A NEW METRIORHYNCHOID (CROCODYLOMORPHA, THALATTOSUCHIA) FROM THE MIDDLE JURASSIC OF OREGON AND THE EVOLUTIONARY TIMING OF MARINE ADAPTATIONS IN THALATTOSUCHIAN CROCODYLOMORPHS

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ABSTRACT—Metriorhynchid thalattosuchians represent the most extreme archosaurian adaptation to the marine realm. Metriorhynchids possess aquatic adaptations throughout the skeleton. These adaptations were so extensive that some have suggested that they lost the ability to move on land, yet their evolutionary timing remains unresolved. The closest relatives of the metriorhynchoids, the teleosauroids, lack these aquatic adaptations, and the earliest metriorhynchoids are known exclusively from cranial material. Here I describe a partial skull with associated forelimb elements of a new marine crocodylomorph, Zoneait nargorum, gen. et sp. nov., of Aalenian–Bajocian age from the Snowshoe Formation of east-central Oregon. Phylogenetic analysis identifies Zoneait as the sister taxon to Metriorhynchidae. It possesses a derived skull with orbits that are more laterally directed and prefrontals that are more expanded than in other basal metriorhynchoids. The preserved forelimb elements are less derived. The humerus is elongate in comparison with that of other metriorhynchids. The ulna is slightly reduced in length and flattened but resembles the teleosauroid condition more so than the plate-like element of metriorhynchids. This suggests that marine adaptations in metriorhynchoids were acquired in mosaic fashion, with modifications of the skull preceding forelimb reduction, with this forelimb reduction occurring first in the zeugopodial elements, prior to reduction of the humerus. This evolutionary timing has important implications for the transition from nearshore ambush predation to pelagic open-marine predation in Thalattosuchia, suggesting that adaptations related to prey detection and capture preceded the locomotor adaptations that allowed these organisms to fully invade the oceans.

http://zoobank.org/urn:lsid:zoobank.org:pub:407671AC-E785-4831-9FB3-560965F15A2E

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Thalattosuchia is a unique group of crocodylomorphs highly adapted to the marine environment. Although thalattosuchians are among the earliest described fossil taxa (e.g., von Sömmering, 1816; Cuvier, 1824; Geoffroy Saint-Hilaire, 1825), they received only sporadic scientific attention until relatively recently. A renewed interest in the group, driven in part by reexamination of known materials (e.g., Pierce and Benton, 2006; Wilkinson et al., 2008; Jouve, 2009; Pierce et al., 2009a, 2009b; Young and Andrade, 2009; Cau and Fantò, 2011; Young et al., 2011a, 2011b, 2012, 2013; Parrilla-Bel et al., 2013; Cau, 2013) and new fossil discoveries (e.g., Frey et al., 2002; Buchy et al., 2006; Gasparini et al., 2006), has revolutionized our understanding of the morphology, ecology, and evolution of Thalattosuchia. Yet, a lack of well-preserved basal members of the group including postcranial material has hindered our understanding of evolutionary patterns during the early history of Thalattosuchia; in particular, the evolutionary timing of the marine adaptations that make thalattosuchians unique among archosaurs.

The two major groups within Thalattosuchia (Teleosauroidea and Metriorhynchoidea) possess differing levels of adaptation to the marine environment (Buffetaut, 1982). Teleosauroids show few adaptations to a marine lifestyle and are found in estuarine and coastal deposits. Based on their morphology, teleosauroids have been characterized as nearshore marine ambush predators, hunting in a manner similar to the extant Indian gharial (Msarane, 1987; Hua and Buffrenil, 1996).

Metriorhynchoids, in particular the metriorhynchids, possess the most extensive marine adaptations of any archosaurian lineage (Langston, 1973). The skull and body were highly streamlined, with paddle-like hind limbs and extremely reduced, hydrofoil-like forelimbs (Fraas, 1901, 1902; Ammon, 1905; Arthaber, 1906; Auer, 1907; Andrews, 1913, 1915). Metriorhynchoids with preserved caudal vertebrae show a modest hypocercal tail fin similar to basal ichthyosaurs (von Meyer, 1831; Fraas, 1901, 1902; Andrews, 1913, 1915; Young et al., 2010), preserved as a carbon film in one specimen (Rhachiosaurus gracilis, NHMUK R3498; Ammon, 1905; Young et al., 2010:fig. 5a). Other features that indicate adaptation to a pelagic lifestyle include the loss of dermal armor, lateral orientation of the orbits (Andrews, 1913; Buffetaut, 1982; Pierce and Benton, 2006; Young et al., 2010), and development of an enlarged preorbital salt gland (Fernández and Gasparini, 2000, 2008; Gandola et al., 2006; Fernández and Herrera, 2009; Young et al., 2010; Leardi et al., 2012; Herrera et al., 2013). Additionally, histological study of Metriorhynchus superciliosus has shown that the skeleton, especially the skull, is greatly lightened, demonstrating a highly cancellous texture (‘osteoporotic-like’ sensu Hua and Buffrenil, 1996). A similar lightening of the skeleton is seen in some cetaceans, ichthyosaurs, and mature plesiosaurs (Buffrenil and Schoevaert, 1988; Buffrenil and Mazin, 1990; Wiffen et al., 1995; Hua and Buffrenil, 1996). This suite of characteristics has led researchers to reconstruct metriorhynchids as passive or active pelagic
predators with a high degree of resource partitioning (e.g., Pierce et al., 2009b; Andrade et al., 2010; Young et al., 2012). However, the timing of acquisition of the adaptations allowing metriorrhynchoids to invade the pelagic realm have remained unresolved due to lack of postcranial materials from the basal-most members.

Until recently, phylogenetic relationships within Thalattosuchia were poorly known. Much recent work has focused on elucidating the relationships of metriorrhynchoids (e.g., Young and Andrade, 2009; Young et al., 2010, 2012, 2013; Cau and Fanti, 2011; Parrilla-Bel et al., 2013); yet, relationships between the tel eosaurus have received less attention (but see Mueller-Töwe, 2006; Jouve, 2009; Young et al., 2012; Parrilla-Bel et al., 2013). Additionally, the relationship between Thalattosuchia and other crocodylomorphs remains contentious (see Clark [1994], Jouve [2009], and Pol and Gasparini [2009] for discussions of this issue). One potential factor driving this uncertainty involves the highly derived morphology of thalattosuchians. A better understanding of the basal-most members, potentially retaining plesiomorphic character states, may help resolve this issue.

New fossil material of a thalattosuchian crocodylomorph from the Middle Jurassic Snowshoe Formation of east-central Oregon has recently been discovered. This specimen represents the earliest known occurrence of Metriorrhynchoidea (Late Aalenian–Early Bajocian), one of only a few known from North America (Gasparini and Iturralde-Vinent, 2001; Frey et al., 2002; Buchy et al., 2008; Buchy, 2008), and the first found from the northern Pacific region. The new material includes the first associated postcranial elements from an early metriorrhynchoid thalattosuchian. Investigation of the morphology of this new taxon will help shed light on the plesiomorphic morphology of metriorrhynchoids and aid in reconstructing the phylogenetic relationships of Thalattosuchia. This will provide a framework upon which to investigate hypotheses of evolutionary timing of marine adaptations.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, New York, U.S.A.; BSPG, Bayerische Staatsammlung für Paläontologie und Geologie, Munich, Germany; CNRST-SUNY, Centre National de Recherche Scientifique et Technologique du Mali–Stony Brook University, Stony Brook, New York, U.S.A.; FMNH, Field Museum of Natural History, Chicago, Illinois, U.S.A.; GPF, Geologisches-Paläontologisches Institut der Universität Tübingen, Tübingen, Germany; IRSNB, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; MLP, Museo de La Plata, La Plata, Argentina; MNHN, Muséum National d’Histoire Naturelle, Paris, France; NMNH, National History Museum, London, U.K.; OXUF, Oxford University Museum, Oxford, U.K.; SUI, University of Iowa Paleontology Repository, Iowa City, Iowa, U.S.A.; SMNH, Saskatchewan Museum of Natural History, Regina, Saskatchewan, Canada; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; UH, Urveltmuseum Hauff, Holzmaiden, Germany; UOMNH, University of Oregon Museum of Natural and Cultural History, Eugene, Oregon, U.S.A.; USNM, United States National Museum, Smithsonian Institution, Washington, D.C., U.S.A.

