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Archosaur Adductor Chamber Evolution: Integration of Musculoskeletal and Topological Criteria in Jaw Muscle Homology

Casey M. Holliday^{1,2*} and Lawrence M. Witmer¹

¹Department of Biomedical Sciences, College of Osteopathic Medicine, Ohio University, Athens, Ohio 45701

²Department of Biological Sciences, Ohio University, Athens, Ohio 45701

ABSTRACT The homologies of jaw muscles among archosaurs and other sauropsids have been unclear, confounding interpretation of adductor chamber morphology and evolution. Relevant topological patterns of muscles, nerves, and blood vessels were compared across a large sample of extant archosaurs (birds and crocodylians) and outgroups (e.g., lepidosaurs and turtles) to test the utility of positional criteria, such as the relative position of the trigeminal divisions, as predictors of jaw muscle homology. Anatomical structures were visualized using dissection, sectioning, computed tomography (CT), and vascular injection. Data gathered provide a new and robust view of jaw muscle homology and introduce the first synthesized nomenclature of sauropsid musculature using multiple lines of evidence. Despite the great divergences in cephalic morphology among birds, crocodylians, and outgroups, several key sensory nerves (e.g., n. anguli oris, n. supraorbitalis, n. caudalis) and arteries proved useful for muscle identification, and vice versa. Extant crocodylians exhibit an apomorphic neuromuscular pattern counter to the trigeminal topological paradigm: the maxillary nerve runs medial, rather than lateral to *M. pseudotemporalis superficialis*. Alternative hypotheses of homology necessitate less parsimonious interpretations of changes in topology. Sensory branches to the rictus, external acoustic meatus, supraorbital region, and other cephalic regions suggest conservative dermatomes among reptiles. Different avian clades exhibit shifts in some muscle positions, but maintain the plesiomorphic, diapsid soft-tissue topological pattern. Positional data suggest *M. intramandibularis* is merely the distal portion of *M. pseudotemporalis* separated by an intramuscular fibrocartilaginous sesamoid. These adductor chamber patterns indicate multiple topological criteria are necessary for interpretations of soft-tissue homology and warrant further investigation into character congruence and developmental connectivity. *J. Morphol.* 268:457–484, 2007. © 2007 Wiley-Liss, Inc.

KEY WORDS: archosaur; feeding; crocodylian; avian; reptile; homology; myology; jaw muscles; trigeminal nerve

Tracking the evolution of jaw adductor muscles through the diversity of amniote evolution has been one of the most perplexing pursuits in cephalic evolutionary morphology. Jaw muscles are integral characters in the development and epigenesis of the skull, promoting the formation and ossification of

the bones they contact (de Beer, 1937; Moss, 1968; Hurov, 1988; Herring, 1993; Kiliardis, 1996; Tarsitano et al., 2001). Jaw muscles power the feeding apparatus via complex, coordinated movements, and are critical to investigations of kinematic (Cleuren and DeVree, 1992; Zweers et al., 1994; Gussekloo and Bout, 2005), motor (Zweers, 1974; Van Drongelen and Dullemeijer, 1982; Gans and De Vree, 1986; Busbey, 1989; Cleuren et al., 1995), and bone strain (Ross and Metzger, 2004) patterns of the head during prey acquisition, handling, and ingestion. Jaw muscles are crucial to the success of an organism and are important adaptive characters that can be used to interpret feeding function in birds and crocodylians, as well as numerous extinct taxa (e.g., sauropods, ceratopsians, ornithopods) that are not represented by living groups today (e.g., Anderson, 1936; Haas, 1955, 1969; Ostrom, 1964; Rayfield et al., 2001).

Many broad, comparative myological studies were conducted in the early 20th century (Lakjer, 1926; Lubosch, 1933; Edgeworth, 1935; Kesteven, 1942–1945) to identify comparative patterns of the trigeminal musculature in Amniota, including archosaurs. Numerous data exist on the cephalic myology of crocodylians, primarily that of *Alligator mississippiensis* (Iordansky, 1964, 2000; Schumacher, 1973; Busbey, 1989), but also caimans (van Drongelen and Dullemeijer, 1982; Cleuren and De Vree, 1992) and longirostrine crocodylians (Endo et al.,

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*Correspondence to: Casey M. Holliday, Department of Anatomy and Pathology, Joan C. Edwards School of Medicine, Marshall University, 1542 Spring Valley Dr., Huntington, WV 25704-9398. E-mail: hollidayc@marshall.edu

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2002). Myological data of birds have been described in comparative works (e.g., Hofer, 1950; Stark and Barnikol, 1954), whereas other studies have focused on particular clades, such as Tinamiformes (Elzansowski, 1987), Anseriformes (Goodman and Fisher, 1962), Galloanserae (Zusi and Livezey, 2000), and Columbiformes (Bhattacharyya, 1980, 1989), or various species, such as ostrich (Webb, 1957), grebes (Zusi and Storer, 1969), cranes (Fisher and Goodman, 1955), cormorants (Dullemeijer, 1951), hummingbirds (Zusi and Bentz, 1984), and numerous others (see Zusi and Livezey, 2000 for a review). However, previous investigations of archosaur jaw muscle evolution have been incomplete in one or more tests of homology (e.g., connectivity, correspondence, congruence) or have focused on only one system (e.g., muscles or nerves). Additionally, despite their taxonomic diversity, these studies have yet to be synthesized in a modern phylogenetic context, and have generated a challenging nomenclature for comparative biologists.

Topological criteria involve correspondences in the relative positions of adductor chamber components. Among the criteria used to identify muscle homology, none is more commonly cited than the trigeminal topological paradigm first implemented by Luther (1914). The relative positions of the ophthalmic, maxillary, and mandibular divisions of the trigeminal nerve discriminate different groups of jaw muscles, separating them into *M. constrictor internus dorsalis*, *M. adductor mandibulae internus*, *M. adductor mandibulae externus*, and *M. adductor mandibulae posterior* (Fig. 1). Despite some minor variations, these homology criteria were further elaborated by Lubosch (1933), Lakjer (1926), Edgeworth (1935), Säve-Söderbergh (1945), and many others [see Haas (1973), Iordansky (2000), and Zusi and Livezey (2000) for reviews]. This scheme is not only generally accepted as a robust criterion for muscle identification, but as the basis for terminology as well.

However, relatively few studies (e.g., Oelrich, 1956; Haas, 1973; Rieppel, 1987, 1988, 1990) have incorporated more than one suite of anatomical structures (e.g., nerves, muscles, vessels). For example, Poglayen-Neuwall (1953a) and Bubień-Waluszewska (1981) illustrated the branches of the trigeminal nerve without any topological reference to other tissues. Although blood vessels are intimately associated with the developing musculature (Ruberte et al., 2003), the paths of vascular structures relative to other adductor chamber soft tissues have only been noted in certain taxa [e.g., *Podarcis*, Rieppel (1987); Charadriiformes, Dzerzhinsky and Yudin (1982); *Struthio*, *Anas*, *Alligator*, Sedlmayr (2002)]. Despite the historical importance of the trigeminal topological paradigm, recent myological literature has generally ignored neurological criteria and simply relied on the relative position of other muscles, their aponeuroses, and their bony

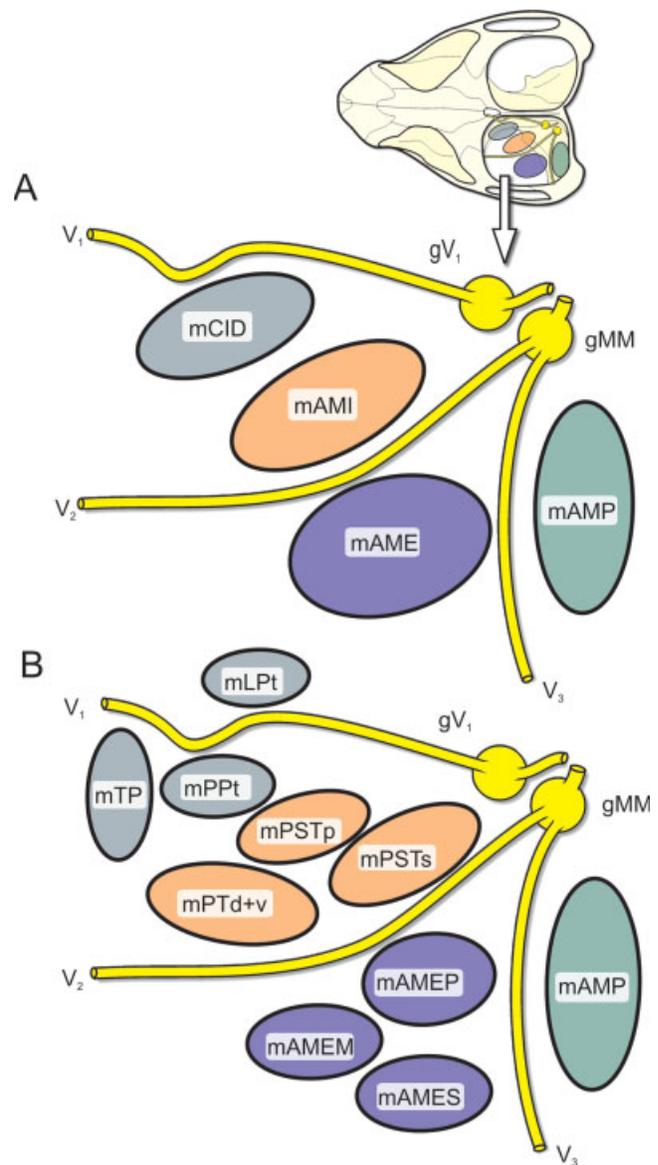


Fig. 1. The trigeminal topological paradigm. Neuromuscular topological organization of the adductor chamber in left dorsal view, as shown in schematic of *Sphenodon*. **A:** Major muscle compartments defined by their positions relative to the trigeminal divisions. **B:** Individual muscles within each compartment. gMM, maxillomandibular ganglion; gV₁, ophthalmic ganglion; mAMI, *Musculus* (M) adductor mandibulae internus; mAME, M. adductor mandibulae externus; mAMEM, M. adductor mandibulae externus medialis; mAMEP, M. adductor mandibulae externus profundus; mAMES, M. adductor mandibulae externus superficialis; mAMP, M. adductor mandibulae posterior; mCID, M. constrictor internus dorsalis; mLpt, M. levator pterygoideus; mPpt, M. protractor pterygoideus; mPSTp, M. pseudotemporalis profundus; mPSTs, M. pseudotemporalis superficialis; mPTd+v, M. pterygoideus dorsalis and ventralis; mTP, M. tensor periorbitae; V₁, ophthalmic nerve; V₂, maxillary nerve; V₃, mandibular nerve.

attachments (e.g., Zusi and Bentz, 1984; Zusi and Livezey, 2000). Focusing on musculoskeletal criteria may be critical in functional investigations (van Drongelen and Dullemeijer, 1982; Busbey, 1989;

Cleuren and De Vree, 1992), but comparisons of neuromuscular function and behavior across even closely related taxa may prove difficult without the integration of muscle-independent hypotheses of homology. Finally, many earlier authors did not frame their analyses within a phylogenetic context, often subjecting Archosauria to the vagaries of paraphyly (i.e., excluding birds).

The adductor chambers of extant crocodylians, birds, and their closest extant outgroups (lepidosaurs and turtles) were investigated to test the trigeminal topological paradigm as a muscle homology criterion and to pursue other topologically and evolutionarily informative soft- and hard-tissue patterns. These patterns will serve as the basis for a discussion of soft-tissue homologies, the utility of topology criteria, and regional evolution. The results of this study are integrated with data from the fossil record in complementary analyses (Holliday, 2006).

MATERIALS AND METHODS

Figure 2 provides the relationships of the major clades of amniotes including many taxa used in this study. This analysis used a conservative consensus phylogeny for character analysis, subjectively collapsing tenuous nodes (particularly among neoavians). This subjectivity does not hamper the conclusions of the study in that we are not reanalyzing archosaur phylogeny, only tracking particular characters in the consensus tree (e.g., Hutchinson, 2001a,b). The phylogeny is based on Gauthier (1986), Cracraft (1986), Benton and Clark (1988), Brochu (1999), Cracraft and Clarke (2001), and Mayr and Clarke (2003). Crocodylians and neornithine birds are the two surviving clades of Archosauria, a group that includes non-avian dinosaurs, pterosaurs, and other extinct groups.

