment & Porro (2010) explicitly test the homology of the “palpebral(s)” of some ornithischian taxa with that of the variously named supraorbital(s) of other clades using Patterson’s (1982) homology tests. In short, they find that the “palpebral(s)” and supraorbital(s) of ornithischian clades are homologous. Their extensive and careful assessment of ornithischian “palpebral(s)” across the clade is welcomed, but in the end, the term “palpebral” is not appropriate for the orbital bone(s), although the first application of the term palpebral to that of the structure in some ornithischians was based on the

inferred homology of the palpebral to those of crocodylians (Gregory & Mook 1925). Using the same methodology for determining homology, we can reject the homology of the ornithischian “palpebral” and crocodylian palpebral, given that the element fails Patterson’s (1982) tests one (the morphology and connectivity differ) and three (the common ancestors of the two clades do not possess a “palpebral”). As a general recommendation, we advocate that ornithischian “palpebral” be renamed to further prevent future confusion.

3. Acknowledgements

We thank Sankar Chatterjee, Hans-Dieter Sues, Thomas Sulej, Patricia Holroyd, Wann Langston and Rainer Schoch for providing access to specimens under their care. Discussions with Randall Irmis, Christopher Brochu, Eric Wilberg, Eugenia Gold and Michael Vickaryous helped improve the manuscript. Wann Langston contributed to the discussion of the paper, provided useful publication, and access to rare specimens; his advice set us on the right track more than once. Critical reviews by James Clark and Christopher Brochu were instrumental to completing this paper. Jeffery Martz provided pictures of *Aetosaurus*. We thank James Clark for access to a cast of *Junggarsuchus* and pictures of the skull prior to full preparation.

4. References

- Alcober, O. 2000. Redescription of the skull of *Saurosuchus galilei* (Archosauria: Rauisuchidae). *Journal of Vertebrate Paleontology* **20**, 302–16.
- Andrade, M. B. & Bertini, R. J. 2008. Morphological and anatomical observations about *Mariliaosuchus amarali* and *Notosuchus terrestris* (Mesoeucrocodylia) and their relationships with other South American notosuchians. *Arquivos do Museu Nacional, Rio de Janeiro* **66**, 5–62.
- Andrade, M. B. & Hornung, J. J. 2011. A new look into the periorbital morphology of *Goniopholis* (Mesoeucrocodylia: Neosuchia) and related forms. *Journal of Vertebrate Paleontology* **31**, 352–68.
- Brochu, C. A. 1996. Closure of neurocentral sutures during crocodylian ontogeny: implications for maturity assessment in fossil archosaurs. *Journal of Vertebrate Paleontology* **16**, 49–62.
- Brochu, C. A. 2001. Progress and future directions in archosaur phylogenetics. *Journal of Paleontology* **75**, 1185–201.
- Brown, B. 1933. An ancestral crocodile. *American Museum Novitates* **638**, 1–4.
- Brown, B. & Schlaikjer, E. M. 1940. The structure and relationships of *Protoceratops*. *Annals of the New York Academy of Sciences* **40**, 133–266.
- Brusatte, S. L., Benton, M. J., Desojo, J. B. & Langer, M. C. 2010. The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). *Journal of Systematic Palaeontology* **8**, 3–47.
- Buffetaut, E. 1982. Radiation evolutive, paleoecologie et biogéographie des crocodiliens mesosuchiens. *Mémoires de la Société Géologique de France* **142**, 1–88.
- Burrow, C. J., Jones, A. S. & Young, G. C. 2005. X-ray microtomography of 410 million year old optic capsules from placoderm fishes. *Micron* **36**, 551–57.
- Butler, R. J., Brusatte, S. L., Reich, M., Nesbitt, S. J., Schoch, R. R. & Hornung, J. J. 2011. The sail-backed reptile ctenosauriscus from the latest Early Triassic of Germany and the timing and biogeography of the early archosaur radiation. *PLoS One* **6**, 1–28.
- Carvalho, I. D. S., Ribeiro, L. C. B. & Avilla, L. D. S. 2004. *Uberabasuchus terrificus* sp. nov., a new Crocodylomorpha from the Bauru Basin (Upper Cretaceous), Brazil. *Gondwana Research* **7**, 975–1002.