Anatomical Abbreviations—a sq, articulation surface for squamosal; a qu, articulation surface for quadrate; ang, angular; art, articular; bo, basioccipital; bsp, basiphenoid; car, internal carotid foramen; ccf, crista cranii frontalis; den, dentary; div 2, diverticulum 2; dpe, deltopectoral crest; dvs, dorsal venous sinus; ec, endocranial cavity; ect, ectoptyerygoid; emc, exposed middle ear cavity; epx, epoxy; exo, exoccipital; fm, foramen magnum; fr, frontal; fs, frontal suture; IV, Trigeminal fossa; ic, internal carotid canal; ie, inner ear; imp, impression of bone on matrix; itf, infratemporal fenestra; jf, jugal foramen; jug, jugal; lu, left humerus; lrap, left retroarticular process; l ul, left ulna; lac, lacrimal; lcf, lacrimal foramen; lfc, canal for the lacrimal foramen; lpsf, laterosphenoid; max, maxilla; meuc, median eustachian canal; nas, nasal; nphd, nasopharyngeal duct; ns, neural spine; orb, orbit; pat, palatine; pal dp, dorsal process of the palatine; pat f, fractured surfaces of the palatine; par, parietal; pmx, premaxilla; pm, postorbital; prf, prefrontal; pro, prootic; pty, pterygoid; qu, quadrate; r ul, right ulna; rib, dorsal rib; sa, surangular; sgl, salt gland; so, supraoccipital; sof, suborbital fenestra; sp, splenial; sq, squamosal; ss, sulcus septalis; stf, supra-temporal fenestra; t, tooth; tc, temporal canal; V, trigeminal (V) foramen; vom, vomer; Xl, hypoglossal (XII) foramen.

GEOLOGIC SETTING

The new material comes from the Weberg Member of the Snowshoe Formation that crops out extensively in east-central Oregon near the towns of Suplee and Izee (Crook and Grant counties) and is geologically part of the Izee terrane (Orr et al., 1992). The Izee terrane represents a forearc basin filled with marine calcareous sandstones, sandy calcilutites, and siltslides up to 65 m thick (Taylor, 1988). This terrane was accreted to the North American plate during the Late Jurassic. The Weberg Member of the Snowshoe Formation is recognized only around Suplee and Izee, Oregon. Invertebrate fossils, particularly ammonoids, are common in the Weberg Member, although other vertebrate material has previously been recovered, including crocodylomorph material (Buffetaut, 1979; Stricker and Taylor, 1989).

The Weberg Member has been interpreted as a tropical warm-water, high-energy, and relatively shallow marine environment. The western part of the Snowshoe Formation has been dated with some precision using ammonite biostratigraphy (Inlay, 1973). The Weberg Member represents the latest Aalenian and most of the Bajocian stages of the Middle Jurassic (Taylor, 1982, 1988). The material comes from the lower portion of the Weberg member, suggesting that it is either latest Aalenian or earliest Bajocian in age (R. Rosé, pers. comm., May 2012). However, precise placement awaits a detailed biostratigraphic analysis.

SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA Walker, 1790
THALATTOSUCHIA Fraas, 1901
METRIORRHYNCHOIDEA Fitzinger, 1843 (sensu Young and Andrade, 2009)
ZONEA T NÄRGÖRUM, gen. et sp. nov. (Figs. 1–13)

Holotype—USNM F39539, partial skull, mandibular fragments, two teeth, two hemi, two ulnae, eight partial dorsal ribs, and one caudal vertebra.

Referred Specimens—USNM 244292 (block containing a partial rostrum and mandible), USNM 244476 (antorbital region of cranium), USNM 256441 (proximal end of right humerus), USNM 256442 (vertebra), USNM 256443 (vertebra), USNM 256444 (vertebra): previously referred to ‘Telesauroidea indet.’ by Buffetaut (1979), from the Weberg Member of the Snowshoe Formation (Aalenian–Bajocian) near Suplee, Oregon, the same region in which the holotype was discovered.

Etymology—‘Large tooth of NARG,’ named after the fearsome water monster ‘Zone Ait Ghahnay’ of Kiowa legend. Zoneait (pronounced ‘zone-eight’) means ‘large tooth’ in Kiowa. The specific epithet is from NARG (North American Research Group), members of which discovered, excavated, and largely prepared the specimen.

Diagnosis—A metriorrhynchoid crocodylomorph possessing large, ‘D’-shaped supratemporal fenestrae and fully laterally directed orbits (autapomorphies indicated by an asterisk, *). The dorsoventrally thickened prefrontal is ovate in dorsal view and...
strongly overhangs the anterior third of the orbit. The posterior roof of the parietal is raised dorsally relative to frontal and tapers sharply anteriorly. The ventral surface of the frontal possesses a ventrally projecting ridge on the roof of the nasal cavity. The lacrimal possesses a large foramen at the dorsoventral midpoint, anterior to the orbital rim. The humeri are elongate (≈75% of the basal width of the skull) and lack curvature. The humeral shaft contributes approximately two-thirds of its total length. The deltopectoral crest is present, but reduced, and occurs at approximately one-third of the length of the humerus. The ulnae are shortened relative to the humerus but retain the plesiomorphic thalattosuchian ‘J’ shape. The distal half of the ulna is very shortened proximodistally and flattened relative to the proximal half.

Differential Diagnosis—Among non-metriorhynchid metriorhynchoids, *Zoneait* differs from *Teleidosaurus calvadosii* in possessing orbits that are fully directed laterally, an expanded prefrontal that overhangs the orbit, a lacrimal that does not contribute to the dorsal margin of the orbit, a completely superficial postorbital bar, and broader supratemporal fossae. *Zoneait* differs from *Eoneustes bathonicus* in possessing prefrontals that are more laterally expanded to overhang the orbit, a dorsal surface of the parietal elevated relative to the frontal, and supratemporal fenestrae that are less expanded anteroposteriorly. *Zoneait* differs from *Eoneustes gaudryi* in possessing more greatly expanded and dorsoventrally thickened prefrontals and a frontal-nasal suture that is strongly posteromedially curved and anteroposteriorly elongate. *Zoneait* differs from Metriorhynchidae (sensu Young and Andrade, 2009) in possessing a relatively elongate retroarticular process in which the articular ascends sharply as it approaches the glenoid fossa anteriorly, similar to *Teleidosaurus calvadosii*, prefrontals that show a less marked lateral expansion, a humerus that is elongate and nearly circular in cross-section (not flattened), and an elongate ulna similar to Teleosauroida.

**DESCRIPTION**

**General Form and Preservation**

*Holotype*—The material is preserved in three dimensions with no obvious postmortem deformation. The partial skull is preserved in two blocks. Much of the surface of the cranial bones is not preserved, especially on the occipital surface, palatines, and interorbital region. The right block includes the entire right orbit and supratemporal fenestra. The left block terminates posteriorly at the anterior border of the supratemporal fenestra and includes the anterior portion of the supratemporal fossa. The entire snout region is not preserved.

The majority of the mandible is not preserved, but portions of both the left and right retroarticular processes are present. The right is preserved in two blocks. Much of the surface of the cranial bones is not preserved, especially on the occipital surface, palatines, and interorbital region. The right block includes the entire right orbit and supratemporal fenestra. The left block terminates posteriorly at the anterior border of the supratemporal fenestra and includes the anterior portion of the supratemporal fossa. The entire snout region is not preserved.

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Other preserved elements include dorsal rib fragments, both humeri, a complete right and a partial left ulna, a partial
of the frontal. The second block (USNM 244292) contains rostral
autapomorphic ventrally projecting ridge on the ventral surface
damaged. This specimen shares with the holotype specimen the
as with the new specimen, most of the surface bone is missing or
prefrontal pillars and some palatal and rostral bones. However,
internal mold of the antorbital region of the snout, including the
ments in particular. The first block (USNM 244476) contains an
preserved in the new, holotype specimen, focusing on two ele-
identical to the new material in all overlapping elements, and is
Snowshoe Formation by Buffetaut (1979). This material is nearly
'teleosaurid' were described from the Weberg Member of the
rhynchids, but due to the disarticulated nature of the specimen,
osteoderms may have been absent in this taxon, as in metrio-
caudal vertebra, and two isolated teeth. No osteoderms were
recovered among the postcranial materials. This suggests that
osteoderms may have been absent in this taxon, as in metrio-
rhynchids, but due to the disarticulated nature of the specimen,
postcranial bones. Including partial premaxillae, maxillae, a
right dentary, and potentially a partial right splenial. The rostral
bones are cleaved nearly along the horizontal plane, slightly
inclined from right to left. This fracture reveals the nasal pas-
sages and intersects the alveoli of the right maxilla. Because
the posterior dorsal surface is missing, the anterior extent of the
nasals is unclear, but they undoubtedly did not reach the
premaxillae.