Extant taxa studied include both intact heads and skeletal specimens (Appendix 1). Numerous specimens prepared by Witmer (1995) and Sedlmayr (2002) were also available. Among the avian sample, the following received the most attention in that at least six individuals of each were studied: commercially raised domestic breeds of chicken (*Gallus gallus*), duck (*Anas platyrhynchos*), goose (*Anser anser*), and ostrich (*Struthio camelus*). Additional bird species representing most avian orders were obtained from zoos, wildlife rehabilitation centers, and local sources for comparison. Among crocodylians, three species received the greatest attention: (1) American alligator (*Alligator mississippiensis*), collected from the Rockefeller Wildlife Refuge, southwestern Louisiana, (2) saltwater crocodile (*Crocodylus porosus*), and (3) New Guinea freshwater crocodile (*C. novaeguineae*). Both *Crocodylus* species were obtained from Papua New Guinea. In addition, single individuals of the common caiman (*Caiman crocodilus*), false gharial (*Tomistoma schlegelli*), and gharial (*Gavialis gangeticus*) were studied for comparison. Ontogenetic series of embryos of *Gallus*, *Anas*, and *Alligator* also were available (see Witmer, 1995 for details). Most data on extant nonarchosaurian amniotes were obtained from the extensive literature, but were confirmed via dissection of the following species: (1) Squamata: *Varanus exanthematicus*, *V. niloticus*, *Iguana iguana*, *Hydrosaurus amboinensis*, *Agama stellio*; (2) Testudines: *Chrysemys picta*, *Chelydra serpentina*, and *Malaclemys terrapene*; and (3) Mammalia: *Ceratotherium simum* and *Homo sapiens*.

Four major anatomical techniques were used: (1) gross dissection; (2) serial gross sectioning; (3) latex and barium/latex vascular injection, and (4) X-ray-computed tomography (CT) and magnetic resonance (MR) imaging. Specimens were CT-scanned at O'Bleness Memorial Hospital, Athens, Ohio, on GE Hi Speed

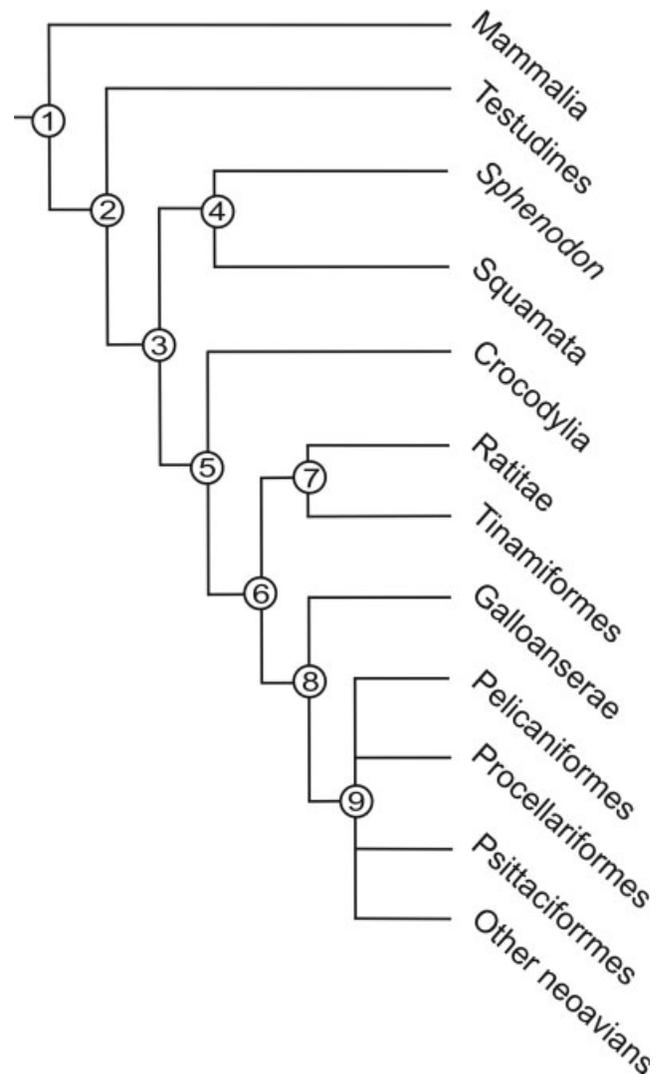


Fig. 2. Cladogram depicting phylogenetic relationships of focal taxa and outgroups used in this study. Numerical codes indicate nodal taxa: 1, Amniota; 2, Sauropsida; 3, Diapsida; 4, Lepidosauria; 5, Archosauria; 6, Neornithes; 7, Paleognathae; 8, Neognathae; 9, Neoaves. Topology follows Gauthier (1986), Cracraft (1986), Brochu (1999), Cracraft and Clarke (2001), and Mayr and Clarke (2003).

FX/i and LightSpeed Ultra Helical CT scanners, and the University of Texas CT Lab, Austin, TX, and MR-imaged at O'Bleness Memorial Hospital using a 1.0T GE Signa Short-Bore MRI system. In some cases, more than one technique was performed on the same specimen (e.g., cephalic arteries were injected with contrast media, followed by CT scanning, serially sectioning, and dissection). All specimens were obtained fresh, frozen, or fixed in 10% neutral buffered formalin and stored in 70% ethanol. All dissections were documented via photography, and occasionally drawings were made with a camera lucida mounted on a Nikon SMZ-U microscope. Most unfixed specimens were skeletonized by dermestid beetles, enzymatic digestion (Terg-a-Zyme, Fisher Scientific Inc.), or cold-water maceration. Several specimens of each focal taxon were frozen and serially sectioned using a bandsaw, hacksaw, or scalpel. All new specimens were accessioned into the Ohio University Vertebrate Collections (OUVC). Additional osteological specimens were studied at the Carnegie Museum of Natural History (CMNH), Field Museum of Natural

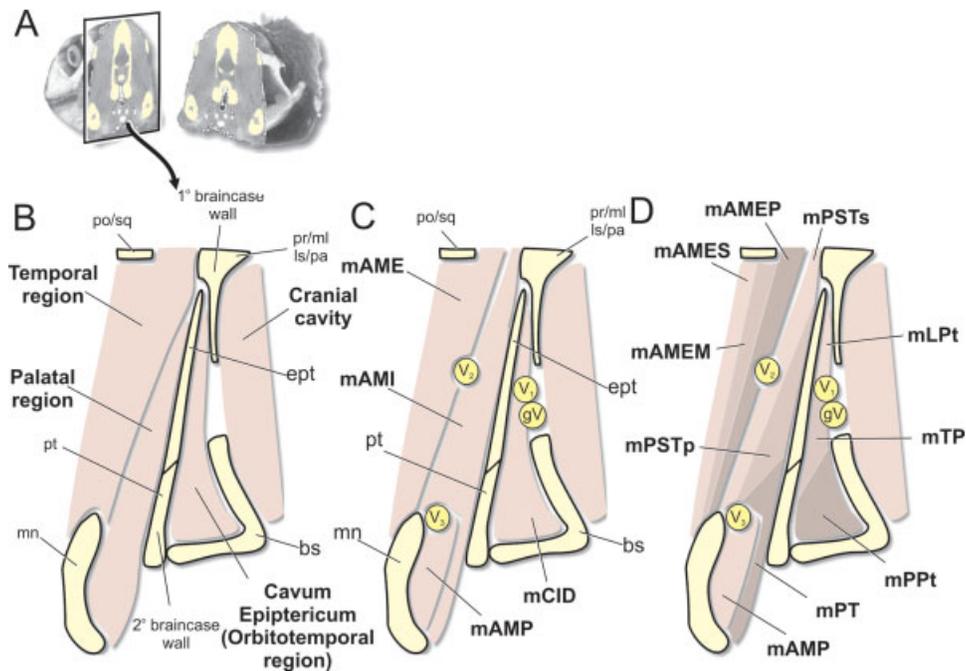


Fig. 3. Overview of adductor chamber and its contents. **A:** Reference image of axial section through *Iguana iguana* depicting the location of the slice schematized in B–D. **B–D:** Schematics of axial sections of plesiomorphic sauropsid adductor chamber in left caudal view. **B:** Major regions and muscular subunits of adductor chamber using musculoskeletal criteria. **C:** Major muscular subunits using trigeminal topological paradigm criteria. **D:** Major muscles of interest discussed in this paper. bs, basisphenoid; ept, epipterygoid; gV, trigeminal ganglion; ls, laterosphenoid; mAMI, Musculus (M) adductor mandibulae internus; mAME, M. adductor mandibulae externus; mAMEP, M. adductor mandibulae externus profundus; mAMEM, M. adductor mandibulae externus medialis; mAMES, M. adductor mandibulae externus superficialis; mAMP, M. adductor mandibulae posterior; mCID, M. constrictor internus dorsalis; mLpt, M. levator pterygoideus; ml, membrane limitans; mn, mandible; mPpt, M. protractor pterygoideus; mPSTp, M. pseudotemporalis profundus; mPSTs, M. pseudotemporalis superficialis; mPT, M. pterygoideus; mTP, M. tensor periorbitae; pa, parietal; po, postorbital; pt, pterygoid; pr, prootic; sq, squamosal; V₁, ophthalmic nerve; V₂, maxillary nerve; V₃, mandibular nerve.

History (FMNH), and the University of California Museum of Paleontology (UCMP).

RESULTS

Organization of the Analysis of Adductor Chamber Similarity

The adductor chamber contents were analyzed proceeding in a medial (deep) to lateral (superficial) direction. Using musculoskeletal criteria, three generalized regions were identified: the palatal, temporal, and orbitotemporal regions. Complementing these regions, trigeminal topological criteria partition the muscles into four separate groups (Figs. 1, 3C): M. constrictor internus dorsalis, M. adductor mandibulae internus, M. adductor mandibulae externus, and M. adductor mandibulae posterior (Luther, 1914; Lakjer, 1926). This paper focuses primarily on the adductor musculature proper (i.e., M. adductor mandibulae) found within the palatal and temporal regions, whereas the orbitotemporal region (housing the protractor musculature and adnexa) is taken up elsewhere (Holliday, 2006). Nonetheless, several orbitotemporal structures are mentioned as landmarks in several figures, namely the ophthalmic nerve, the motor branch to M. con-

strictor internus dorsalis, and the protractor musculature (M. protractor pterygoideus and M. levator pterygoideus). Tables 1 and 2 list the hypotheses of muscular homology and nomenclature for each major muscular group in reference to past works on sauropsid adductor muscles. Cranial (Fig. 4, Table 3) and mandibular (Table 4) attachments are reported for each muscle in each major diapsid clade. These data are followed by specific and informative neurovascular patterns associated with the musculature.

The Palatal Region

M. adductor mandibulae internus. Defined by its relationship medial to the maxillary nerve (Luther, 1914) and lateral to the palatal bones, M. adductor mandibulae internus has classically included both the pterygoideus musculature (e.g., M. pterygoideus dorsalis and ventralis) and M. pseudotemporalis (e.g., Luther, 1914; Lakjer, 1926; Hofer, 1950; Schumacher, 1973). In contrast, Edgeworth (1935) categorized M. pseudotemporalis as M. adductor mandibulae medius based on its early separation from the M. adductor mandibulae internus anlage during development and its disparate

TABLE 2. Synonyms of *M. adductor mandibulae externus* and posterior among diapsids used in this study and selected literature

Author (Top row, crocodylians; Bottom row, birds)	M. adductor mandibulae externus (mAME)		M. adductor mandibulae posterior (mAMP)
This Study	M. adductor mandibulae externus profundus	M. adductor mandibulae externus medialis	M. adductor mandibulae posterior
Lakjer, 1926	M. adductor mandibulae externus IIIb	M. adductor mandibulae externus IIIa,b	M. adductor mandibulae externus IIIc
Edgeworth, 1935	M. adductor mandibulae externus II, Ia, b, c, M. adductor mandibulae externus	M. adductor mandibulae externus III rostralis	+ M. adductor mandibulae externus pars III caudalis
Adams, 1919	M. capitimandibularis medius	M. capitimandibularis superficialis	M. adductor mandibulae medius M. capitimandibularis medius
Kesteven, 1942-1945	M. pterygoideus externus	M. capitimandibularis superficialis	
Schumacher, 1973 ^a	M. temporalis	M. temporo-massetericus	M. pterygoideus medius
Iordansky, 2000 ^d	M. pseudotemporalis	M. massetericus	M. quadratomandibularis
Busbey, 1989 ^a	+ M. adductor mandibulae externus profundus pars posterior	+ M. quadrato-mandibularis	+ M. adductor mandibulae externus profundus
Hofer, 1950 ^b	+ M. adductor mandibulae externus caudolateralis, part of M. adductor mandibulae externus rostromedialis	+ M. adductor mandibulae externus superficialis	+ +
Elzanowski, 1987 ^b	M. adductor mandibulae externus profundus	M. adductor mandibulae externus rostromedialis	+ +
Vanden Berge and Zweers, 1993 ^b	M. adductor mandibulae externus profundus externus ventralis		M. adductor mandibulae externus pars profunda, M. adductor mandibulae externus ossis quadrati
Zusi and Livezey, 2000 ^b	M. adductor mandibulae externus coronoideus, M. adductor mandibulae externus zygomaticus, M. adductor mandibulae externus superficialis	M. adductor mandibulae externus rostralis	+ M. adductor mandibulae externus externus articularis internus
Oelrich, 1956 ^c	+ M. adductor mandibulae externus superficialis		+ +
Haas, 1973 ^c	+ M. adductor mandibulae externus levator anguli oris	+ M. adductor mandibulae externus rostralis	+ +

+ , Same terminology as this study.