- Carvalho, I. D. S., Campos, A. D. C. A. & Nobre, P. H. 2005. *Baurusuchus salgadoensis*, a new Crocodylomorpha from the Bauru Basin (Cretaceous), Brazil. *Gondwana Research* **8**, 11–30.
- Carvalho, I. D. S., Vascocellos, F. M. D. & Tavares, S. A. S. 2007. *Montealtosuchus arrudacamposi*, a new peirosaurid crocodile (Mesoeucrocodylia) from the Late Cretaceous Adamantina Formation of Brazil. *Zootaxa* **607**, 35–46.
- Chatterjee, S. 1985. *Postosuchus*, a new thecodontian reptile from the Triassic of Texas and the origin of tyrannosaurs. *Philosophical Transactions of the Royal Society, London B* **309**, 395–460.

- Clark, J. M. 1986. *Phylogenetic relationships of the crocodylomorph archosaurs*. PhD Dissertation, University of Chicago, USA. 556 pp.
- Clark, J. M. 2012. A new shartegosuchid crocodyliform from the Upper Jurassic Morrison Formation of western Colorado. *Zoological Journal of the Linnean Society* **163**(Supplement 1), S152–72.
- Clark, J. M., H. D. Sues, and D. S. Berman 2000. A new specimen of *Hesperosuchus agilis* from the Upper Triassic of New Mexico and the interrelationships of basal crocodylomorph archosaurs. *Journal of Vertebrate Paleontology* **20**, 683–704.
- Clark, J. M., Xing, X., Forster, C. A. & Wang, Y. 2004. A Middle Jurassic 'sphenosuchian' from China and the origin of the crocodylian skull. *Nature* **430**, 1021–24.
- Clark, J. M. & Sues, H.-D. 2002. Two new basal crocodylomorph archosaurs from the Lower Jurassic and the monophyly of the Sphenosuchia. *Zoological Journal of the Linnean Society* **136**, 77–95.
- Colbert, E. H. 1946. *Sebecus*, representative of a peculiar suborder of fossil Crocodylia from Patagonia. *Bulletin of the American Museum of Natural History* **87**, 221–70.
- Colbert, E. H. 1961. The Triassic reptile *Poposaurus*. *Fieldiana* **14**, 59–78.
- Colbert, E. H. & Mook, C. C. 1951. The ancestral crocodylian *Protosuchus*. *Bulletin of the American Museum of Natural History* **97**, 143–82.
- Coombs, W. P. J. 1972. The eyelid of *Euoplocephalus*. *Journal of Paleontology* **46**, 637–50.
- Coulombre, A. J. 1965. The eye. In De Haan, R. L. & Ursprung, H. (eds) *Organogenesis*, 219–51. New York: Holt.
- Crompton, A. W. & Smith, K. K. 1980. A new genus and species of crocodylian from the Kayenta Formation (Late Triassic?) of Northern Arizona. In Jacobs, L. L. (ed.) *Aspects of Vertebrate History*, 193–217. Flagstaff: Museum of Northern Arizona Press.
- Crush, P. J. 1984. A Late upper Triassic sphenosuchid crocodylian from Wales. *Palaeontology* **27**, 131–57.
- Curtis, E. L. & Miller, R. C. 1938. The sclerotic ring in North American birds. *Auk* **55**, 225–43.
- Dal Sasso, C. & Maganuco, S. 2011. *Scipionyx sammiticus* (Theropoda: Compsognathidae) from the Lower Cretaceous of Italy: osteology, ontogenetic assessment, phylogeny, soft tissue anatomy, taphonomy and palaeobiology. *Memorie della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* **37**, 1–281.
- Daly, E. 1973. A Lower Permian vertebrate fauna from southern Oklahoma. *Journal of Paleontology* **47**, 562–89.
- Desojo, J. B. & Baez, A. M. 2007. Cranial morphology of the Late Triassic South American archosaur *Neoaetosauroides engaeus*: evidence of aetosaurian diversity. *Palaeontology* **50**, 267–76.
- Estes, R., De Queiroz, K. K. & Gauthier, J. 1988. Phylogenetic relationships within Squamata. In Estes, R. K. & Pregill, G. (eds) *Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp*, 119–281. Stanford, California: Stanford University Press.