The referred proximal right humerus (USNM 25644; Fig. S1)
shows the same morphology as the humeri in UOMNH F39539,
including the slightly reduced deltopectoral crest (differing from
other known thalattosuchians) and a humeral shaft that is circular
in cross-section (differing from Metriorhynchidae). Three verte-
brae (USNM 256442, USNM 256443, USNM 256444) are here
tentatively referred to Z. nargorum. The complete caudal
(USNM 256442; Buffetaut, 1979:fig. 2f, g) is consistent with the
morphology of the preserved caudal of UOMNH F39539, and the
other two vertebrae were associated with USNM 256442. How-
ever, these elements are not diagnostic among thalattosuchians.

**Comment on the Stricker and Taylor Specimen**—An abstract
was presented at the 1989 Society of Vertebrate Paleontology
Annual Meeting (Stricker and Taylor, 1989) regarding a thalat-
tosuchian specimen from a similar location in the Weberg Mem-
er of the Snowshoe Formation. This specimen, as described by
these authors, is very similar to the currently described material
and may represent the same species. Unfortunately, the speci-
men was never formally described nor reposited in a public insti-
tution. In spite of inquiries by the author, this specimen appears
to be no longer available for scientific study.

**Cranial Openings**

**Orbits**—Both the left and right orbits are preserved in some
fashion (Figs. 1–3). The right orbit retains complete ventral and
posterior borders, whereas the left orbit possesses full dorsal and
anterior borders. Thus, the entire orbit can be described. The
orbits are ovoid, being slightly longer anteroposteriorly than
dorsoventrally. They are directed fully laterally, with the ventral
margin slightly lateral to the dorsal margin. The anterior one-
third of the orbit is overhanging a lateral expansion of the pre-
frontal. No sclerotic ossicles are preserved; however, given the
disarticulated nature of the skeleton, this cannot be used as evi-
dence against the presence of these thin, fragile bones.

**Postnasal Fenestrae**—The right postnasal fenestra is pre-
served and visible in USNM 244476. It is ‘D’-shaped, with the
curved margin facing laterally (Fig. 4). The dorsolateral, dorsal,
dorsomedial margins are formed by the prefrontal. The palat-
tine forms the medial (and presumably ventral) margin, whereas
the lacrimal forms the lateral margin. This fenestra is larger than
in dyrosaurs (e.g., *Rhabdognathus aslerensis*—CNRS-SUNY-
190; *Dyrosaurus phosphaticus*—Jouve, 2005; *Congosaurus bequaerti*—Jouve and Schwarz, 2004) but similar in size to other
metriorhynchoids (e.g., *Metriorhynchus superciliosus*—MNHN
8922).

**Suborbital Fenestrae**—The suborbital fenestrae are partially
preserved on both sides, but both lack the anterior border
(Fig. 5). They taper sharply anteriorly between the palatines and
maxillae and are interpreted to extend approximately to the
anterior margin of the orbit. The suborbital fenestrae terminate
posteriorly at the posterior border of the orbit and are formed by
roughly equal contributions from the ectopterygoid and pterygoid.

**Supratemporal Fenestrae**—The complete right and partial left
supratemporal fenestrae are preserved (Fig. 1). They are ‘D’-
shaped, with a straight lateral margin. The fenestrae are slightly
longer than wide and possess broad fossae along the anterior,
medial, and posterior margins. The supratemporal fenestrae are
slightly larger than the orbit (approximately 1.15 times the length).

**Infratemporal Fenestrae**—The dorsal and anterior borders of the right infratemporal fenestra are preserved (Fig. 3). It appears to be anteroposteriorly shorter than the supratemporal fenestra (terminating prior to the anterior limit of the supratemporal fenestra) and tapers towards its anterior margin.

**Internal Choana**—The internal choana does not seem to be preserved. Parts of the palatines are preserved between the suborbital fenestrae. The posterior-most limit of the palatines could represent the anterior border of the choana, but it does not correspond closely in location or shape with that of other metriorhynchosids.

**Otic Aperture**—The right otic aperture is partially preserved, but the lateral-most portion has been eroded away (Fig. 3). The otic canal is ‘D’-shaped from lateral view, with a straight posterior margin and differs greatly from that of *Maledictosuchus ricaensis* in which the otic canal is dorsoventrally elongate and anteriorly inclined (Parrilla-Bel et al., 2013). The otic canal is mediolaterally elongate as in all thalattosuchians due to the postmortem dorsoventral crushing of the skull. The posterior process of the otic canal is ‘D’-shaped from lateral view, with a straight posterior margin and differs greatly from that of *Maledictosuchus ricaensis* in which the otic canal is dorsoventrally elongate and anteriorly inclined (Parrilla-Bel et al., 2013). The otic canal is mediolaterally elongate as in all thalattosuchians due to the postmortem dorsoventral crushing of the skull. The posterior process of the otic canal is ‘D’-shaped from lateral view, with a straight posterior margin and differs greatly from that of *Maledictosuchus ricaensis* in which the otic canal is dorsoventrally elongate and anteriorly inclined (Parrilla-Bel et al., 2013). The otic canal is mediolaterally elongate as in all thalattosuchians due to the postmortem dorsoventral crushing of the skull.

**Maxilla**—Only the posteroventral process of the maxilla is preserved on both the right and left halves of the skull (Figs. 4, 5). They extend ventrally to approximately the anteroposterior midpoint of the orbit. These processes do not contact the ectopterygoids. A small portion of the posterior palatal process of the maxilla is present on the right side (Fig. 4), forming the anterolateral border of the suborbital fenestra.

Portions of both maxillae are preserved in USNM 244292 and USNM 244476. The dorsal surface of the right and left maxillae is preserved in USNM 244292 (Fig. 6). The maxillae form an elongate and slender rostrum that broadens slightly posteriorly. Most of the surface bone is damaged except for the anterodorsal portion of the left maxilla, where no sculpture is visible. The right maxilla has been cleaved such that the roots of at least 12 alveoli are visible in dorsal view.

The posterior portion of the palatal processes of the left and right maxillae is preserved in USNM 244476 (Fig. 4). These contact the palatines medially and form the floor of diverticulum 2 of Fernández and Herrera (2009). Diverticulum 2 may be homologous with the cavichonchal recess of modern crocodylians. However, more detailed investigation is required to test this hypothesis.

**Lacrimal**—The vertically oriented lacrimal is preserved on the left side of the skull (Fig. 2). This element forms most of the anterior margin of the orbit and is quite broad mediolaterally. Ventrolaterally, the lacrimal is sutured with the jugal, forming the anterovelar corner of the orbital margin. The anterior process is not preserved. Portions of the right and left lacrimals are preserved in USNM 244476. The lacrimal forms the lateral margin of the postnasal fenestrae. Anteromedially, the lacrimal contacts the dorsal process of the palatines and forms the lateral wall of the nasal cavity and the dorsolateral wall of diverticulum 2.

A foramen is present on the lateral surface of the lacrimal of the holotype specimen just below the dorsoventral midpoint, slightly anterior to the orbital margin and opens posterolaterally (Fig. 2). This could represent the nasolacrimal duct. The canal extends anteromedially and may be visible along the fractured anterior surface of the lacrimal. However, the highly cancellous nature of skull bones hampers this identification (Fig. 7). In modern crocodylians, the posterior opening of the nasolacrimal duct lies very near the prefrontal-lacrimal suture along the inner rim of the orbit. The location and orientation of the foramen in *Zoneait* is rather different; thus, the two ducts may not be homologous.

It is more likely that this foramen accommodates an enlarged vascular canal. Although this area is not well known among metriorhynchosids due to the postmortem dorsoventral crushing of most specimens, a few specimens are of note. *Eoneustes gaudryi* (NHMUK R3353) possesses a similarly sized foramen on the lacrimal, but the opening is nearer the lacrimal-prefrontal suture, more consistent with the nasolacrimal duct of extant crocodylians. A well-preserved *Metriorhynchus moreli* specimen (NHMUK R3900) shows a group of small foramina in this location, rather than a single large opening as in *Zoneait*, but also lacks any openings clearly homologous with the nasolacrimal duct. A better understanding of these lacrimal canals requires additional material from undistorted metriorhynchosid specimens.