^aCrocodylian terminology only.^bAvian terminology only.^cLepidosaurian terminology only.

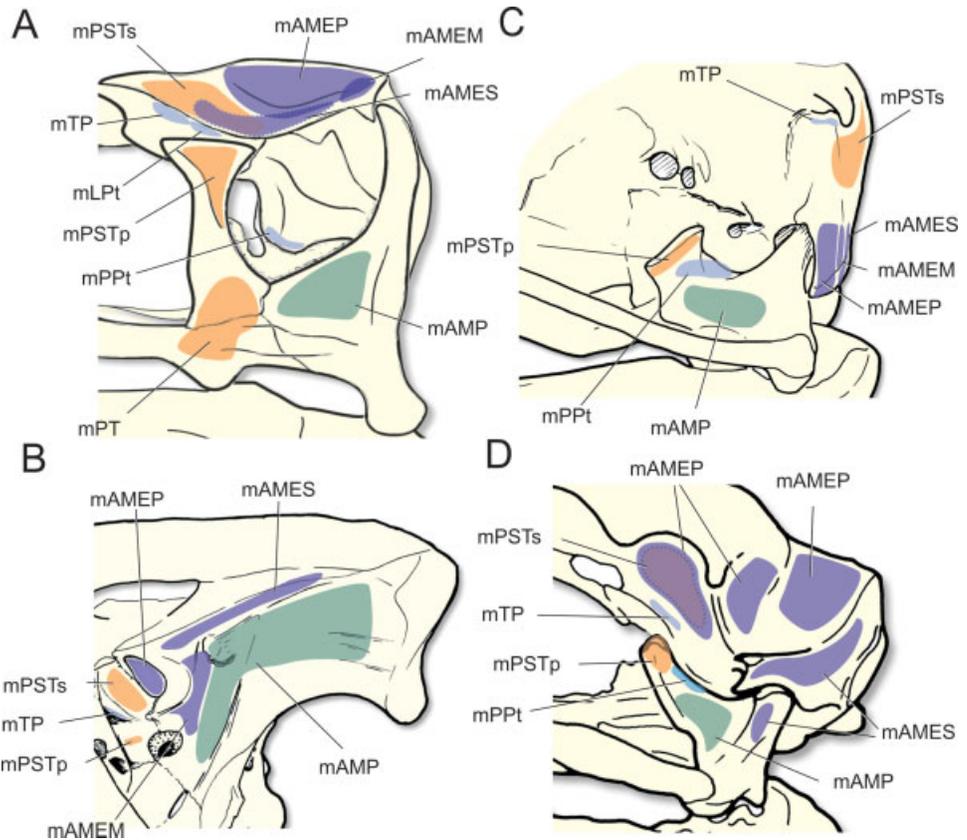


Fig. 4. Skulls of representative sauropsid taxa in left lateral view indicating attachment areas of important muscles. **A:** *Sphenodon punctatus*. **B:** *Alligator mississippiensis*. **C:** *Struthio camelus*. **D:** *Ardea herodias*. mAMI, Musculus (M) adductor mandibulae internus; mAME, M. adductor mandibulae externus; mAMEP, M. adductor mandibulae externus profundus; mAMEM, M. adductor mandibulae externus medialis; mAMES, M. adductor mandibulae externus superficialis; mAMP, M. adductor mandibulae posterior; mCID, M. constrictor internus dorsalis; mLpT, M. levator pterygoideus; mLPt, M. levator pterygoideus; mPPt, M. protractor pterygoideus; mPSTp, M. pseudotemporalis profundus; mPSTs, M. pseudotemporalis superficialis; mPT, M. pterygoideus; mTP, M. tensor periorbitae.

fiber direction compared to the pterygoideus muscles. Nevertheless, based on position and innervation, the pseudotemporalis muscles are best included within M. adductor mandibulae internus, and we join other workers in doing so.

Partitioning of the pterygoideus musculature has occurred in varying ways in the different sauropsid clades, obscuring general patterns. For example, Lakjer (1926) and Iordansky (1964) proposed anterior (rostral) and posterior (caudal) parts in crocodylians, Zusi and Storer (1969) and Vanden Berge and Zweers (1993) identified lateral and ventral parts in birds, and Schumacher (1973) used dorsal and ventral constructs in turtles. The present study failed to identify any criteria independent of the respective bony attachments of the muscles that discriminate subdivisions of the pterygoideus musculature. Thus, this study defers to the dorsalis/ventralis nomenclature based on the dorsal and ventral attachments of the muscles to the palate and their mandibular insertions in crocodylians and birds. However, it appears that other reptiles (i.e., turtles and *Sphenodon*) also have more than one distinct pterygoideus belly, suggesting it may be a shared feature that was elaborated by archosaurs and potentially lost in squamates (Witmer, 1995).

M. pterygoideus dorsalis—*Crocodylia*. The dorsal pterygoideus [M. pterygoideus anterior of Iordansky (1964)] occupies a substantial portion of the

heads of crocodylians, particularly the dorsal surface of the palate and suborbital space (Figs. 5E, 8). The cranial attachments of the muscle include the caviconchal fossa (Witmer, 1995) of the maxilla/palatine articulation, the caudolateral surface of the postconchal nasal cartilage, the dorsomedial surface of the palatine, the ventrolateral surface of the lacrimal, the dorsomedial surface of the maxilla/ectopterygoid articulation, the suborbital fenestra, the cartilaginous interorbital septum, the lateral surface of the cultriform process, and the ascending process of the pterygoid (Figs. 5, 8). The muscle runs caudally through the postnasal fenestra, ventral to M. tensor periorbitae and M. depressor auriculae inferioris in the suborbital space, medial to the maxilla, jugal, ectopterygoid, and ventral to M. pseudotemporalis profundus and M. adductor mandibulae posterior, medial to M. intramandibularis, and lateral to M. pterygoideus ventralis in the temporal region.

Musculus pterygoideus dorsalis attaches to the ventromedial surface of the angular and articular of the lower jaw, just ventral to the jaw joint (Figs. 5E, 8). The medial surface of the muscle attaches as a strong tendon to the ventromedial edge of the medial mandibular fossa, just caudal to the pterygoid flange. The lateral surface of the muscle attaches as a tendon to the dorsomedial edge of the articular, just medial to the jaw joint and retroartic-

TABLE 3. Origins (dorsal attachments) of homologous adductor chamber muscles of *Lepidosauria*, *Crocodylia*, and *Neornithes*

Muscle	Origin		
	Lepidosauria	Crocodylia	Neornithes
M. adductor mandibulae internus	Caudal surface of interorbital septum. Dorsal surface of palatine, pterygoid, ectopterygoid and interorbital septum	Dorsal surface of palatine, pterygoid, ectopterygoid, ventral surface of interorbital septum	Dorsal surface of palatine and pterygoid
M. pterygoideus ventralis	Ventral edge of pterygoid, and quadrate, separate aponeurosis	Caudomedial and caudolateral edge of pterygoid	Ventral surface of palatine and pterygoid
M. pseudotemporalis profundus	Lateral surface of epipterygoid and prootic	Ventrolateral surface of laterosphenoid lateral bridge	Rostral surface of quadrate orbital process
M. pseudotemporalis superficialis	Lateral surface of prootic, membrane limitans, rostrolateral surface of parietal	Caudodorsal surface of laterosphenoid	Rostradorsolateral surface of laterosphenoid
M. adductor mandibulae externus	Caudolateral surface of parietal, rostromedial surface of squamosal	Ventrolateral surface parietal	Lateral surface of parietal, squamosal, and laterosphenoid
M. adductor mandibulae externus medialis	Rostrrolateral surface of squamosal	Rostromedial surface of quadrate	Lateral surface of squamosal
M. adductor mandibulae externus superficialis	Rostrrolateral surface of squamosal, ventromedial surface of squamosal and postorbital	Rostrrolateral surface of quadrate and quadratojugal	Lateral surface of squamosal, dorsolateral surface of quadrate otic process
M. adductor mandibulae posterior	Ventrolateral surface of quadrate	Rostral surface of quadrate	Rostrrolateral surface of quadrate

TABLE 4. Insertions (ventral attachments) of homologous adductor chamber muscles of *Lepidosauria*, *Crocodylia*, and *Neornithes*

Muscle	Origin		
	Lepidosauria	Crocodylia	Neornithes
M. adductor mandibulae internus	Caudomedial surface of angular and articular	Caudomedial surface of angular and articular	Rostradorsolateral surface of medial mandibular process
M. pterygoideus ventralis	Caudovertrrolateral surface of angular and articular, lateral surface of jugal, postorbital	Caudovertrrolateral surface of angular and articular, lateral surface of jugal, postorbital	Rostovertrrolateral surface of medial mandibular process, lateral surface of mandible
M. pseudotemporalis profundus	Dorsomedial surface of surangular and coronoid	Dorsomedial surface of angular	Ventromedial surface of coronoid process, medial mandibular fossa
M. pseudotemporalis superficialis	Medial surface of coronoid process	Cartilago transiliens	Medial surface of coronoid process
M. adductor mandibulae externus profundus	Dorsolateral surface of coronoid process	Dorsomedial surface of coronoid eminence of surangular	Dorsolateral surface of coronoid process
M. adductor mandibulae externus medialis	Dorsolateral surface of surangular	Dorsolateral surface of coronoid eminence of surangular	Dorsolateral surface of lower jaw
M. adductor mandibulae externus superficialis	Dorsolateral surface of surangular	Dorsal surface of surangular	Lateral surface of lower jaw, lateral mandibular process
M. adductor mandibulae posterior	Medial mandibular fossa, dorsomedial surface of angular and articular	Medial mandibular fossa, dorsomedial surface of angular and articular	Caudodorsomedial and caudodorsal surface of lower jaw