- Ewer, R. F. 1965. The anatomy of the thecodont reptile *Euparkeria capensis* Broom. *Philosophical Transactions of the Royal Society, London, Series B* **248**, 379–435.
- Fernandez, M. & Gasparini, Z. 2008. Salt glands in the Jurassic metriorhynchid *Geosaurus*: implications for the evolution of osmoregulation in Mesozoic marine crocodyliform. *Naturwissenschaften* **95**, 79–84.
- Fiorelli, L. E. & Calvo, J. O. 2007. The first "protosuchian" (Archosauria: Crocodyliformes) from the Cretaceous (Santonian) of Gondwana. *Arquivos do Museu Nacional, Rio de Janeiro* **65**, 417–59.
- Fraas, O. 1877. *Aëtosaurus ferratus* Fr. Die gepanzerte Vogel-Escheaus dem Stubensandstein bei Stuttgart. *Württembergische naturwissenschaftliche Jahreshefte* **33**, 1–22.
- Franz-Odenaal, T. A. & Vickaryous, M. K. 2006. Skeletal elements in the vertebrate eye and adnexa: morphological and developmental perspectives. *Developmental Dynamics* **235**, 1244–55.
- Gasparini, Z., Chiappe, L. M. & Fernandez, M. 1991. A new senonian peirosaurid (Crocodylomorpha) from Argentina and a synopsis of the South American Cretaceous crocodylians. *Journal of Vertebrate Paleontology* **11**, 316–33.
- Gasparini, Z., Pol, D. & Spalletti, L. 2006. An unusual marine crocodyliform from the Jurassic–Cretaceous boundary of Patagonia. *Science* **311**, 70–73.
- Gauthier, J. A., Nesbitt, S. J., Schachner, E., Bever, G. S. & Joyce, W. G. 2011. The bipedal stem crocodylian *Poposaurus gracilis*: inferring function in fossils and innovation in archosaur locomotion. *Bulletin of the Peabody Museum of Natural History* **52**, 107–26.
- Georgi, J. A. & Krause, D. W. 2010. Postcranial axial skeleton of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* **30**(Supplement 1), 99–121.
- Gordon, I. & Shapiro, H.A. 1975. *Forensic medicine: a guide to principles*. New York: Churchill Livingstone. 396 pp.
- Gower, D. J. 1999. The cranial and mandibular osteology of a new rauisuchian archosaur from the Middle Triassic of southern Germany. *Stuttgarter Beitrage zur Naturkunde Serie B (Geologie und Palaeontologie)* **280**, 1–49.
- Gower, D. J. 2000. Rauisuchian archosaurs (Reptilia, Diapsida): An overview. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **218**, 447–88.
- Gower, D. J. 2002. Braincase evolution in suchian archosaurs (Reptilia: Diapsida): Evidence from the rauisuchian *Batrachotomus kupferzellensis*. *Zoological Journal of the Linnean Society* **136**, 49–76.
- Gower, D. J. & Schoch, R. 2009. Postcranial anatomy of the rauisuchian archosaur *Batrachotomus kupferzellensis*. *Journal of Vertebrate Paleontology* **29**, 103–22.
- Gregory, W. K. & Mook, C. C. 1925. On *Protoceratops*, a primitive ceratopsian dinosaur from the Lower Cretaceous of Mongolia. *American Museum Novitates* **156**, 1–9.
- Hall, B. K. 2005. *Bones and Cartilage*. London: Elsevier Academic Press. 760 pp.
- Hall, M. I., Kirk, E. C., Kamilar, J. M. & Carrano, M. T. 2011. Comment on "Nocturnality in dinosaurs inferred from scleral ring and orbit morphology". *Science* **334**, 1641.
- Hill, R. V. 2005. Integration of morphological data sets for phylogenetic analysis of Amniota: the importance of integumentary characters and increased taxonomic sampling. *Systematic Biology* **54**, 530–47.
- Heckert, A. B. & Lucas, S. G. 2000. Taxonomy, phylogeny, biostratigraphy, biochronology, paleobiogeography and evolution of the Late Triassic Aetosauria (Archosauria: Crurotarsi). *Zentralblatt für Geologie und Paläontologie, Teil I Heft 11–12*, 1539–87.
- Irmis, R. B. 2007. Axial skeleton ontogeny in the parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs. *Journal of Vertebrate Paleontology* **27**, 350–61.