**Prefrontal**—Only the left prefrontal is preserved. This element is ovoid in dorsal aspect. It forms much of the dorsal margin of the orbit, reducing the contribution of the frontal to the orbit. It is expanded laterally to overlap the anterior third of the orbit (Fig. 1). The lateral-most margin of the prefrontal overhangs is between the maxillae. The posterior process of the premaxilla does not contact the nasals, because they are excluded by the midline contact between the maxillae as in other thalattosuchians.
slightly damaged, so the full extent of the overhang is not entirely clear, but the overhang is dorsoventrally thickened. The ventral process is inset from the lateral margin, extending ventrally to contact the lacrimal. The prefrontal forms approximately the dorsal quarter of the anterior margin of the orbit. Laterally, the suture between the prefrontal and lacrimal is flush with the orbital rim, not elevated as a ridge as in some metriorhynchids. It is, however, raised along the anterior wall of the orbit. The medial suture with the frontal is angled anteromedially, continuing as an arc into the medial suture with the posterior process of the nasal. The anterior process of the prefrontal is missing; thus, its extent is unclear. Due to sediment infilling, the prefrontal pillar is not visible in this specimen, but the exposed portion is mediolaterally broad, forming the anterodorsal wall of the orbit.

Ventral to the prefrontal is a large open region within the nasal cavity (Fig. 7). This cavity is slightly expanded laterally into the lateral expansion of the prefrontal. In other metriorhynchids, this region housed an enlarged nasal salt gland (Fernández and Gasparini, 2008; Fernández and Herrera, 2009). Although no trace of the gland itself is preserved (as in natural endocasts of Cricosaurus araucanensis; Fernández and Gasparini, 2008), the large open space is consistent with its presence and is nearly identical to the morphology of this region in computed tomography (CT) scans of C. araucanensis (Fernández and Herrera, 2009:fig. 4D).

The right and partial left prefrontal pillars are preserved in USNM 244476. The descending process of the prefrontal is mediolaterally broad, forming the anterodorsal wall of the orbit and the dorsal margin of the postnasal fenestra. The prefrontal pillars are divided by a dorsoventrally elongate opening for the olfactory nerves. This opening is very wide dorsally and narrows to approximately one-third its maximum width ventrally. This architecture is rather different from most crocodyliforms in which this opening is a similar width both dorsally and ventrally (e.g., Rhadobdognathus aslerensis—CNRST-SUNY-190; Brochu et al., 2002; and in modern crocodylians—Iordansky, 1973).

As preserved, the prefrontal pillar does not contact the palate, although it comes quite close to the vomer and the dorsal process of the palate. Unfortunately, the incomplete preservation and lack of well-preserved surface bone make this interpretation tenuous. The preserved portion of the descending process is much closer to the palate than in Pelagosaurus typus (NHMUK OR32599), in which it clearly does not contact the palate. Thus, it is possible that the prefrontal pillar of Zoneait contacted the palate as in more derived forms such as Metriorhynchus superciliosus (MNHN 8922; Wenz, 1968).

Frontal—Much of the frontal is preserved, although most of the surface bone is missing (Fig. 1). The frontal is cruciform, with anterior, posterior, and lateral processes. It is very broad between the orbits, forming part of the medial border of the
The anterior process is partly preserved and extended beyond the anterior border of the orbit. Anteriorly, the anterior process of the frontal is wedge-shaped, separating the posterior processes of the nasals; however, due to breakage, the anterior extent is unclear.

Posterolaterally, the frontal contacts the postorbital. The suture begins near the midpoint of the orbit and extends posterolaterally, forming a sharp 'V' shape, overlapping the postorbital as in all metriorhynchids. These lateral processes are at near right angles to the main body of the frontal, similar to *Eoneustes gaudryi* (NHMUK R3353) and distinctly different from the highly acute angle in *Dakosaurus* (Gasparini et al., 2006; Pol and Gasparini, 2009) and *Cricosaurus* (e.g., MLP 72-IV-7-1; Young and Andrade, 2009:fig. 5c). The suture with the postorbital continues posteromedially into the supratemporal fossa, but breakage prevents following it further. The posterior process is only partly preserved. It clearly formed part of the interfenestral bar, meeting the parietal posteriorly, but this region is missing and has been filled in with epoxy.

Due to the vertical fracture anterior to the orbit, the cross-section of the frontal at this level is visible (Fig. 7). In cross-section, it is evident that this and other bones in this region of the skull exhibit an osteoporotic-like state, as in *Metriorhynchus superciliosus* (Hua and Buffrenil, 1996). Additionally, the ventral margin of the anterior process is ventrally expanded, forming a pronounced ridge along the roof of the nasal cavity. This ridge has not been observed in other metriorhynchoids, although sampling is limited to specimens broken to expose the ventral surface of the frontal (e.g., *Suchodus durobrivensis*—NHMUK R2618; *Metriorhynchus superciliosus*—NHMUK R2036, NHMUK R2049) or CT scans (e.g., *C. araucanensis*; Fernández and Herrera, 2009). A dorsoventrally aligned linear feature is present in this ridge, reaching the dorsal-most preserved portion of the anterior process (Fig. 5). This could potentially represent a ventrally open frontal suture, indicating that the frontals were not completely fused as in most crocodyliforms. A similar partly closed frontal suture is also present in a CT-scanned...
**Pelagosaurus typus** skull (BSPG 1890 I5; Mueller-Töwe, 2006). However, the highly cancellous nature of the bone makes this interpretation uncertain.

The anterior process of the frontal is preserved in USNM 244476 (Fig. 4). This specimen also shows a distinct ventral ridge extending from the frontal into the nasal cavity. The anterior process is quite long relative to other metriorhynchoids, clearly extending well anterior to the orbits and apparently further than the prefrontals (Fig. 4C). It is possible that the frontal would have been overlain by the nasals in this region, but the lack of surface bone makes this interpretation uncertain. A dorsoventrally aligned linear feature is also present within the ventral ridge of this smaller individual. Again, this could be an open frontal suture, but the same osteoporo tic-like texture hinders confident identification. Between the prefrontal pillars, the frontal forms the roof of the opening for the olfactory nerves and bears a shallow crista cranii frontalis (Fig. 4A).

**Parietal**—The parietal is also partly preserved, but an anteroposterior fracture splits it just left of the sagittal plane (Fig. 1). It extends from the postorbital into the nasal cavity. The anterior process is extensive and laps onto the lateral surface of the squamosal. The posterior process forms much of the lateral margin of the supratemporal fenestra and is much longer anteroposteriorly than the squamosal. The posterior process is dorsoventrally tall and mediolaterally thin (Fig. 3). Ventrally, the posterior process forms the dorsal margin of the infratemporal fenestra. Based on the preserved articulation surface on the lateral portion of the squamosal, it appears that the postorbital would have contacted the quadrate, but much of the bone is damaged in this region.

The ventral process forms the lateral surface of the postorbital bar and lies lateral to the jugal as in all thalattosuchians (Clark, 1986). The postorbital bar is anteroposteriorly broad and mediolaterally flattened and oriented slightly anteroventrally to postero-odorsally. The ventral process forms the dorsal half of the posterior margin of the orbit. Externally, the suture between the postorbital and jugal is posteroventrally directed and ends at the anterior corner of the infratemporal fenestra (Fig. 3). The ventral margin of the postorbital is much more dorsally located than in teleosaurids where it often reaches or nearly reaches the ventral margin of the skull, and slightly more dorsal than that of *Teleidosaurus calvadosii* (Jouve, 2009). The postorbital bar is vertically oriented and entirely superficial, showing no medial inset as in several metriorhynchids (e.g., *Dakosaurus andiensis*; Pol and Gasparini, 2009) and most crocodyliforms (see Jouve [2009] for a discussion of postorbital bar morphology among thalattosuchians). However, because the superficial portion of the posterior region is missing, I cannot exclude the possibility of it being slightly inserted posteriorly in *T. calvadosii.*

**Squamosal**—A partial right squamosal is preserved (Fig. 1). As preserved, the squamosal is ‘L’-shaped, with anterior and mediolateral processes. The anterior process is sutured with the postorbital, forming the posterolateral margin of the supratemporal fenestra. The medial process articulates with the parietal. This process is dorsoventrally tall, contributing to the steep posterior...
margin of the supratemporal fenestra. The medial-most portion of the squamosal is not preserved, but the articulation surface on the parietal shows that it would have extended medially, forming the lateral and dorsolateral margins of the temporal canal. Ventrally, the medial process contacts the exposed middle ear canal where the quadrate would have articulated with the squamosal. Medially, between the anterior and medial processes, the squamosal slopes into the supratemporal fenestra, forming a broad posterolateral supratemporal fossa. In lateral view, dorsal to the external otic aperture, the squamosal can be seen to overlie the quadrate and is excluded from the aperture (Fig. 3). Because much of the exoccipital has been eroded away, the squamosal forms a broad portion of the preserved occipital surface.