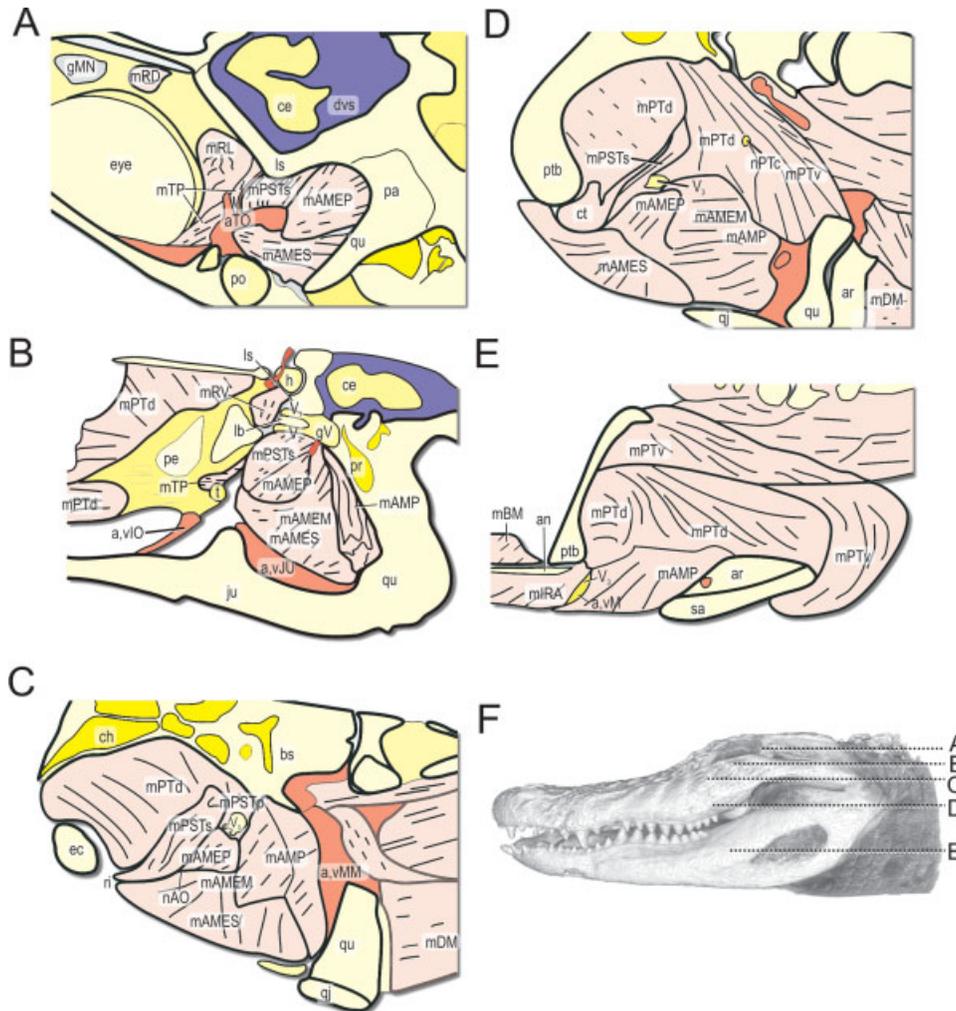


Fig. 5. Schematics of serial, horizontal sections of the left adductor chamber of *Alligator mississippiensis* in dorsal view. **A–E:** Sections proceed dorsal to ventral. **F:** Denotes location of sections in head. a, vIO, infraorbital artery and vein; a, vJU, jugal artery and vein; a, vM, mandibular artery and vein; a, vMM, maxillomandibular artery and vein; an, angular; ar, articular; aTO, temporo-orbital artery; ce, cerebrum; ch, choana; ct, cartilago transiliens; dvs, dural venous sinus; ec, ectopterygoid; gMN; harderian gland; gV, trigeminal ganglion; h, hypophysis; ju, jugal; lb, lateral bridge of the laterosphenoid; ls, laterosphenoid; mAMEP, M. adductor mandibulae externus profundus; mAMEM, M. adductor mandibulae externus medialis; mAMES, M. adductor mandibulae superficialis; mAMP, M. adductor mandibulae posterior; mBM, M. branchiomandibularis; mDM, M. depressor mandibulae; mIRA, M. intramandibularis; mOD, M. obliquus dorsalis; mPSTp, M. pseudotemporalis profundus; mPSTs, M. pseudotemporalis superficialis; mPTd, M. pterygoideus dorsalis; mPTv, M. pterygoideus ventralis; mRD, M. rectus dorsalis; mRL, M. rectus lateralis; mRV, M. rectus ventralis; mTP, M. tensor periorbitae; nAO, ramus to the corner of the mouth (anguli oris) of the mandibular nerve; nPTc, caudal branch of the pterygoid ramus of the mandibular nerve; pa, parietal; pe, periorbita; pr, prootic; ptb, pterygoid buttress; qj, quadratojugal; qu, quadrate; ri, rictus; sa, surangular; t, tarsus for M. depressor auriculae inferioris; V₁, ophthalmic nerve; V₂, maxillary nerve; V₃, mandibular nerve.

ular process. Generally, the muscle excavates a large fossa on the caudomedial surface of the mandible, caudal to the medial mandibular fossa and ventral to the articular and retroarticular process.

M. pterygoideus ventralis—*Crocodylia*. The ventral pterygoideus tendinously attaches via Jordan-sky's (1964) "U" tendon to the caudal rim of the pterygoid flange (Fig. 5D) and the caudolateral surface of the ascending process of the pterygoid (Fig. 5E). It then passes lateral to the cervical musculature and conspicuously wraps around mPTd and the retroarticular process to attach to the caudolat-

eral surface of the angular (Fig. 8). The muscle is generally parallel fibered with several large intramuscular tendons contributing to its internal architecture.

M. pterygoideus dorsalis—*Neornithes*. The dorsal pterygoideus of birds consistently attaches to the dorsal and lateral surfaces of the palatine and pterygoids. In most cases, separate medial and lateral bellies individually attach to the surfaces of the pterygoids and palatines, respectively (e.g., Lakjer, 1926; Hofer, 1950; Goodman and Fisher, 1962; Zusi and Bentz, 1984; Figs. 6, 9). In palaeognaths (e.g.,

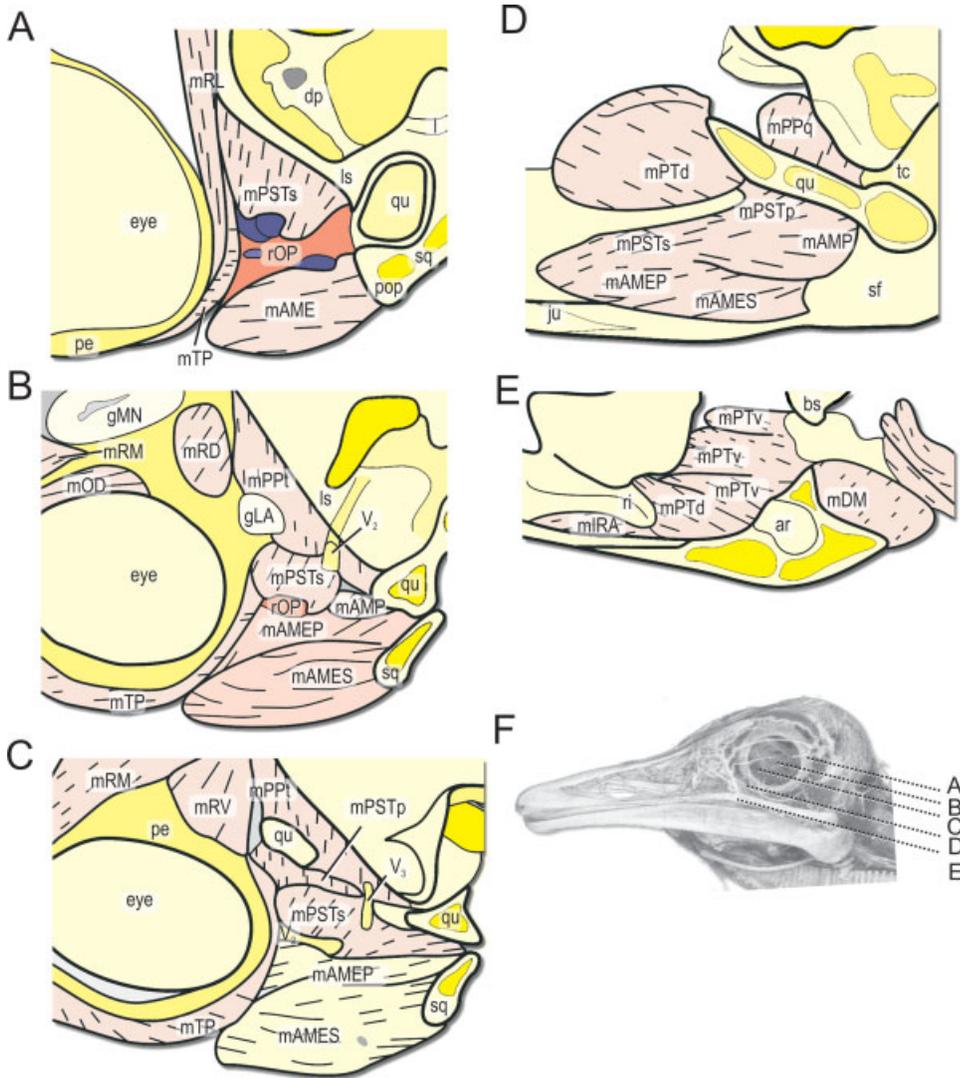


Fig. 6. Schematics of serial, horizontal sections of the left adductor chamber of *Struthio camelus* in dorsal view. **A–E**: Sections proceed dorsal to ventral. **F**: Denotes location of sections in head. ar, articular; bs, basisphenoid; dp, diploe; gLA, lacrimal gland; gMN, Harderian gland; ju, jugal; l, labyrinth; ls, laterosphenoid; mAME, musculus (M) adductor mandibulae externus; mAMEP, M. adductor mandibulae externus profundus; mAMES, M. adductor mandibulae externus superficialis; mAMP, M. adductor mandibulae posterior; mDM, M. depressor mandibulae; mIRA, M. intramandibularis; mOD, M. obliquus dorsalis; mPPq, M. protractor quadratus; mPPT, M. protractor pterygoideus; mPST; M. pseudotemporalis profundus; mPSTs, M. pseudotemporalis superficialis; mPTd, M. pterygoideus dorsalis; mPTv, M. pterygoideus ventralis; mRD, M. rectus dorsalis; mRL, M. rectus lateralis; mRM, M. rectus medialis; mRV, M. rectus ventralis; mTP, M. tensor periorbitae; pe, periorbita; pop, postorbital process; q, quadrate; ri, rictus; rOP, ophthalmic rete; sf, superficial fatty tissue; sq, squamosal; tc, tympanic cavity; V₂, maxillary nerve; V₃, mandibular nerve.

Struthio, *Rhea*, *Eudromia*), mPTd attaches to the dorsal surface of the lateral palatine lamina and passes lateral to the ventral pterygoideus bellies (Fig. 6D). Psittaciformes evolved a remarkable, enlarged belly of M. pterygoideus dorsalis, the M. ethmomandibularis, which attaches to the interorbital septum rostral to the septal attachments of M. protractor pterygoideus (Zusi, 1993; Tokita, 2004). Along its path in the palate, M. pterygoideus dorsalis is bordered dorsally by the suborbital air sinus (Witmer, 1995) and laterally by the jugal and M. pseudotemporalis profundus. Distally, M. pterygoideus dorsalis attaches to the medial surface of the mandible, ventral to the jaw joint, and to the rostral surface of the medial mandibular process, bordered ventrally and medially by M. pterygoideus ventralis and laterally by M. pseudotemporalis profundus (Fig. 9). Despite slight taxonomic differences in muscle morphology, M. pterygoideus dorsalis consistently runs from the dorsal surface of the palate to the medial surface of the mandible either imme-

diately rostral or ventral to the medial cotyla of the jaw joint and always runs between M. pseudotemporalis profundus and M. pterygoideus ventralis.

M. pterygoideus ventralis—*Neornithes*. The ventral pterygoideus attaches to the ventral surfaces of the palatine and pterygoid. Separate bellies often arise from the ventral or medial surface of the palatine and pterygoid. Palaeognaths evolved a complex set of ventral pterygoideus muscles (e.g., lateral and medial bellies) that attach mediolaterally across the ventral surface of the pterygoid and enclose the choana. Palaeognaths also evolved a novel M. pterygoideus ventralis belly, M. retractor palatini (Webb, 1957; Burton, 1974), which attaches to the palatal mucosa rostradorsal to the other M. pterygoideus ventralis bellies, passes dorsal to the medial mandibular process, and inserts on the parasphenoid lamina between the internal carotid foramen and the ala parasphenoidale. Distally, ventral pterygoideus attaches along the ventral rim of the medial mandibular process in most neognaths, bor-

dered dorsally by mPTd and ventrolaterally by *M. serpihyoideus*, a hyolingual muscle. Representatives of several avian clades (Lakjer, 1926; Hofer, 1950; pers. obs.) including pelicaniforms, procellariiforms, owls, parrots, penguins, and auks are characterized by *M. pterygoideus ventralis* muscles that attach to the lateral surface of the mandible similar to the condition found in crocodylians (Fig. 9).

M. pseudotemporalis profundus—*Crocodylia*. A small slip of muscle attaches to the lateral bridge of the laterosphenoid, ventral to *M. pseudotemporalis superficialis*, with some fibers attaching to the ventrolateral surface of the maxillary nerve. This muscle melds with the dorsal fibers of *M. pterygoideus dorsalis* near the caudodorsal surface of the angular (Fig. 8). Iordansky (1964) identified this muscle as *M. adductor mandibulae intermedius*, but Busbey (1989) identified it as *M. pseudotemporalis*. Topological and attachment criteria (see Discussion) indicate that this muscle is most likely a rudimentary belly of *M. pseudotemporalis profundus*, and in general, is indistinguishable from mPTd at its mandibular insertion.

M. pseudotemporalis profundus—*Neornithes*. This muscle attaches to the quadrate orbital process in extant birds [*M. quadratomandibularis*, Hofer (1950) and Elzanowski (1987); *M. adductor mandibulae caudalis*, Vanden Berge and Zweers (1993)], and is generally parallel fibered with a strong tendinous attachment to the caudolateral edge of the muscle (Fig. 9). In *Struthio* and tinamous (e.g., *Nothoprocta*, *Tinamus*, and *Eudromia*), a short, taut ligament (orbitoquadrate ligament; Elzanowski, 1987) connects the ventral margin of *M. pseudotemporalis superficialis* with the dorsal aspect of *M. pseudotemporalis profundus* (with some blended muscle fibers). Dzerhinsky and Yudin (1982) regarded this shared ligament as evidence for evolution of the two pseudotemporal muscles from a common developmental rudiment. *Musculus pseudotemporalis profundus* typically attaches dorsal to the medial mandibular fossa, medial to the entry of the mandibular nerve into the Meckelian canal (Figs. 9, 10), rostroventral to *M. pseudotemporalis superficialis*, ventral to *M. adductor mandibulae externus profundus*, and lateral and rostral to the mandibular attachment of *pterygoideus dorsalis*. Neighboring soft tissues of *M. pseudotemporalis profundus* are discussed with *M. pseudotemporalis superficialis* below.