- Juul, L. 1994. The phylogeny of basal archosaurs. *Palaeontologia Africana* **31**, 1–38.
- Kofron, P. C. 1992. Status and habitats of the three African crocodiles in Liberia. *Journal of Tropical Ecology* **8**, 265–73.
- Larsson, H. C. E. & Sues, H.-D. 2007. Cranial osteology and phylogenetic relationships of *Hamadasuchus rebouli* (Crocodyliformes: Mesoeucrocodylia) from the Cretaceous of Morocco. *Zoological Journal of the Linnean Society* **149**, 533–67.
- Lee, M. S. Y. 1997. The phylogeny of varanoid lizards and the affinities of snakes. *Philosophical Transactions of the Royal Society, London B: Biological Sciences* **352**, 53–91.
- Li, C., Wu, X.-C., Cheng, Y.-N., Sato, T. & Wang, L. 2006. An unusual archosaurian from the marine Triassic of China. *Naturwissenschaften* **93**, 200–06.
- Long, R. A. & Ballew, K. L. 1985. Aetosaur dermal armor from the Late Triassic of southwestern North America, with special reference to the Chinle Formation of Petrified Forest National Park. *Museum of Northern Arizona Bulletin* **54**, 45–68.
- Long, R. A. & Murry, P. A. 1995. Late Triassic (Carnian and Norian) tetrapods from the southwestern United States *New Mexico Museum of Natural History and Science Bulletin* **4**. Albuquerque: New Mexico Museum of Natural History and Science. 254 pp.
- Maidment, S. C. R. & Porro, L. B. 2010. Homology of the palpebral and origin of supraorbital ossifications in ornithischian dinosaurs. *Lethaia* **43**, 95–111.
- Marinho, T. S. & Carvalho, I. D. S. 2009. An armadillo-like sphagesaurid crocodyliform from the Late Cretaceous of Brazil. *Journal of South American Earth Sciences* **27**, 36–41.
- Mayr, G. 2005. The postcranial osteology and phylogenetic position of the middle Eocene *Messelastur gratulator* Peters, 1994: a morphological link between owls (Strigiformes) and falconiform birds? *Journal of Vertebrate Paleontology* **25**, 635–45.
- Mehl, M. G. 1915. *Poposaurus gracilis*, a new reptile from the Triassic of Wyoming. *Journal of Geology* **23**, 516–22.
- Motani, R., Rothschild, B. M. & Wahl, W. 1999. Large eyeballs in diving ichthyosaurs. *Nature* **401**, 747.
- Nesbitt, S. J. 2003. *Arizonasaurus* and its implications for archosaur divergences. *Proceedings of the Royal Society of London, B* **270**(Supplement 2), S234–37.
- Nesbitt, S. J. 2005. The osteology of the Middle Triassic pseudosuchian archosaur *Arizonasaurus babbitti*. *Historical Biology* **17**, 19–47.
- Nesbitt, S. J. 2007. The anatomy of *Effigia okeeffeae* (Archosauria, Suchia), theropod convergence, and the distribution of related taxa. *Bulletin of the American Museum of Natural History* **302**, 1–84.

- Nesbitt, S. J. 2011. The early evolution of Archosauria: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History* **352**, 1–292.
- Nesbitt, S. J., Stocker, M. R., Small, B. J. & Downs, A. 2009. The osteology and relationships of *Vancleavea campi* (Reptilia: Archosauriformes). *Zoological Journal of the Linnean Society* **157**, 814–64.
- Nesbitt, S. J., Liu, J. & Li, C. 2011. A sail-backed suchian from the Heshangou Formation (Early Triassic: Olenekian) of China. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **101**(for 2010), 271–84.
- Nesbitt, S. J. & Norell, M. A. 2006. Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimid dinosaurs (Theropoda). *Proceedings of the Royal Society, London B* **273**, 1045–48.
- Nobre, P. H. & Carvalho, I. D. S. 2006. *Adamantinasuchus navae*: A new Gondwanan Crocodylomorpha (Mesoeucrocodylia) from the Late Cretaceous of Brazil. *Gondwana Research* **10**, 370–78.
- Novas, F. E., Pais, D. F., Pol, D., Carvalho, I. D. S., Mones, A., Scaferla, A. & Riglos, M. S. 2009. Bizarre notosuchian crocodyliform with associated eggs from the Upper Cretaceous of Bolivia. *Journal of Vertebrate Paleontology* **29**, 1316–20.