**Jugal**—Portions of both the left and right jugals are preserved, although neither is complete. The jugal is triradiate, with anterior, dorsal, and posterior processes. The preserved portion of the anterior process of the left jugal extends anterior to the orbit and is sutured dorsally with the lacrimal (Fig. 2). The ventral surface of this fragment preserves a concave articulation surface for the suture with the posterior process of the maxilla. The anterior-most portions of the jugals are not preserved, thus the anterior extent is unknown. The right jugal is preserved from the anterior border of the orbit to the anterior border of the infra-temporal fenestra (Fig. 3). The jugal forms the entire lateral border of the orbit is in this region flattened, with the external surface oriented ventrolaterally.

Posterior to the orbit, much of the lateral surface of the dorsal process is overlain by the descending process of the postorbital. Thus, the jugal lies medial to the postorbital within the postorbital bar and contributes to the posterior margin of the orbit. Ventromedially, just anterior to the postorbital bar, the jugal is sutured with the ectopterygoid (Fig. 5). Ventrally, this suture begins near the midpoint of the orbit and extends posteriorly, ending at the posterior margin of the orbit. In dorsal view, a large vascular foramen is present in the jugal lateral to the midpoint of the suture with the ectopterygoid.

The posterior process is not well preserved. Posterior to the postorbital bar, remnants of the jugal form the ventral border of the infratemporal fenestra. A smooth surface preserved in the matrix indicates that the medial surface of the jugal in this region was mediolaterally flattened, and not rod-like as in many thalattosuchians (Fig. 3).

**Palatine**—Fragmentary portions of the left and right palatines are preserved. The palatines clearly met at the midline, forming the floor of the nasopharyngeal duct (Figs. 4, 5, 7). In ventral view, large portions of the palatines are visible between the suborbital fenestrae, ending just posterior to the posterior process of the maxilla (Fig. 5). However, this margin appears broken, and the palatines likely extended posteriorly to form the anterior margin of the internal choana as in other thalattosuchians. The palatines appear to possess a linear array of pits just lateral to the midline suture between the two elements. This feature is shared with many metriorhynchids and may be related to the palatomaxillary grooves characteristic of thalattosuchians. However, the ventral surface of the palatines appears damaged, at least on the left side, making this interpretation uncertain. The palatines form the medial border of the suborbital fenestrae.

In anterior view, the palatines contribute to separations of the nasal cavity (Fig. 5). At the lateral extent of the palatines, a process extends dorsolaterally, forming the lateral wall of the nasopharyngeal duct, separating it from diverticulum 2 of Fernández and Herrera (2009). Along the medial contact between the palatines, a small dorsal process extends to meet the descending process of the vomer, contributing to the median septum between the nasopharyngeal ducts.

**Ectopterygoid**—The complete right ectopterygoid is preserved (Fig. 5). The ectopterygoid is an hourglass-shaped element oriented anterolaterally to posteromedially and concave ventrally. The ectopterygoid forms the posterolateral margin of the suborbital fenestra. Laterally, it has a broad, curved suture with the jugal. This suture extends posteriorly to the level of the postorbital bar. However, the ectopterygoid does not contact the
postorbital (because the postorbital forms the lateral portion of the postorbital bar). The anterior extent of the suture with the jugal does not appear to reach the posterior process of the maxilla, being separated by 1.5 cm, although there is some damage in this region.

The medial portion of the ectopterygoid is oriented ventromedially. It underlaps the pterygoid, covering its ventrolateral surface. In ventral view, the exposed suture is a broad curve oriented anteromedially to posterolaterally. The ectopterygoid does not extend to the torus transiliens.

Pterygoid—Portions of both pterygoids are preserved, including the lateral process of the right and part of the anterior process of the left (Fig. 5). Laterally, it contacts the ectopterygoid, extending posteriorly beyond and forming an anteroposteriorly short, but dorsoventrally tall torus transiliens. The anterior margin of the lateral process forms the posteromedial border of the suborbital fenestra. The posterior margin is concave anteriorly. Medially, the pterygoid is inclined dorsoconically. The preserved portion would likely have formed the lateral margin of the large depression posterior to the internal choana.

The anterior process of the pterygoid is visible on the posterior surface of the block containing the left orbit. This thin projection forms the roof and lateral wall of the nasopharyngeal duct, contacting the vomer and dorsal process of the palatines anteriorly. The roof of the nasopharyngeal duct is gently concave ventrally and lacks a ventrally projecting septum, which would have divided the internal choana.

Vomer—The vomer is visible anteriorly where fractures have cleaved the skull in the transverse plane. Anteriorly (at the level of the anterior margin of the orbit), the vomer is visible as a thin ‘Y’-shaped element dividing the nasopharyngeal duct. Dorsally, two smaller curved, sheet-like projections rest along the side of the vomer. Based on CT scans of the well-preserved *C. arauca-nensis* skull (Fernández and Herrara, 2009), these sheets were likely extensions of the dorsolateral processes that would have formed the roof of the nasopharyngeal duct in this region. The posterior extension of the vomerine septum of the nasopharyngeal duct is unknown. But based on what is visible, it does not appear to have extended to the internal choana.

The vomer is also preserved in USNM 244476 (Fig. 4). Anteriorly, the vomer is a small ‘Y’-shaped element with a broad ventral contact with the palatines. This represents the anterior-most portion of the primary choana. As the vomer proceeds posteriorly, it develops an elongate ventral process, becoming ‘Y’-shaped, and dividing the nasopharyngeal ducts. At the level of the anterior margin of the orbits, the vomer is strongly ‘Y’-shaped, with the ventral process slightly expanded ventrally at the contact with the palatines. The dorsolateral processes possess a laterally directed shelf. This shelf appears to have articulated with the dorsal processes of the palatine, completely enclosing the nasopharyngeal ducts. The vomer forms the ventral surface of the sulcus septalis, unlike in other crocodyliforms (e.g., *Dyrosaurus phosphaticus*; Jouve, 2005).

**Chondrocranium**

**Laterosphenoid**—The laterosphenoid is partially preserved on the right side (Fig. 1). The anterior region, including the capitate process, is not preserved. The posterior region forms the lateral wall of the anterior portion of the braincase. It abuts the prootic posteriorly and is not sutured with the quadrate. The suture with the prootic is elevated, forming a slight, dorsoventrally oriented crest. This crest is interpreted as separating the attachment areas for the M. pseudotemporalis superficialis (anteriorly) and M. adductor mandibulae externus profundus (posteriorly) (Holliday and Witmer, 2009; Fernández et al., 2011). The laterosphenoid forms the anterior and anterodorsal border of the trigeminal foramen (Fig. 5). Its ventral extent and contact with the basicranial bone is not well preserved.

**Prootic**—The right and partial left prootics are preserved. The right prootic is widely exposed on the lateral surface of the braincase (Fig. 1) as in other thalattosuchians (Wenz, 1968; Clark, 1986). It also contributes to the posterior wall of the supratemporal fenestra and forms the medial portion of the ventral border of the external carotid canal. It is sutured dorsally with the parietal. Anteriorly, it contacts the laterosphenoid immediately dorsal to the trigeminal foramen. The prootic forms the posterodorsal and posterior and ventral margins of the trigeminal foramen (Fig. 5). Posterodorsal and posterior to the trigeminal foramen, the prootic possesses articulation surfaces where the quadrate would have abutted the braincase.

Part of the left prootic is visible where the braincase is nearly hemisected (Fig. 8). Sutures on this surface are rather unclear, but the prootic appears to form the anterodorsal third of the otic capsule as in extant crocodylians. It also encloses the trigeminal fossa.

**Basisphenoid**—The base of the skull is missing, but part of the basisphenoid is present on the left and right sides. On the right side, the basisphenoid is visible at the ventral margin of the skull (Fig. 5). Posterodorsally it articulates with the prootic and anterodorsally with the laterosphenoid. Posteriorly it articulates with the basioccipital. Much of the posterior region possesses articulation surfaces for the quadrate.

On the left side, the basioccipital is hemisected, showing some of its internal morphology (Fig. 8). Two canals are visible piercing the basisphenoid. The dorso-most canal lies just ventral to the dorsal suture with the prootic. This is interpreted as the internal carotid canal. Ventral and slightly medial to this is another...
canal that is slightly taller dorsoventrally. Based on the position, this canal is interpreted as the medial eustachian canal.

**Basioccipital**—The right half of the basioccipital is preserved as a thick element forming the floor of the foramen magnum. In posterior view, it is dorsoventrally taller than the foramen magnum (Fig. 9). However, the ventral-most portion is not preserved; thus, it is not clear if well-developed basioccipital tubera were present as in other thalattosuchians. The posterior surface is missing, including the occipital condyle. The basioccipital articulates laterally with the exoccipital and anteriorly with the basisphenoid. It forms the posterior floor of the endocranial cavity (Fig. 8).