M. adductor mandibulae posterior. This muscle maintains a consistent position on the body of the quadrate among all sauropsids, bordered by *M. pterygoideus rostromedialis*, *M. pseudotemporalis rostralis*, *M. adductor mandibulae externus profundus* rostrally, *M. adductor mandibulae externus superficialis* laterally. Because *M. adductor mandibulae posterior* develops from either *M. adductor mandibulae internus* or *M. adductor mandibulae externus* in lepidosaurs and turtles, respec-

tively (Edgeworth, 1935), Rieppel (1987, 1990) expressed concern about their homology. However, the consistent musculoskeletal and other relevant criteria in adult forms support the homology of these muscles and they will be treated as such. *Adductor mandibulae posterior* has intimate developmental ties to Meckel's cartilage during the development of the mandible (Edgeworth, 1935; de Beer, 1937), maintaining attachments on the cartilage when present in adults (e.g., crocodylians) and occupying the majority of the medial mandibular fossa.

M. adductor mandibulae posterior—*Crocodylia*. This is one of the larger muscles of the adductor chamber of crocodylians (Schumacher, 1973; Busbey, 1989). The large quadrangular muscle attaches to most of the quadrate, medial to *M. adductor mandibulae externus superficialis*, ventral to *M. adductor mandibulae externus medialis*, and lateral to *M. pterygoideus ventralis* (Figs. 5, 8). The muscle is composed of a number of intramuscular aponeuroses that often leave specific crests and tubercles on the quadrate (see Iordansky, 1964; Fig. 4B) and that give it a parallel-fibered orientation from a lateral view but a pinnate one in cross section. The thickened mandibular adductor tendon serves as the rostralateral boundary of the muscle and its primary tendinous anchor to the quadrate body. The muscle inserts on the medial aspect of the mandible, occupying the majority of the medial mandibular fossa where it attaches to the dorsal surface of the angular, rostral surface of the articular, and the medial surface of the dermis overlying the external mandibular fenestra (Fig. 10B). The muscle borders *M. pterygoideus dorsalis* dorsolaterally, *M. adductor mandibulae externus profundus* and *M. adductor mandibulae externus superficialis* caudomedially, and *M. intramandibularis* caudally in the medial mandibular fossa.

M. adductor mandibulae posterior—*Neornithes*. In ratites, *M. adductor mandibulae posterior* attaches to the dorsomedial surface of the mandible, caudal to the mandibular attachments of *M. adductor mandibulae externus profundus*, a characteristic similar to that found in other non-avian sauropsids (Fig. 10A–C). On the other hand, *M. adductor mandibulae posterior* [synonymous with *M. adductor mandibulae ossis quadrati*, Vanden Berge and Zweers (1993); *M. adductor mandibulae caudalis*, Bühler (1981)] of most neoavians typically attaches to the dorsal and lateral surface of the mandible (Fig. 10D). In galloanserines and some neoavians, *M. adductor mandibulae posterior* has two parts, a large belly that attaches to the lateral portion of the orbital process and body of the quadrate (here defined as *M. adductor mandibulae posterior medialis*), and a thin belly that attaches to the otic process of the quadrate (*M. adductor mandibulae posterior lateralis*) [synonymous with *M. adductor mandibulae articularis internus*, Zusi and Livezey (2000); Figs. 4D, 9C]. The muscle is bor-

dered caudomedially by *M. pseudotemporalis profundus*, rostrolaterally by *M. adductor mandibulae externus superficialis*, and rostromedially by *M. adductor mandibulae externus profundus*. Among Galloanserae, *M. adductor mandibulae posterior medialis* is often large and pinnate, fanning out across the lateral surface of the mandible, whereas *M. adductor mandibulae posterior lateralis* is slim and parallel-fibered, running from the otic tubercle to the caudodorsal part of the mandible, caudodorsal to the attachment of *M. adductor mandibulae posterior medialis* and rostrolateral to the jaw joint. In most birds, *M. adductor mandibulae posterior lateralis* maintains a consistent position immediately rostral to the jaw joint and quadratomandibular ligament, similar to the pattern found in galloanserines. However, the mandibular attachments of *M. adductor mandibulae posterior medialis* vary greatly among neoavians, ranging from positions in the caudal medial mandibular fossa to large lateral mandibular attachments (Fig. 10D).

M. constrictor ventralis. The constrictor ventralis muscles include *M. intermandibularis* and possibly *M. intramandibularis*. The intermandibularis spans the space between the two mandibles with transversely oriented fibers. In birds, the two sides meet at a midline raphe, whereas in crocodylians, the two sides are more continuous with one another. The homology of *M. intramandibularis* is contentious. The two hypotheses of homology for the *M. intramandibularis* are (1) it is a lateral and dorsal extension of the *M. intermandibularis* (Rieppel, 1990), or (2) it is part of *pseudotemporalis* (Elzanowski, 1987). Crocodylia, Palaeognathae (Elzanowski, 1987), Sphenisciformes, Pelicaniformes (Dzerhinsky and Yudin, 1982), and Procellariiformes (Hofer, 1950) possess robust *M. intramandibularis* muscles that occupy the rostral portion of the medial mandibular fossa (Figs. 5E, 6E, 8, 10). In both archosaur clades, *M. intramandibularis* connects to the ventral portion of *M. pseudotemporalis superficialis* and is innervated by the same proximal alveolar branch (Poglayen-Neuwall, 1953b) of the mandibular nerve that also innervates *M. intermandibularis*. In ratites (e.g., *Struthio*, *Rhea*) and other birds, a thin intertendon connects *M. pseudotemporalis* and *M. intramandibularis*. In crocodylians, this tendon develops a large fibrocartilaginous sesamoid cartilage, the cartilago transiliens (Figs. 5, 8D), and *M. intramandibularis* attaches to it ventrally. The presence of sesamoids and intertendons suggests that the *M. intramandibularis* and *M. pseudotemporalis superficialis* are parts of one homologous muscle rather than two separate muscles. Hypothesis 2 is further supported by the topological patterns these muscle share with neighboring neurovasculature.

Neurovasculature in the palatal region. The boundaries of the pterygoideus muscles, as well as the adductor chamber as a whole, are well circum-

scribed by characteristic patterns of nerves and blood vessels. Among all taxa sampled, the maxillary nerve, the pterygoid branch of the mandibular nerve (i.e., the pterygoid nerve) (discussed with *M. pseudotemporalis superficialis* below), and the sphenopalatine artery (Weber, 1996; Sedlmayr, 2002) pass between *M. pterygoideus dorsalis* and either the extraocular muscles, as in turtles, lizards, and crocodylians, or the suborbital air sac in birds. In crocodylians, the large caudal branch of pterygoid nerve passes along the dorsal surface of *M. pterygoideus ventralis*, whereas among birds the pterygoid nerve merely pierces *M. pterygoideus dorsalis* to innervate *M. pterygoideus ventralis* (Figs. 8, 9). The external jugular vein, external carotid artery, and cranial nerves IX–XI bound the caudomedial surface of *M. pterygoideus ventralis*, running between this muscle and the cervical musculature. Hyolingual muscles (e.g., *M. serpihyoideus*, *M. branchiomandibularis*, and *M. stylohyoideus*) bound the medial and ventral portions of *M. pterygoideus ventralis* and pharyngeal mucosa borders the ventral surface of the *M. pterygoideus ventralis* in birds. These different structures can be used to isolate the pterygoideus musculature from surrounding tissues. However, no other structures can be used to separate individual bellies of the muscle.

There are no neurovascular structures that differentiate either *M. intramandibularis* from *M. intermandibularis* or *M. intramandibularis* from *M. pseudotemporalis*. Yet, both the mandibular nerve and its accompanying mandibular artery pass between *M. intermandibularis* and *M. adductor mandibulae posterior* and then subsequently lateral to *M. intramandibularis* within the medial mandibular fossa. After branching from the mandibular nerve, the proximal part of the inferior alveolar nerve runs medially through the rostral portion of *M. intramandibularis* and exits the medial surface of the mandible to ramify across the ventral part of *M. intermandibularis*. The similar topological relationships these muscles share with neighboring neurovasculature further supports the homologous link between *M. intramandibularis* and *M. pseudotemporalis superficialis* noted above.

The Temporal Region

M. adductor mandibulae internus.

M. pseudotemporalis superficialis—Crocodylia. The homology of *M. pseudotemporalis* has been contentious in the crocodylian myological literature. We recognize the presence of *M. pseudotemporalis* in crocodylians (Lakjer, 1926), but disagree with the interpretations of its attachments presented by Iordansky (1964), Schumacher (1973), and Busbey (1989). Homology of *M. pseudotemporalis* is taken up in the Discussion, and synonymies are presented in Tables 1 and 2. *Musculus pseudotemporalis*

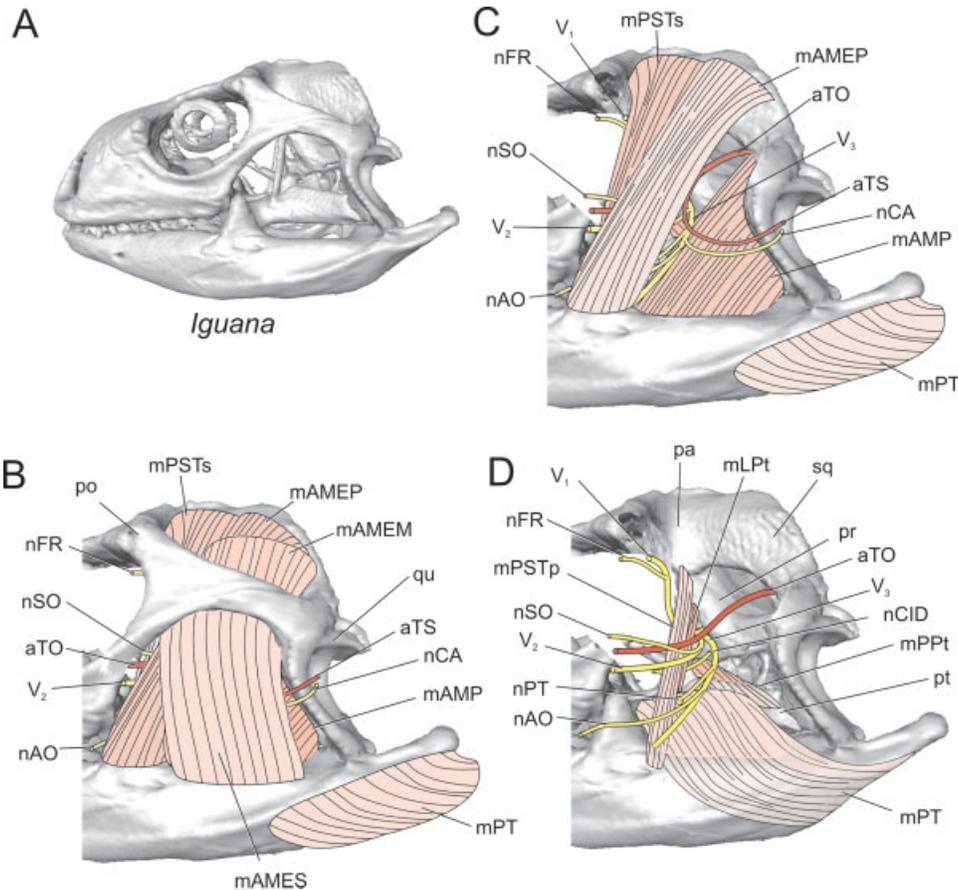


Fig. 7. Major features of the adductor chamber of *Iguana iguana* in left lateral view. Image is composite based on CT data for skeletal anatomy and dissections for soft-tissue anatomy. **A:** Head skeleton. **B:** Superficial dissection (M. levator anguli oris omitted). **C:** Intermediate depth. **D:** Deep dissection. aTO, temporoorbital artery; aTS, superficial temporal artery; mAMEM, musculus (M) adductor mandibulae externus medialis; mAMEP, M. adductor mandibulae externus profundus; mAMES, M. adductor mandibulae externus superficialis; mAMP, M. adductor mandibulae posterior; mLpt, M. levator pterygoideus; mPPt, M. protractor pterygoideus; mPSTp, M. pseudotemporalis profundus; mPSTs, M. pseudotemporalis superficialis; mPT, M. pterygoideus; nAO, ramus to the constrictor internus dorsalis muscles of the mandibular nerve; nFR, frontal ramus of the ophthalmic nerve; nPT, pterygoid ramus of the mandibular nerve; nSO, supraorbital ramus of the maxillary nerve; pa, parietal; po, postorbital; pr, prootic; pt, pterygoid; qu, quadrate; sq, squamosal; V₁, ophthalmic nerve; V₂, maxillary nerve; V₃, mandibular nerve.

superficialis attaches to the caudal surface of the postorbital process of the laterosphenoid, caudal to M. tensor periorbitae (Figs. 4B, 8, 11), rostral to M. adductor mandibulae externus profundus, and rostradorsal to the maxillomandibular foramen (Fig. 5A,B). It attaches ventrally to the dorsomedial surface of the cartilago transiliens, with some fibers merging with M. adductor mandibulae externus profundus near the medial surface of the coronoid eminence (Figs. 5D, 8, 10B).