- Patterson, C. 1982. Morphological characters and homology. In Joysey, K. A. & Friday, A. E. (eds) *Problems of Phylogenetic Reconstruction. Systematics Association Special Volume 21*. London: Academic Press.
- Peters, J. A. 1964. *Dictionary of herpetology, a brief and meaningful definition of words and terms used in herpetology*. New York: Hafner Publication Company. 392 pp.
- Peyer, K., Carter, J. G., Sues, H.-D., Novak, S. E. & Olsen, P. E. 2008. A new suchian archosaur from the Upper Triassic of North Carolina. *Journal of Vertebrate Paleontology* **28**, 363–81.
- Pol, D., Turner, A. H. & Norell, M. A. 2009. Morphology of the Late Cretaceous crocodylomorph *Shamosuchus djadochtaensis* and a discussion of neosuchian phylogeny as related to the origin of Eusuchia. *Bulletin of the American Museum of Natural History* **324**, 1–103.
- Pol, D. & Gasparini, Z. 2009. Skull anatomy of *Dakosaurus andiniensis* (Thalattosuchia: Crocodylomorpha) and the phylogenetic position of Thalattosuchia. *Journal of Systematic Palaeontology* **7**, 163–97.
- Pol, D. & Norell, M. A. 2004. New gobiosuchid crocodyliform taxon from the Cretaceous of Mongolia. *American Museum Novitates* **3458**, 1–31.
- Pritchard, A. C., Turner, A. H., Allen, E. R. & Norell, M. A. In press. Osteology of a North American goniopholidid (*Eutretauranosuchus delfsi*) and palate evolution in Neosuchia. *American Museum Novitates*.
- Reig, O. A. 1959. Primeros datos descriptivos sobre nuevos reptiles arcosaurios del Triásico de Ischigualasto (San Juan, Argentina). *Revista de la Asociación Argentina de Geología* **13**, 257–70.
- Ritchie, A. 1968. New evidence on *Jamoytius kerwoodi* White, an important ostracoderm from the Silurian of Lanarkshire, Scotland. *Palaeontology* **11**, 21–39.
- Romer, A. S. 1956. *Osteology of the Reptiles*. Malabar, Florida: Kreiger Publishing Company. 772 pp.
- Romer, A. S. 1972. The Chafiáres (Argentina) Triassic reptile fauna. XIII. An early ornithosuchid pseudosuchian, *Gracilisuchus stipanicorum*, gen. et sp. nov. *Breviora* **389**, 1–24.
- Schachner, E., Manning, P. L. & Dodson, P. 2011. Pelvic and hindlimb myology of the basal archosaur *Poposaurus gracilis* (archosauria: Poposauroida). *Journal of Morphology* **272**(12), 1464–91.
- Schoch, R. R. 2007. Osteology of the small archosaur *Aetosaurus* from the Upper Triassic of Germany. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **246**, 1–35.
- Schmidt, K. P. 1941. A new fossil alligator from Nebraska. *Fieldiana: Geology* **8**, 27–32.
- Schmitz, L. & Motani, R. 2011. Nocturnality in dinosaurs inferred from scleral ring and orbit morphology. *Science* **332**, 705–08.
- Sereno, P. C. 1991. Basal archosaurs: phylogenetic relationships and functional implications. *Journal of Vertebrate Paleontology* **10**(supplement to 3), 1–53.
- Sereno, P. C., McAllister, S. & Brusatte, S. L. 2005. TaxonSearch: a relational database for suprageneric taxa and phylogenetic definitions. *PhyloInformatics* **8**, 1–21.
- Sereno, P. C. & Larsson, H. C. E. 2009. Cretaceous crocodyliforms from the Sahara. *ZooKeys* **28**, 1–143.
- Sertich, J. J. W. 2011. *Basal Mesoeucrocodylian Phylogenetics and Cretaceous Gondwanan biogeography*. Unpublished Dissertation, Stony Brook University, NY, USA.
- Sertich, J. J. W. & Groenke, J. R. 2010. Appendicular skeleton of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* **30**(supplement 1), 122–53.