**Exoccipital**—The exoccipitals are partly preserved on the damaged occipital surface of the skull (Fig. 9). The exoccipitals meet above the foramen magnum, separating the supraoccipital from its dorsal margin. They appear to have been dorsoventrally expansive, but much of the posterior surface has been eroded away. Two foramina pierce the preserved portion of the exoccipital. The first foramen lies lateral to the ventral border of the foramen magnum and is interpreted as the opening for the hypoglossal nerve (XII). Ventral and slightly lateral to this is a much larger foramen. This is interpreted as the opening for the internal carotid artery. The internal carotid foramen is large in all known metriorhynchids, much larger than the opening of most crocodyliforms. The exoccipital forms the posterolateral wall of the endocranial cavity. Within the braincase, it forms the posterior-most portion of the roof of the endocranial cavity (Fig. 8). It also contributes greatly to the posterior wall of the otic capsule as in extant crocodylians.

**Supraoccipital**—The supraoccipital is trapezoidal in occipital view, longer dorsally than ventrally (Fig. 9). It contacts the parietal dorsally and the exoccipitals laterally and ventrally. This bone would have formed the ventral border of the posttemporal fenestrae, but encrusting calcite makes the location of the fenestrae difficult to discern. The supraoccipital is visible in dorsal view but does not contribute to the skull roof. The supraoccipital forms the posteriormost portion of the roof of the endocranial cavity (Fig. 8). Breakage through the bone demonstrates that it is solid, without a transverse canal joining the mastoid antra on either side of the skull. It also contributes to the anterodorsal portion of the otic capsule.

**Splanchnocranium**

**Quadrate**—Only a small portion of the quadrate is preserved (Figs. 3, 5). The main preserved portion forms the dorsal and anterior margins of the otic aperture. The articulation surface for the anteromedial process of the quadrate is present along the posteroventral region of the bone. The quadrate does not appear to have been strongly connected to the skull roof. The supraoccipital forms the posterior roof of the bone. The preserved portion of the retroarticular process suggests that it was more elongate than in most metriorhynchids, similar to *Teleidosaurus calvadosii* (NHMUK R2681). The dorsal half of the lateral face of the articular is sutured with the anterior process of the surangular. The ventral half is sutured with the angular.

**Dermal Bones of the Mandible**

**Dentary**—Part of the right dentary is preserved in USNM 244292 (Fig. 6). This portion appears to be part of the symphysis that has been cleaved near the mid sagittal plane. Anteriorly, the roots of at least four alveoli are visible. This suggests that the
teeth in this region were oriented dorsolaterally. Posteromedially, the dentary articulates with a narrow strip of bone interpreted as the splenial.

**Splenial**—A small strip of bone sutured with the posteromedial region of the dentary in USNM 244292 is here interpreted as the splenial (Fig. 6). Thus, the splenial contributed to the mandibular symphysis as in all other thalattosuchians, but its extent cannot be determined.

**Surangular**—The posterior-most portions of both surangulars are preserved (Figs. 10, 12A). The surangular abuts the articular medially and extends along the length of the retroarticular process. The left retroarticular process preserves the posterior-most region, and it appears that the surangular would have reached or nearly reached the posterior terminus of the retroarticular process (Fig. S2).

**Angular**—The posterior-most part of the right angular is preserved in articulation with the surangular and articular (Figs. 10, S2). The dorsal suture with the surangular is anteroposteriorly straight and extends along much of the length of the retroarticular process. On the retroarticular process, the angular is angled slightly ventromedially, forming the ventrolateral and ventral surfaces of the retroarticular process.

**Dentition**

Only two teeth are preserved. Neither is in articulation, so their location in the tooth row cannot be determined with confidence. One tooth is elongate with a deep root and is slightly mediolaterally compressed (Figs. 11, S3). It possesses strong anterior and posterior carinae that lack serrations. A second tooth crown is preserved (Fig. S4). This tooth is shorter and broader than the first. This is interpreted as a posterior tooth due to its blunter morphology and the similarity to posterior teeth in other metriorhynchoids. The second tooth lacks carinae, although this could be a preservational artifact because the enamel is poorly preserved. Several partial teeth are also preserved in USNM 244292. All teeth appear elongate and somewhat slender. Where the enamel is preserved, the teeth possess strong, unserrated anterior and posterior carinae similar to those of the new specimen.

**Axial Skeleton**

**Vertebrae**—Only a single caudal vertebra is preserved (Fig. 11). This vertebra is split along the sagittal plane. Due to the size of the vertebra in comparison with the other skeletal elements, this is interpreted as coming from the medial portion of the caudal series. It possesses a tall and narrow neural spine, which is dorsoventrally as tall as the anteroposterior length of the centrum and anteroposteriorly one-third the length of the
centrum. The anterior articular surface is not preserved. The posterior surface is fractured but appears to be amphicoelous.

**Ribs**—Nine fragmentary dorsal ribs are preserved and are generally similar to the ribs of extant crocodylians (Figs. 11, 12). Two of these can be identified as left middle dorsal ribs and possess very short diaphyses and elongate parapophyses. The distal ends of all ribs are missing. The body of the rib is ovoid in cross-section with a strong crest along the posterior margin, presumably to house the intercostal nerves and blood vessels. Similar to the vertebra, in cross-section the ribs do not appear to possess an osteoporotic-like state as in the ribs of at least some metriorhynchids (Hua and Buffrenil, 1996).

**Forelimb**

**Humerus**—Both humeri are complete (Figs. 12A, 13). The body of the humerus is essentially straight, with the proximal articulation surface very slightly offset posteriorly, unlike many crocodyliforms. The shaft of the humerus is very slightly bowed ventrally. The proximal articulation surface is anteroposteriorly broad and ovate. Approximately one-third of the length down the humerus, the deltopectoral crest projects anteroventrally (Fig. 13). The deltopectoral crest is relatively small and dorsoventrally thin but is much more robust than in metriorhynchids (e.g., *C. araucanensis*; Herrera et al., 2009). The distal articulation surface is quadrangular, with the anteroposterior axis slightly twisted ventrally relative to the proximal articulation surface.

The humerus is very elongate (21.6 cm) when compared with metriorhynchids. Metriorhynchids possess extremely shortened and flattened humeri. The shaft of the humerus of *Zoneait* is nearly circular in cross-section and shows no flattening. The shaft of the right humerus is missing much of the surface bone, exposing the interior. This bone appears to have the osteoporotic-like texture noted by Hua and Buffrenil (1996) in the hind limbs of *Metriorhynchus superciliosus*, suggesting that this texture may have been widespread in the limb bones.

**Ulna**—The complete right and partial left ulnae are preserved (Fig. 12B). The ulna is ‘J’-shaped, with a distinct bend occurring near the midpoint of the bone. The proximal half of the bone is very broad (~2.5 times the width of the distal half). The anterior margin of the ulna is gently curved from proximal to distal articulation surface. The posterior margin is nearly straight from the proximal surface to the midpoint, where a sharp bend occurs. The distal half of the posterior margin is slightly concave.

The proximal articulation surface is rather large and is twice the width of the distal articulation surface. The proximal surface is anteroposteriorly elongate, but relatively deep dorsoventrally, similar in size to the distal articulation surface of the humerus. The distal half of the bone is very flattened, with a small, ovoid distal articulation surface. The ulna is reduced relative to the humerus, being slightly less than half of its length (10.5 cm). In spite of this reduction, the ulna of *Zoneait* is large relative to those of metriorhynchids (e.g., *C. suevicus*—Fraas, 1902; *M. superciliosus*—Andrews, 1915), where the ulna and radius are reduced to plate-like elements to support a small, flipper-like forelimb.

**PHyLOGENETIC ANALYSIS**

**Taxon and Character Sampling**

To test the relationships of *Zoneait magerorum* with other thalattosuchian crocodylomorphs, I performed a phylogenetic analysis of 375 morphological characters scored for 76 taxa including 22 thalattosuchian species (10 teleosauroids, 12 metriorhynchoids). *Postosuchus kirkpatricki* was selected as the primary outgroup based on its completeness and putative sister-group relationship with Crocodylomorpha. The sphenosuchians *Sphenosuchus acutus* and *Dibothrosuchus* were also included. A sphenosuchian was not selected as the primary outgroup due to the uncertainty surrounding their relationships to each other and to crocodyliforms (e.g., Clark and Sue, 2002; Clark et al., 2004). Taxon sampling among thalattosuchians aimed to capture a broad sample of both teleosauroids and metriorhynchoids, including *Peihepsuchus teleorhinus*, a purportedly basal teleosauroid (Vignaud, 1995), and *Teleidosaurus calvadosii* and both species of *Eoneutes*, all basal metriorhynchoids. The character set was largely modified from the analysis of Jouve (2009). Character sampling was increased from previous analyses, with a focus on characters relevant to thalattosuchian relationships. The materials studied, complete character descriptions, and a nexus file of the phylogenetic data matrix are available in Supplementary Data.