M. pseudotemporalis superficialis—*Neornithes*. Avian clades differ with regard to attachment site of M. pseudotemporalis superficialis on the laterosphenoid (Vanden Berge and Zweers, 1993; Baumel and Witmer, 1993). For example, in tinamous (e.g., *Eudromia*) and ratites (e.g., *Struthio*, *Rhea*) other than *Apteryx*, M. pseudotemporalis superficialis solely excavates the dorsotemporal fossa (Webb,

1957; Elzanowski, 1987; Figs. 4C, 6, 11C) and is bordered rostrally by M. tensor periorbitae, ventromedially by the maxillomandibular foramen, and ventrolaterally by M. adductor mandibulae externus profundus (Fig. 6A). *Apteryx* has a greatly enlarged M. pseudotemporalis superficialis that occupies the rostrolateral surface of the laterosphenoid and is bordered laterally by an expansive periorbital fat pad (Hofer, 1950), which is likely associated with the ophthalmic rete and temporal vessels. Among neognaths (e.g., Galloanserae, *Gavia*, *Puffinus*, Falconiformes, Gruiformes, Sphenisciformes, Psittaciformes, Passeriformes), M. pseudotemporalis superficialis attaches to the rostral (orbital) surface of the laterosphenoid just ventral to M. tensor periorbitae, lateral to M. rectus lateralis, and rostromedial to M. adductor mandibulae externus profundus. In some birds, (e.g., *Aechmophorus*,

Anhinga, *Apteryx*, *Ardea*, *Pelicanus*, *Phalacrocorax*, and *Ciconiiformes*), *M. pseudotemporalis superficialis* attaches to the lateral surface of the laterosphenoid and shares the rostral surface of the dorsotemporal fossa with *M. adductor mandibulae externus profundus*, which covers *M. pseudotemporalis superficialis* laterally (Fig. 4D). In strigids (e.g., *Bubo*, *Otus*) and caprimulgids (e.g., *Caprimulgus*) and other neoavians with enlarged eyes, *M. pseudotemporalis superficialis* remains on the rostromedial part of the laterosphenoid and is usually displaced ventrally by the eye and merges with the rostromedial portion of *M. adductor mandibulae externus profundus*. Pelicaniformes (e.g., *Phalacrocorax*, *Pelicanus*), Procellariiformes (e.g., *Phoebastria*), and others (Dzerhinsky and Yudin, 1982) have a second caudal belly of *M. pseudotemporalis superficialis*, Hofer's (1950) "caput absconditum" (Fig. 9C). This muscle is a small, thin fleshy belly that attaches in the dorsal tympanic recess. Strikingly, the muscle is orthogonal to the main *M. pseudotemporalis superficialis* belly and merges with its caudolateral surface as only a thin tendon. Distally, *M. pseudotemporalis superficialis* consistently attaches to the dorsomedial surface of the mandible, dorsal to the medial mandibular fossa, medial and ventral to the attachments of *M. adductor mandibulae externus profundus* and the coronoid process, and rostral to the attachments of *M. adductor mandibulae posterior* (Figs. 10C,D).

M. adductor mandibulae externus. *Musculus adductor mandibulae externus* is the most functionally and anatomically variable group of the jaw musculature (Table 3). The *M. adductor mandibulae externus* is defined by its position lateral and rostral to the maxillary and mandibular nerves, respectively (Lakjer, 1926; Fig. 1). The group represents an amalgam of variably constructed "temporal" muscles typically partitioned into superficial (*M. adductor mandibulae externus superficialis*), medial (*M. adductor mandibulae externus medialis*), and deep (*M. adductor mandibulae externus profundus*) parts in non-avian sauropsids (Fig. 7), or, among birds, *M. adductor mandibulae externus rostralis* and *M. adductor mandibulae externus temporalis* (Vanden Berge and Zweers, 1993). Smaller, identifiable bellies also arise within these muscles in various clades (e.g., *M. adductor mandibulae externus profundus anterior*, *M. adductor mandibulae externus zygomaticus*, *M. levator anguli oris*). Generally, *M. adductor mandibulae externus* occupies most of the temporal fossa and lateral region of the adductor chamber. It has broad attachments to the dorsotemporal fossa and medial surfaces of the laterally bounding dermatocranium (postorbital, squamosal; Figs. 4, 7–9, 11) and generally has a vertical fiber orientation as it inserts on primarily the dorsal and lateral surfaces of the surangular (Fig. 10).

Among outgroup taxa, the *M. adductor mandibulae externus* of turtles splits into a large *M. adduc-*

tor mandibulae externus profundus that fills the temporal fossa and expands caudally into the posttemporal fenestra (Schumacher, 1973; Rieppel, 1990) and smaller *M. adductor mandibulae externus medialis* and *M. adductor mandibulae externus superficialis* bellies that occupy the rostromedial surface of the quadrate and medial surface of the postorbital, quadratojugal, and jugal, respectively. These morphologies are similar to those found among lepidosaurs where *M. adductor mandibulae externus profundus*, *M. adductor mandibulae externus medialis*, and *M. adductor mandibulae externus superficialis* all occupy respective positions within the dorsotemporal fossa (Haas, 1973; Figs. 4, 7, 11).

M. adductor mandibulae externus profundus—*Crocodylia*. *Musculus adductor mandibulae externus profundus* [Schumacher's (1973) *M. pseudotemporalis*] is the only muscle in the dorsotemporal fossa and attaches to the lateral surface of the parietal and rostral surface of the squamosal (Figs. 4B, 5A, 8, 11B). The muscle is small, semicircular in cross-section, and conically pinnate among brevirostrines including alligatorids and many *Crocodylus* species. Among these taxa, *M. pseudotemporalis superficialis* forms its complement such that together they form a two-part circular muscle group that occupies the temporal region (Fig. 5B). In longirostrine taxa (e.g., *Gavialis*, *C. johnstoni*, and *Tomistoma*; Iordansky, 1973; Langston, 1973; Endo et al., 2002), *M. adductor mandibulae externus profundus* has a larger, circular cross-section. The caudolateral portion of *M. adductor mandibulae externus profundus* attaches to the rostromedial surface of the mandibular adductor tendon, and attaches distally as a strong tendon at the rostral edge of the dorsal surface of the surangular, just caudal to the rictus in all crocodylian taxa (Figs. 5C, 8, 10B). It is bordered medially by the cartilago transiliens and *M. pseudotemporalis superficialis*, rostromedially by the rictus, and caudally by *M. adductor mandibulae externus medialis* and *M. adductor mandibulae externus superficialis*.

M. adductor mandibulae externus profundus—*Neornithes*. *M. adductor mandibulae externus profundus* is characterized by a variety of different subunits, and, except for palaeognaths, is consistently responsible for excavating the dorsotemporal fossa (Figs. 4D, 11C,D). Among palaeognaths (e.g., *Eudromia*, *Struthio*, *Rhea*), *M. adductor mandibulae externus profundus* attaches to the postorbital process and is divisible into several, variable, smaller bellies (Webb, 1957; Elzanowski, 1987; Figs. 4C, 6D). Despite the partitioning of *M. adductor mandibulae externus profundus* into different bellies (Zweers, 1974; Weber, 1996; Zusi and Livezey, 2000), the basal *M. adductor mandibulae externus profundus* pattern of attachments is retained in galloanserines. The main belly of *M. adductor mandibulae externus profundus* (*M. adductor mandibulae externus coronoideus*; Zusi and Livezey,

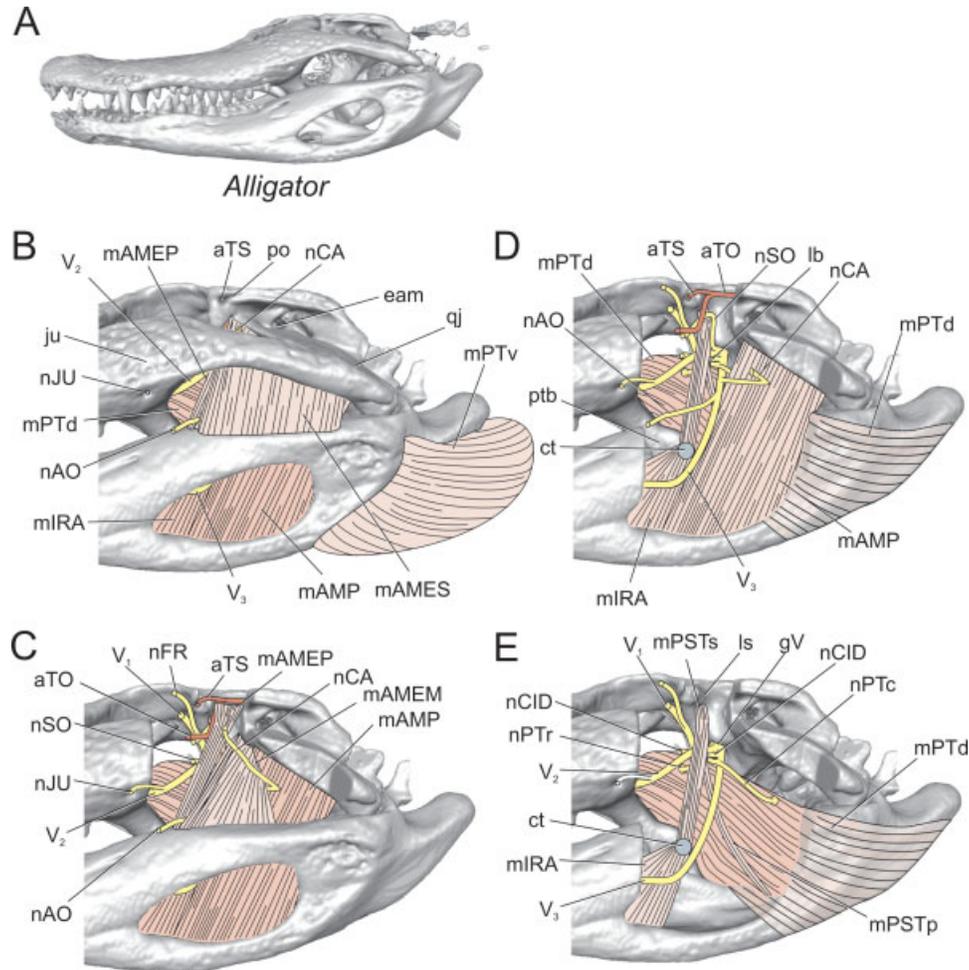


Fig. 8. Major features of the adductor chamber of *Alligator mississippiensis* in left lateral view. Image is composite based on CT data for skeletal anatomy and dissections for soft-tissue anatomy. **A:** Head skeleton. **B:** Superficial dissection. **C:** Intermediate depth. **D:** Deep dissection. **E:** deepest dissection. aTO, temporoorbital artery; aTS, superficial temporal artery; ct, cartilago transiliens; eam, external acoustic meatus; gV, trigeminal ganglion; ju, jugal; lb, lateral bridge of the laterosphenoid; ls, laterosphenoid; mAMEM, musculus (M) adductor mandibulae medialis; mAMEP, M. adductor mandibulae externus profundus; M. adductor mandibulae externus superficialis; mAMP, M. adductor mandibulae posterior; mIRA, M. intramandibularis; mPSTp, M. pseudotemporalis profundus; mPSTs, M. pseudotemporalis superficialis; mPTd, M. pterygoideus dorsalis; mPTv, M. pterygoideus ventralis; nAO, ramus to the corner of the mouth (anguli oris) of the mandibular nerve; nCA, caudal ramus of the mandibular nerve; nCID, motor ramus to the constrictor internus dorsalis muscles of the mandibular nerve; nFR, frontal ramus of the ophthalmic nerve; nJU, jugal branch of the maxillary nerve; nPTc, caudal branch of the pterygoid ramus of the mandibular nerve; nPTr, rostral branch of the pterygoid ramus of the mandibular nerve; nSO, supraorbital branch of the maxillary nerve; po, postorbital; ptb, pterygoid buttress; qj, quadratojugal; V₁, ophthalmic nerve; V₂, maxillary nerve; V₃, mandibular nerve.