- Sill, W. D. 1974. The anatomy of *Saurosuchus galilei* and the relationships of the rauisuchid thecodonts. *Bulletin of the Museum of Comparative Zoology* **146**, 317–62.
- Simpson, G. G. 1937. New reptiles from the Eocene of South America. *American Museum Novitates* **927**, 1–3.
- Small, B. J. 1998. The occurrence of *Aetosaurus* in the Chinle Formation (Late Triassic, USA) and its biostratigraphic significance. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* **5**, 285–96.
- Sues, H.-D., Olsen, P. E., Carter, J. G. & Scott, D. M. 2003. A new crocodylomorph archosaur from the Upper Triassic of North Carolina. *Journal of Vertebrate Paleontology* **23**, 329–43.
- Sulej, T. 2005. A new rauisuchian reptile (Diapsida: Archosauria) from the Late Triassic of Poland. *Journal of Vertebrate Paleontology* **25**, 78–86.
- Trotteyn, M. J., Desojo, J. B. & Alcober, O. A. 2011. Nuevo material postcranio de *Saurosuchus galilei* Reig (Archosauria: Crurotarsi) del Triásico Superior del centrooeste de Argentina. *Ameghiniana* **48**, 605–20.
- Turner, A. H. & Buckley, G. A. 2008. *Mahajangasuchus insignis* (Crocodyliformes: Mesoeucrocodylia) cranial anatomy and new data on the origin of the eusuchian-style palate. *Journal of Vertebrate Paleontology* **28**, 382–408.
- Turner, A. H. & Sertich, J. J. W. 2010. Phylogenetic history of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* **30**(supplement 1), 177–236.
- Vickaryous, M. K. & Hall, B. K. 2008. Development of the dermal skeleton in *Alligator mississippiensis* (Archosauria, Crocodylia) with comments on the homology of osteoderms. *Journal of Morphology* **269**, 398–422.
- Vickaryous, M. K. & Sire, J.-Y. 2009. The integumentary skeleton of tetrapods: origin, evolution, and development. *Journal of Anatomy* **214**, 441–64.
- Walker, A. D. 1961. Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus*, and their allies. *Philosophical Transactions of the Royal Society of London* **244**, 103–204.
- Walker, A. D. 1968. *Protosuchus*, *Proterochampsia*, and the origin of phytosaurs and crocodiles. *Geological Magazine* **105**, 1–14.
- Wang, X., Kellner, A. W. A., Zhou, Z. & Campos, D. D. A. C. 2007. A new pterosaur (Ctenochasmidae, Archaeopterygiformes) from the Lower Cretaceous Yixian Formation of China. *Cretaceous Research* **28**, 245–60.
- Weinbaum, J. C. 2011. The skull of *Postosuchus kirkpatricki* (Archosauria: Paracrocodyliformes) from the Upper Triassic of the United States. *PaleoBios* **30**, 18–44.
- Weinbaum, J. C. & Hungerbühler, A. 2007. A revision of *Poposaurus gracilis* (Archosauria: Suchia) based on two new specimens from the Late Triassic of the southwestern U.S.A. *Paläontologische Zeitschrift* **81**(2), 131–45.
- Whiteside, D. I. & Marshall, J. E. A. 2008. The age, fauna and palaeoenvironment of the Late Triassic fissure deposits of Tytherington, South Gloucestershire, UK. *Geological Magazine* **145**, 105–47.
- Witmer, L. M. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In Thomason, J. J. (ed.) *Functional morphology in vertebrate paleontology*, 19–33. Cambridge, UK: Cambridge University Press.
- Wu, X.-C., Russell, A. P. & Cumbaa, S. L. 2001. *Terminonaris* (Archosauria: Crocodyliformes): new material from Saskatchewan, Canada, and comments on its phylogenetic relationships. *Journal of Vertebrate Paleontology* **21**, 492–514.
- Zaher, H., Pol, D., Carvalho, A. B., Riccomini, C., Campos, D. D. A. C. & Nava, W. 2006. Redescription of the cranial morphology of *Mariliaosuchus amarali*, and its phylogenetic affinities (Crocodyliformes, Notosuchia). *American Museum Novitates* **3512**, 1–40.
- Zhang, F. K. 1975. A new thecodont *Lotosaurus*, from the Middle Triassic of Hunan. *Vertebrata Palasiatica* **13**, 144–47.