**Parsimony Analysis**

The phylogenetic data set was analyzed in TNT version 1.1 (Goloboff et al., 2008) using equally weighted parsimony. Minimal length trees were found using a heuristic search with 1000 replicates of Wagner trees (with TBR branch swapping). Zero-length branches were collapsed if they lacked support under any of the minimal length trees (Rule 1 of Coddington and Scharff, 1994). All characters were treated as unordered.

**Nodal Support**

Nodal support and stability were assessed using Bremer support (Bremer, 1988, 1994) and jackknife resampling as applied to character data (Farris et al., 1996). Bremer support was calculated in TNT using the BREMER.RUN script. This script calculates the number of additional steps required to collapse a clade using negative constraints. Jackknife support was also calculated in TNT using 1000 replicates with the probability of independent character removal set at 0.37 (~e−1; as recommended in Farris et al., 1996). A heuristic search was employed with each replicate consisting of 10 random addition sequences, saving 10 trees per replicate. The resulting topologies were summarized using GC frequencies (difference between the frequency of recovering a given group and the most frequent contradictory group; Goloboff et al., 2003). GC frequencies are preferred over absolute frequencies (the standard method of counting frequencies in bootstrap and jackknife analyses) because they account for the evidence in support of a clade as well as the amount of evidence falsifying that clade.

**Results**

The parsimony analysis resulted in nine most parsimonious trees (MPTs) of length 1606 steps (Fig. 14; consistency index = 0.29, retention index = 0.68). In all MPTs, thalattosuchians are sister to Crocodyliformes, rather than falling within the group. This result comes in spite of the inclusion of numerous non-thalattosuchian long-snouted taxa (dyrosaurids and pholidosaurs) previously suggested to draw thalattosuchians crownward to the Mesoeucoauroidea (as recovered in some analyses: e.g., Sereno and Larson, 2009; Young and Andrade, 2009). Topologies uniting Thalattosuchia with the dyrosaurids and pholidosaurs (the ‘longirostrine clade’) require nine additional steps. Monophyly of Thalattosuchia is robustly supported by a jackknife index of 99 and Bremer support of 14.

Relationships among major crocodyliform groups are identical to previous iterations of this matrix (e.g., Wilberg, 2009, 2012) and similar to other published hypotheses (with the exception of the monophyly of Protosuchia). This analysis recovered a
FIGURE 14. Strict consensus of nine most parsimonious trees of length 1606 steps (consistency index = 0.29; retention index = 0.68). Numbers above nodes are GC jackknife frequencies; numbers below nodes are Bremer support values. Thalattosuchia is shaded in gray.
monophyletic Protosuchia and Notosuchia (excluding the peirosaurids), but neither of these clades is particularly well supported (Fig. 14). This analysis robustly supports the sister-taxon relationship between Elasmosuchus and the pholidosaur/dyrosaurid clade, rather than with Stelosaurus as originally proposed (Lapparent de Broin, 2002). Similar to other analyses of crocodyliform relationships, many of the nodes forming the trunk of the tree lack robust support, suggesting that additional taxon and character sampling could dramatically alter the structure of the tree and thus our understanding of crocodyliform evolution.

Within Thalattosuchia, Teleosauridae is recovered as monophyletic, with two Liassic species of Steneosaurus sister to all other teleosaurids (Fig. 15). The genus Steneosaurus is polyphyletic and in need of taxonomic revision (as suggested also by the analyses of Mueller-Töwe, 2006; Jouve, 2009; Young et al., 2012; Parrilla-Bel et al., 2013). Pelagosaurus typos, a thalattosuchian of controversial affinity (see Pierce and Benton, 2006), is here found nested with teleosaurids, sister to 'Steneosaurus' larteti. Platypterus multisericbulatus is recovered as the sister taxon to Steneosaurus bollensis.

Zoneait nargorum is robustly recovered as the sister taxon to Metriorhynchidae, congruent with previous results (Wilber, 2009; Young and Andrade, 2009; Young et al., 2010, 2012; Cau and Fanti, 2011; Parrilla-Bel et al., 2013). Three unambiguous synapomorphies unite Zoneait with Metriorhynchidae: dorsal margin of the orbit 'V'-shaped in dorsal view (248-1); lacrimal not visible in dorsal view (305-1); and prefrontal overhang greatly enlarged (>10% of its width; 351-1).

The three species previously attributed to Teleidosaurus (including Eoneustes) are not recovered as a monophyletic group. However, the topology recovered differs from that of Jouve (2009) or Young and Andrade (2009; and subsequent studies utilizing the matrix of Young). Eoneustes borthonicus and T. calvadosii are recovered as sister taxa. Jouve (2009) recovered T. calvadosii as the basal-most metriorhynchoid and the two species of Eoneustes as a paraphyletic assemblage at the base of Metriorhynchidae, whereas Eoneustes borthonicus and E. gaudryi were recovered as sister taxa by Young and Andrade (2009). The relationships between Teleidosaurus and Eoneustes are not strongly supported and are likely to change with the addition of new taxa or characters. Only one additional step is required to make Eoneustes form a paraphyletic grade at the base of Metriorhynchidae, whereas two additional steps are required to place E. borthonicus as sister to E. gaudryi. Unfortunately the holotypes (and only known material) of both E. borthonicus and T. calvadosii have been lost. Teleidosaurus calvadosii exists only as a plastotype (NHMUK R2681), whereas E. borthonicus must be coded from the original description (Mercier, 1933). New material would help greatly in resolving their relationships.

Metriorhynchus is also recovered as paraphyletic (Fig. 15). This genus was also determined to be paraphyletic by Young and Andrade (2009), and these authors subsequently reassigned many members of Metriorhynchus to other genera (Young et al., 2010). Their generic assignments are followed here. However, the relationships recovered here are quite different. Species previously assigned to Metriorhynchus included in this analysis form a paraphyletic grade leading to the geologically later-occurring members of Cricosaurus and Dakosaurus. Young and Andrade (2009) recovered a divide between species of Metriorhynchus with elongate slender snouts (more closely related to Cricosaurus: Metriorhynchidae) and those with shorter, taller snouts (more closely related to Dakosaurus: Geosaurinae). The current analysis requires an additional four steps to place Gracilinuastes leedsii and M. superficilus (the slender-snouted species) with Cricosaurus and Suchodus durobrivensis and Purransaurus casa-miquelai (the short-snouted species) with Dakosaurus, as reported by Young and Andrade (2009). Relationships between the metriorhynchid species are not robustly supported in this analysis, and taxon sampling of metriorhynchoids is much lower than in Young and Andrade (2009). Additional taxon and character sampling is necessary to address the issue and to fully test the phylogenetic hypothesis of Young and Andrade (2009; and subsequent analyses based on their data set).

**DISCUSSION**

**Zoneait nargorum** is the oldest known metriorhynchoid, coming potentially from the Aalenian (minimally earliest Bajocian). Phylogenetic analysis places it as the sister taxon of Metriorhynchidae (sensu Young and Andrade, 2009). It possesses orbits that are directed laterally, rather than dorsally (the plesiomorphic condition for Thalattosuchia). As the basal-most metriorhynchid with preserved limb bones, Zoneait offers insights into the evolutionary timing of the extreme morphological changes in the forelimbs of metriorhynchoids. Zoneait retains an elongate humerus, unlike any other known metriorhynchoid. The ulna is reduced but retains the plesiomorphic ‘J’ shape of thalattosuchians, rather than the flattened polygonal plate of metriorhynchids.