2000) occupies the dorsotemporal fossa proper (impressio coronoideus; Zusi and Livezey, 2000), and the rest of the muscle is subdivided along ventral surfaces of the postorbital and zygomatic processes (Weber, 1996). The medial muscles of the group (e.g., M. adductor mandibulae externus coronoideus) attach to the coronoid process. The lateral muscles of this group (e.g., M. adductor mandibulae externus zygomaticus) attach along the rostralateral surface of the mandible and to the lateral mandibular process, rostral to the attachments of M. adductor mandibulae externus superficialis (Fig. 10). Among neoavians, two basic M. adductor mandibulae externus profundus patterns are prevalent.

In the first and most common state (e.g., Passeriformes, Falconiformes, Columbiformes, Laridae, Caprimulgiformes, Psittaciformes), M. adductor mandibulae externus profundus excavates a simple dorsotemporal fossa and attaches to the coronoid eminence (Fig. 11D). The second common pattern is that of many Pelecaniformes (*Pelicanus*, *Phalacrocorax*, *Anhinga*), Podicipediformes (*Aechmophorus*), and Ciconiiformes (*Ardea*), in which the caudal, proper fossa is expanded rostrally into an orbital lamina formed by the laterosphenoid (Burton, 1974). In this case, M. adductor mandibulae externus profundus occupies the caudal part of the dorsotemporal fossa, and a rostral expansion of

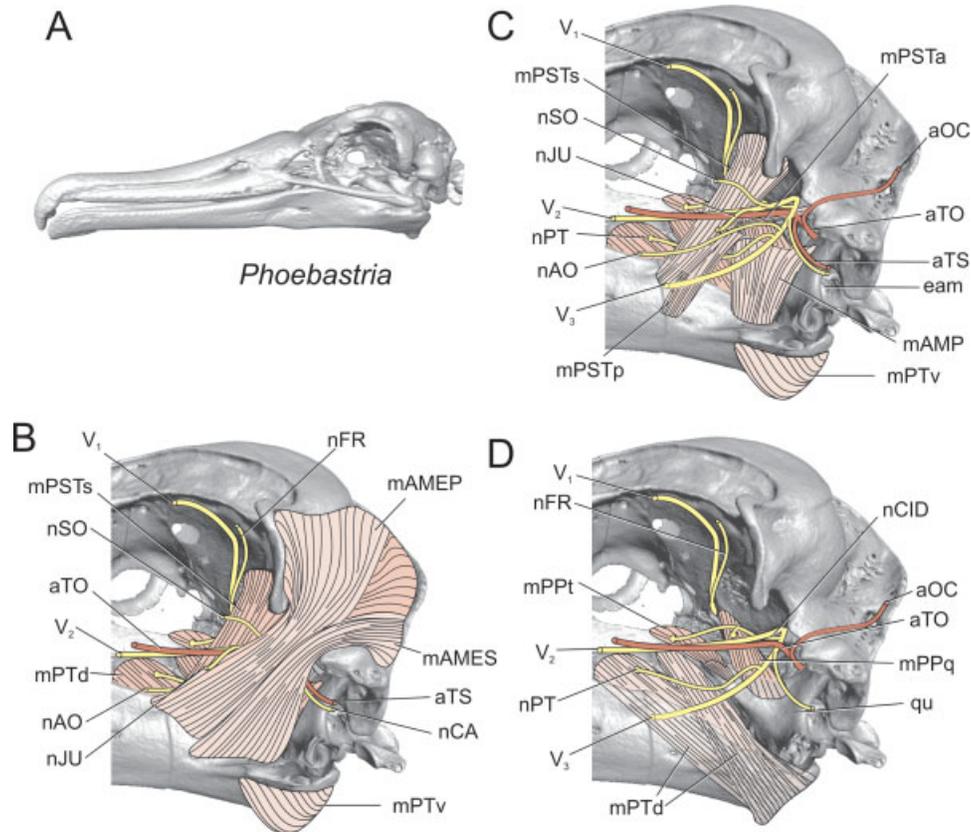


Fig. 9. Major features of the adductor chamber of *Phoebastria immutabilis* in left lateral view. Image is composite based on CT data for skeletal anatomy and dissections for soft-tissue anatomy. **A:** Head skeleton. **B:** Superficial dissection (jugal omitted). **C:** Intermediate depth. **D:** Deep dissection. aOC, occipital artery; aTO, temporoorbital artery; aTS, superficial temporal artery; eam, external acoustic meatus; mAMEP, *M. adductor mandibulae externus profundus*; mAMES, *M. adductor mandibulae externus superficialis*; mAMP, *M. adductor mandibulae posterior*; mIRA, *M. intramandibularis*; mPSTp, *M. pseudotemporalis profundus*; mPSTs, *M. pseudotemporalis superficialis*; mPSTa, *M. pseudotemporalis superficialis pars absconditum*; mPSTp, *M. pseudotemporalis profundus*; mPSTs, *M. pseudotemporalis superficialis*; mPTd, *M. pterygoideus dorsalis*; mPTv, *M. pterygoideus ventralis*; mPPq, *M. protractor quadratus*; mPPt, *M. protractor pterygoideus*; mPSTa, *M. pseudotemporalis superficialis pars absconditum*; mPSTp, *M. pseudotemporalis profundus*; mPSTs, *M. pseudotemporalis superficialis*; mPTd, *M. pterygoideus dorsalis*; mPTv, *M. pterygoideus ventralis*; nAO, ramus to the corner of the mouth (anguli oris) of the mandibular nerve; nCA, caudal ramus of the mandibular nerve; nCID, motor ramus to the constrictor internus dorsalis muscles of the mandibular nerve; nFR, frontal ramus of the ophthalmic nerve; nJU, jugal branch of the maxillary nerve; nPT, pterygoid ramus of the mandibular nerve; nSO, supraorbital branch of the maxillary nerve; qu, quadrate; V₁, ophthalmic nerve; V₂, maxillary nerve; V₃, mandibular nerve.

this muscle occupies the lateral portion of the orbital lamina, bordered medially by *M. pseudotemporalis superficialis* and relevant neurovascular structures (Fig. 11D).

M. adductor mandibulae externus medialis—Crocodylia. This muscle occupies an intermediate position, lodged among the other muscles of the adductor chamber. It attaches to the trapezoidal region of the quadrate just caudoventral to the trigeminal foramen, dorsolateral to the attachment for *M. adductor mandibulae posterior* and ventromedial to *M. adductor mandibulae externus profundus* (Busbey, 1989; Figs. 4B, 8). The muscle shares attachments to the cranial adductor tendon with *M. adductor mandibulae externus profundus* and *M. adductor mandibulae posterior*. It merges laterally with *M. adductor mandibulae externus superficialis* and rostrrolaterally with *M. adductor mandibulae externus profundus* to attach onto the coronoid emi-

nence (Figs. 5C, 8). The remaining fibers attach to the surangular ventromedial to the attachments of *M. adductor mandibulae externus superficialis* and dorsal to the medial mandibular fossa (Fig. 10B).

M. adductor mandibulae externus medialis—Neornithes. *M. adductor mandibulae externus medialis* is not sufficiently distinct to be reliably identified in birds. The problems underlying this assessment are elaborated on in the Discussion.

M. adductor mandibulae externus superficialis—Crocodylia. Rather than attaching within the dorsotemporal fossa as in other non-avian sauropsids (Figs. 4A, 7), *M. adductor mandibulae externus superficialis* attaches to the ventrolateral surface of the quadrate and quadratojugal (Figs. 4B, 8). It then descends caudally as a parallel-fibered muscle. The lateral margin of the *M. adductor mandibulae externus superficialis* is generally free of the dermatocranium, and its investing fascia has only

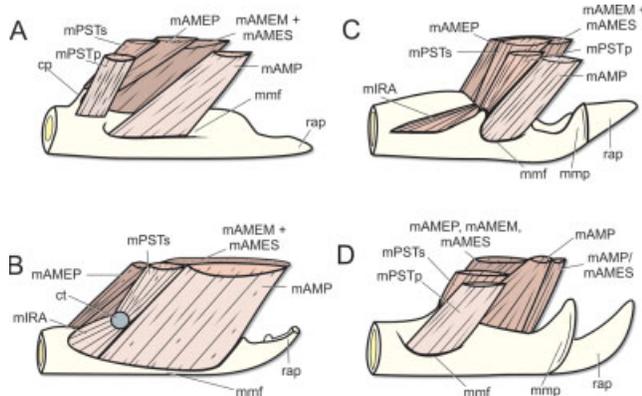


Fig. 10. Musculoskeletal patterns of right mandible in representative diapsid clades in medial view. **A:** Lepidosauria. **B:** Crocodylia. **C:** Palaeognathae. **D:** Neognathae. Note: pterygoideus muscles are not figured for sake of clarity. cp, coronoid process; ct, cartilago transiliens; mAMEM, musculus (M) adductor mandibulae externus medialis; mAMEP, M. adductor mandibulae externus profundus; M. adductor mandibulae externus superficialis; mAMP, M. adductor mandibulae posterior; mIRA, M. intramandibularis; mmf, medial mandibular fossa; mmp, medial mandibular process; rap, retroarticular process.

minor attachments to the dermis and the periosteum of the medial surface of the jugal (Fig. 5). The medial surface of the muscle has numerous fibers that attach to the lateral lamina of the mandibular adductor tendon and M. adductor mandibulae posterior. It then attaches along the dorsal surface of the surangular and rostral to the quadratomandibular ligament and synovial capsule (Figs. 8B, 10B).

M. adductor mandibulae externus superficialis—*Neornithes*. This muscle is thin in palaeognaths and attaches to the temporal fascia dorsomedial to the jugal with only minor attachments on the postorbital process (Figs. 4C, 6C). Among most neognaths, *M. adductor mandibulae externus superficialis* attaches to the subtemporal fossa of the squamosal (i.e., suprameatal process; Zusi and Storer, 1969) as a long pinnate muscle with tendinous attachments to the zygomatic process and nuchal crest (Figs. 4D, 9, 11D). A separate muscle slip of *M. adductor mandibulae externus superficialis* also occasionally attaches to the quadrate otic process [synonymous with *M. adductor externus pars profundus*, Hofer (1950); *M. articularis externus*, Weber (1996), Zusi and Livezey (2000); Fig. 4D]. However, among many birds, the lateral surface of the quadrate is devoid of muscle attachment. In cormorants and possibly other Pelicaniformes, a sesamoid develops in the medial portion of *M. adductor mandibulae externus superficialis* as it wraps over the lateral quadrate cotyla of the squamosal at the rostralateral margin of the subtemporal fossa. The muscle then attaches to the dorsolateral surface of the mandible rostral to the mandibular attachments of *M. adductor mandibulae posterior* and

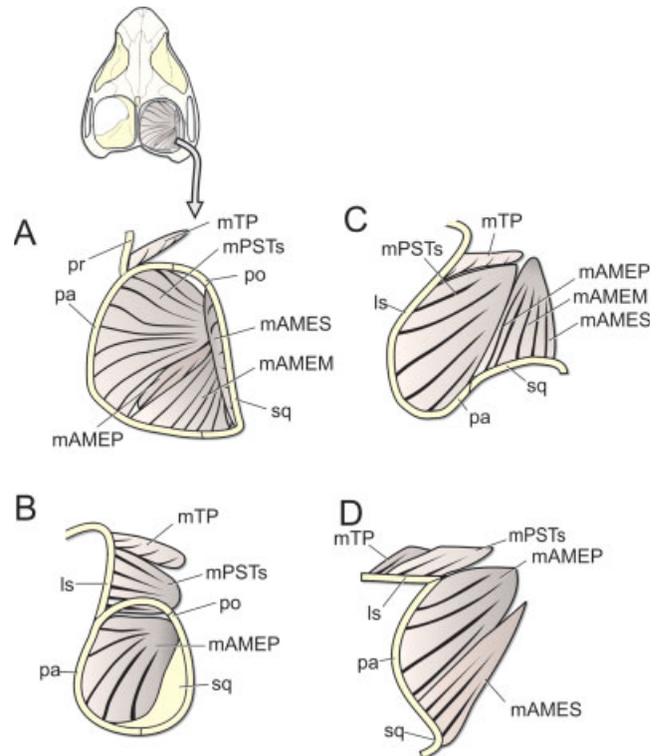


Fig. 11. Musculoskeletal patterns of the right dorsotemporal fossa in representative diapsid clades in dorsal view. **A:** Lepidosauria. **B:** Crocodylia. **C:** Paleognathae. **D:** Neoaves. ls, laterosphenoid; mAMEM, musculus (M) adductor mandibulae externus medialis; mAMEP, M. adductor mandibulae externus profundus; M. adductor mandibulae externus superficialis; mPSTs, M. pseudotemporalis superficialis; mTP, M. tensor periorbitae; pa, parietal; po, postorbital; pr, prootic; sq, squamosal.

caudal to the attachments of *M. adductor mandibulae externus profundus* (Fig. 10D).

Neurovascular structures of the temporal region.