**Evolution of Aquatic Lifestyle in Crocodylomorphs**

The position of thalattosuchians as the sister group to Crocodyliformes impacts numerous evolutionary hypotheses, including the number of times the group has become adapted to an aquatic lifestyle. Crocodyliforms are generally seen as semiaquatic predators similar to extant crocodilians. However, outside of Neosuchia, many groups are much more cursorial and adapted to a terrestrial lifestyle, including protosuchians (e.g., Colbert and Mook, 1951; Osmólska et al., 1997; Wu et al., 1997; Pol and Norrell, 2004a, 2004b; Pol et al., 2004) and notosuchians (e.g., Garparini, 1971; Pol, 2005; Fiorelli and Calvo, 2008; Sereno and Larsson, 2009; Turner and Sertich, 2010). These taxa lack the specializations for aquatic life seen in extant crocodilians. If thalattosuchians are members of the ‘longirostrine clade’ (as in Garparini et al., 2006; Turner and Buckley, 2008; Jouve, 2009; Pol and Garparini, 2009), this suggests that the ancestral ecology of
crocodileiforms was terrestrial, and the transition to an aquatic lifestyle occurred only once, late in crocodileiform history (in neosuchians; Pol and Gasparini, 2009). However, if thalattosuchians are the sister group to Crocodyliformes, this implies at least two independent transitions to the aquatic realm.

This also raises an interesting point relating to the development of salt tolerance in marine crocodiles. If the closest relatives of the fully marine thalattosuchians were fully terrestrial (as in the phylogenetic hypothesis presented here), then it is not intuitive how these animals could have adapted to a saline environment so rapidly. There are no known thalattosuchian taxa showing an intermediate stage of fresh water ecology (as in pholcodosaurs and dyrosaurids); even known juveniles are found in marine environments so rapidly. There are no known thalattosuchian taxa showing an intermediate stage of fresh water ecology (as in pholcodosaurs and dyrosaurids). This transformation appears to have been stepwise, with the orbits becoming more laterally directed through the evolution of basal metriorhynchoids.

Evolutionary Timing of Marine Adaptations in Thalattosuchians

Based on the phylogenetic hypothesis presented here, adaptations in the skull relevant to the change in ecology from a coastal ambush predator (the condition present ancestrally for Thalattosuchia) to an open-water pelagic predator occur only once. The reorientation of the orbits from dorsally to laterally directed occurs in the lineage leading to Metriorhynchidae. This transformation appears to have been stepwise, with the orbits becoming more laterally directed through the evolution of basal metriorhynchoids. Teleidosaurus calvadosii possesses orbits that are directed dorsolaterally, whereas in E. gaudryi the orbits are directed nearly laterally. They are fully laterally directed in Zoneait and all metriorhynchoids. The timing of this reorientation of the orbits occurred prior to the dramatic reduction of the forelimb, as demonstrated by the forelimb of Zoneait, suggesting that the marine adaptations of metriorhynchids evolved in a mosaic fashion. The first stages involved cranial modifications: gradual reorientation of the orbits to a laterally directed position (possibly in response to a change in prey-capture strategy; Hua and Buffrenil, 1996) and the development of hypertrophied salt glands (Gandola et al., 2006; Fernández and Gasparini, 2008). Changes in forelimb morphology, including reduction in size and changes in shape, occurred in several stages following the cranial modifications.

The evolutionary timing of forelimb adaptations in thalattosuchians (based on the phylogeny presented here) follows such that reduction of humerus occurs twice independently, once in Metriorhynchidae and once in derived Steneosaurus (e.g., S. leedsi, S. durobrivensis; Fig. 16). However, the mode of reduction is different in each clade. In S. leedsi and S. durobrivensis, the humerus is reduced by shortening the proximal portion, moving the deltopectoral crest nearer to the posteriorly offset proximal articulation surface. The humerus in these species of Steneosaurus is not noticeably flattened and the distal region remains slender and rod-like. In metriorhynchids, the humerus initially becomes reduced, with little change in shape. The deltopectoral crest remains in approximately the same position (relative to Zoneait), but the entire element becomes greatly reduced and flattened. A second step in the modification of the forelimb occurs in the most derived forms, Cricosaurus and Dakosaurus, where the humerus is further reduced in length and expanded anteroposteriorly. Additionally, the shortening of the proximal region brings the deltopectoral crest very near the proximal articulation surface forming a continuous arc (see Wilkinson et al., 2008 and Herrera et al., 2009 for illustrations of this feature).

The reduction of the zeugopod (radius and ulna) occurs only once, in metriorhynchoids (Fig. 16). This transformation also occurs in a stepwise fashion. In Zoneait, the ulna becomes reduced relative to the humerus, with the distal portion becoming shorter. In Metriorhynchus, the distal portion of the ulna becomes so short that it no longer resembles a long bone and is reduced to a plate-like element slightly longer proximodistally than anteroposteriorly (NHMUK R4696; Andrews, 1915; Herrera et al., 2009). In Cricosaurus, the ulna becomes more reduced such that it is more developed anteroposteriorly than proximodistally (see Herrera et al., 2009, for a detailed discussion of Cricosaurus forelimbs).

The anteroposterior expansion of the proximal region of the ulna occurs twice independently, in metriorhynchoids and in the sister taxa S. durobrivensis and S. leedsi (Fig. 16). The proximal region of the ulna in both Zoneait and the derived species of Steneosaurus widens, making it more plate-like. However, in Zoneait, the distal portion of the ulna becomes flattened, whereas in Steneosaurus it remains circular in cross-section. The flattening becomes more pronounced still in metriorhynchids, where the zeugopodial elements are flattened into polygonal plates and is continued in the more derived clade containing Cricosaurus and Dakosaurus. The proposed developmental mechanism responsible for the change from normal long bone morphology (dumbbell shape) to the polygonal plates of metriorhynchids involves the loss of perichondral bone (Caldwell, 1997). This loss of perichondral bone in metriorhynchids is convergent with other marine reptiles in which limb elements are reduced to plates (e.g., ichthyosaurs, plesiosaurs; Caldwell, 1997; Herrera et al., 2009). It should be noted that the phylogenetic hypothesis of Young and Andrade (2009) implies independent forelimb reduction events within Metriorhynchidae: once in the lineage including Cricosaurus (Metriorhynchinae) and once in the lineage including Dakosaurus (Geosaurinae).

The origin of hypertrophied salt glands in metriorhynchoids was crucial for their shift to a fully pelagic lifestyle. In several instances, evidence of these glands have been preserved as detailed depressions on the inner surface of the prefrontals (in specimens of Metriorhynchus superciliosus; Gandola et al., 2006) or as natural endocasts (in specimens of Cricosaurus araucanensis; Fernández and Gasparini, 2000, 2008; Fernández and Herrera 2009; Herrera et al., 2013). However, as soft tissue structures, their preservation is rare. It is thus uncertain where in the evolution of metriorhynchoids these enlarged salt glands first appear. Zoneait possesses two features to suggest the presence of these glands. Because birds with well-developed salt glands show an increased diversion of carotid arterial blood flow to salt glands during periods of maximal salt excretion (Gerstberger, 1991), Herrera et al. (2013) suggested that the conspicuous enlargement of the carotid foramen and carotid canal in metriorhynchids may be correlated with the presence of an enlarged salt gland. Zoneait possesses a greatly enlarged carotid foramen (Fig. 9) and a large internal carotid canal (Fig. 8). Additionally, large open spaces exist ventral to the prefrontals in the region that houses the hypertrophied salt glands of Metriorhynchus and Cricosaurus. Additional evidence will be required to test this hypothesis.

Additional features related to marine life include the loss of heavy dermal armor, modifications to the pelvis, and the distinct tail bend supporting a caudal fin in derived metriorhynchids (Fraas, 1901; Andrews, 1913; Hua and Buffrenil, 1997; Young et al., 2010). Because maneuverability in aquatic organisms is limited by body mass and inertia (Webb and Buffrenil 1990; Hua and Buffrenil, 1996), the loss of osteoderms would act to decrease skeletal mass and increase maneuverability (Hua and
CONCLUSIONS

Zoneait represents the earliest known metriorhynchoid thalattosuchian and is the sister taxon to Metriorhynchidae. The preserved postcranial remains are the first known from a non-metriorhynchid metriorhynchoid and fill an important gap in our understanding of the early evolution of the group. This study adds to the growing body of work on thalattosuchian phylogenetics, increasing the taxon sampling of teleosauroids. Although Teleosauroidea was recovered as monophyletic in this study, the group is in need of taxonomic revision. Increased taxon sampling of teleosauroids should provide a better-supported phylogeny upon which to base these revisions. Steneosaurus in particular must be revised; however, the type species, S. megistorhynchus, was not included in the current study. Thus, it is unclear which taxa currently named Steneosaurus should retain the name.

The discovery of Zoneait allows us to fill in some important missing data in the evolution of the forelimb within metriorhynchoids. Based on this new material, it is clear that marine adaptations of metriorhynchoids appeared in a mosaic fashion, with streamlining of the skull and reorientation of the orbits preceding the locomotor adaptations that allowed these animals to fully exploit the marine realm.

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