Maxillary nerve. The position of the maxillary nerve has received the most attention (Luther, 1914; Lakjer, 1926; Lubosch, 1933; Edgeworth, 1935) as a criterion of the trigeminal topological paradigm that distinguishes the adductor mandibulae internus group (e.g., *M. pseudotemporalis superficialis*) medially from the adductor mandibulae externus (e.g., *M. adductor mandibulae externus profundus*) group laterally (Figs. 1, 7–9, 12). This criterion holds for all birds, such that even in palaeognaths, where *M. pseudotemporalis superficialis* occupies the dorsotemporal fossa somewhat caudolaterally to the maxillomandibular foramen, the nerve maintains a plesiomorphic course, wrapping around the caudolateral surface of the muscle, and passes between *M. pseudotemporalis superficialis* and *M. adductor mandibulae externus profundus* before entering the suborbital region (Fig. 6B). Among crocodylians, the maxillary nerve has a short path through the temporal region, exiting the rostral edge of the maxillo-

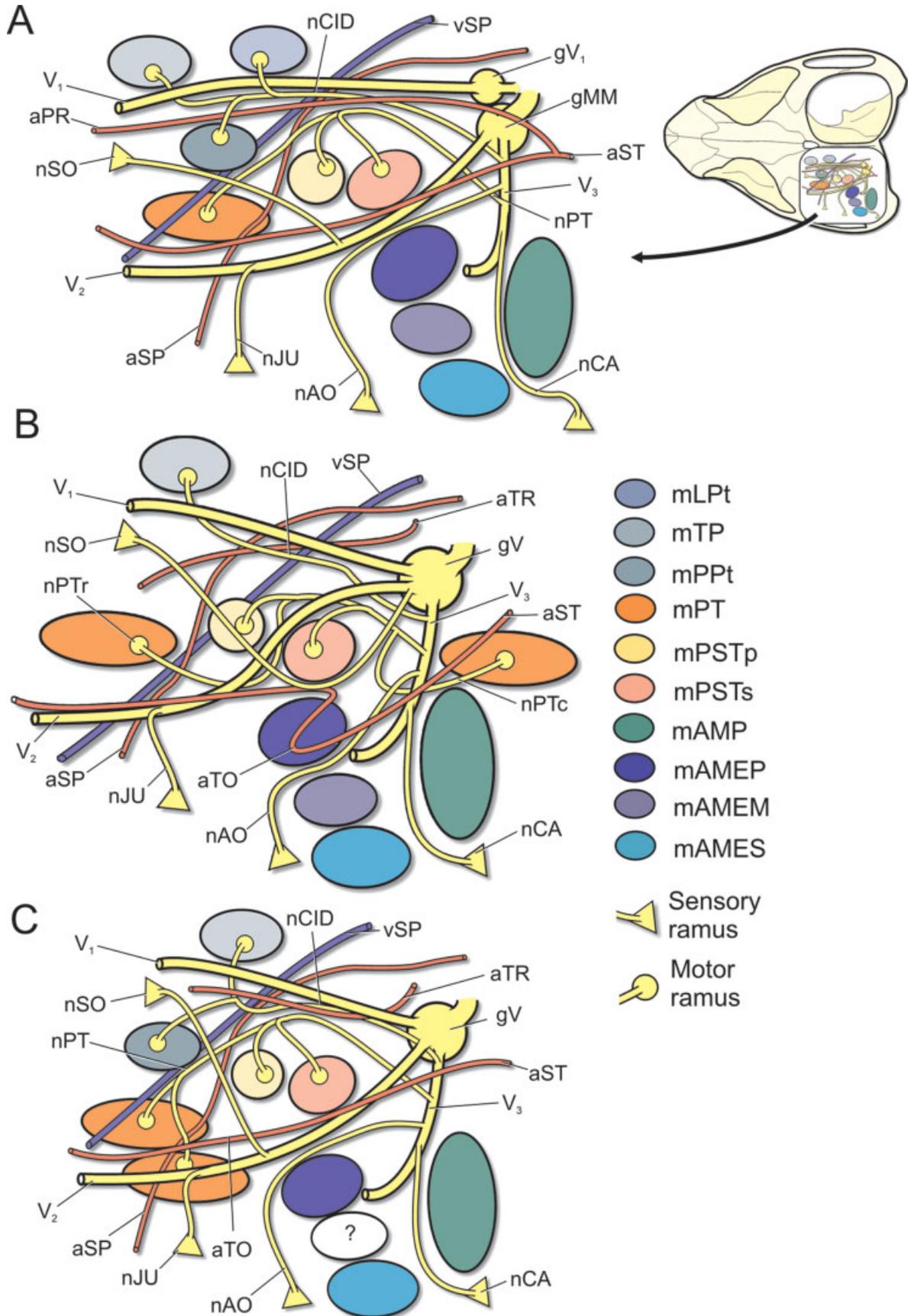


Fig. 12.

mandibular foramen, running between the lateral bridge of the laterosphenoid medially and *M. pseudotemporalis superficialis* laterally and dorsomedial to *M. pterygoideus dorsalis* and *M. pseudotemporalis profundus* (Figs. 5, 8). Therefore, based on these and other data analyzed in the Discussion, the jaw musculature of crocodylians does not conform to the trigeminal topological paradigm as originally described (e.g., Luther, 1914; Lakjer, 1926; Edgeworth, 1935).

Ramus supraorbitalis of the maxillary nerve. The supraorbital nerve is the first branch of the maxillary nerve [Oelrich, 1956; Webb, 1957; Soliman's (1963) ramus frontalis; Bubiń-Waluszewska, 1981] and typically branches dorsally from the maxillary division and passing lateral to *M. pseudotemporalis superficialis* and *M. tensor periorbitae* at the boundary between the orbital and temporal regions (Figs. 7–9, 12). The nerve then ramifies throughout the caudolateral part of the orbit, lacrimal gland, and skin. Being a branch of the maxillary nerve, the supraorbital nerve usually maintains a positionally equivalent intermuscular course, passing between *M. adductor mandibulae internus* and *externus* in birds and lepidosaurs (Fig. 12A,C). However, in crocodylians, the supraorbital nerve uncouples from the maxillary division, instead of arising from the trigeminal ganglion within the caudodorsal region of the trigeminal fossa (Figs. 8, 12B). While the maxillary nerve passes rostrally just lateral to the lateral bridge of the laterosphenoid and ventromedial to *M. pseudotemporalis superficialis*, the supraorbital nerve runs dorsomedially, passing either through the caudal part of the laterosphenoid or within the suture between the laterosphenoid and the quadrate, often running through a separate foramen. The nerve enters dorsally into the dorsotemporal fossa between the parietal and *M. adductor mandibulae externus profundus* (Fig. 8), and then passes between *M. adductor mandibulae externus profundus* and *M. pseudotemporalis superficialis* (Fig. 12B), before joining the temporoorbital artery and the maxillary nerve and ramifying across the back of the orbit and lacrimal gland.

Ramus jugalis of the maxillary nerve. Bounding the rostralateral margin of the adductor chamber is the second branch of the maxillary nerve, here called

the jugal branch of the maxillary nerve (i.e., jugal nerve) (Figs. 7–9, 12). Although Oelrich (1956) found this nerve in *Ctenosaura* to have orbital branches similar to those of the supraorbital nerve, this study failed to find equivalent branches among the sample. The nerve runs rostral to *M. adductor mandibulae externus profundus* and *M. adductor mandibulae externus superficialis*, dorsal to *M. pterygoideus dorsalis*, and ramifies across the skin below the orbit. In general, this nerve lies rostral to the orbitotemporal boundary and dorsal to the pterygoideus muscles, therefore outside of the adductor chamber. In doing so, the nerve forms one of the boundary structures of the adductor chamber.

Ramus pterygoideus of the mandibular nerve. The pterygoid branch of the mandibular nerve (i.e., pterygoid nerve) is the primary motor nerve of the adductor mandibulae internus muscles. In crocodylians, the pterygoid nerve splits into rostral and a caudal branches near its separation from the mandibular nerve (Fig. 8). The rostral branch apomorphically passes between *M. pseudotemporalis superficialis* and *profundus* and then passes between *M. pseudotemporalis profundus* and *M. pterygoideus dorsalis*, subsequently ramifying across the dorsal surface of *M. pterygoideus dorsalis* (Fig. 12B). The caudal branch of the pterygoid nerve passes medial to *M. adductor mandibulae posterior*, often giving off motor rami to this muscle (Poglayen-Neuwall, 1953b; pers. obs.), and ramifies between *M. pterygoideus dorsalis* and *M. pterygoideus ventralis* in the caudal portion of the adductor chamber. The path of the pterygoid nerve is well documented among birds (Hofer, 1950; Dzerzhinsky and Yudin, 1982; Vanden Berge and Zweers, 1993; Weber, 1996). The nerve always passes rostroventrally across the quadrate between the otic and orbital processes and then between *M. pseudotemporalis profundus* and *M. adductor mandibulae posterior* lateral to the quadrate and between *M. pseudotemporalis profundus* and *M. pterygoideus dorsalis* medial to the quadrate (Figs. 9, 12C). It sends off branches to *M. pseudotemporalis profundus* and *M. pseudotemporalis superficialis* and then ramifies across the dorsal surface of *M. pterygoideus dorsalis* to innervate *M. pterygoideus ventralis*. The pterygoid nerve also often carries motor

Fig. 12. Topological patterns of muscles, nerves, and vessels in the adductor chamber of sauropsids. Orientation as in Figure 1. **A:** Plesiomorphic condition common to Lepidosauria and Testudines. **B:** Extant crocodylian condition. **C:** Typical extant avian condition. ?, unclear presence of mAMEM; aPR, profundus branch of the temporoorbital artery; aSP, sphenopalatine artery; aST, stapedial artery; aTO, temporoorbital artery; aTR, rostral trigeminal artery; gMM, maxillomandibular ganglion; gV₁, ophthalmic ganglion; mAMEM, musculus (M) adductor mandibulae externus medialis; mAMEP, M. adductor mandibulae externus profundus; mAMES, M. adductor mandibulae externus superficialis; mAMP, M. adductor mandibulae posterior; mLPT, M. levator pterygoideus; mPPt, M. protractor pterygoideus; mPSTp, M. pseudotemporalis profundus; mPSTs, M. pseudotemporalis superficialis; mPT, M. pterygoideus; mTP, M. tensor periorbitae; nAO, ramus to the corner of the mouth (anguli oris) of the mandibular nerve; nCA, caudal ramus of the mandibular nerve; nCID, motor ramus to the constrictor internus dorsalis muscles of the mandibular nerve; nFR, frontal ramus of the ophthalmic nerve; nJU, jugal branch of the maxillary nerve; nPT, pterygoid ramus of the mandibular nerve; nPTc, caudal branch of the pterygoid ramus of the mandibular nerve; nPTr, rostral branch of the pterygoid ramus of the mandibular nerve; nSO, supraorbital branch of the maxillary nerve; V₁, ophthalmic nerve; V₂, maxillary nerve; V₃, mandibular nerve; vSP, sphenopalatine vein.

fibers to *M. adductor mandibulae posterior* that branch off near the rostroventral surface of the muscle as the nerve travels across the quadrata.

Ramus anguli oris of the mandibular nerve. The nerve to the corner of the mouth (i.e., rictal nerve) is a relatively large sensory nerve that has previously been identified among several sauropsids (Poglayen-Neuwall, 1953a,b; Barnikol, 1954; Oelrich, 1956; Bubieñ-Waluszewska, 1981; McDowell, 1986). The rictal nerve passes rostrally from the mandibular nerve between the muscles of *M. adductor mandibulae internus* and *externus* and ramifies across the rictus (i.e., the corner of the mouth; Figs. 5C, 6E, 7–9, 12). Along its course, the rictal nerve joins with communicating branches of the palatine ramus of the facial nerve that have crossed laterally over the dorsal surface of *M. pterygoideus dorsalis*. With few exceptions, the rictal nerve in birds and lepidosaurs always starts between *M. pseudotemporalis superficialis* and *M. adductor mandibulae externus profundus* and ends between the same muscles at the corner of the mouth. However, in crocodylians, the nerve diverges from this pattern, passing between *M. adductor mandibulae externus profundus* and *M. adductor mandibulae externus medialis*, and subsequently ramifies at the rictus (Figs. 8, 12).

Ramus caudalis of the mandibular nerve. The caudal branch of the mandibular nerve (i.e., caudal nerve) maintains a position rostral to *M. adductor mandibulae posterior* among non-archosaurian sauropsids (Poglayen-Neuwall, 1953a; Oelrich, 1956; Soliman, 1963; Haas, 1973; Dzerzhinsky and Yudin, 1982; Rieppel, 1990; Figs. 7–9, 12). The caudal nerve is the motor supply to *M. adductor mandibulae posterior* and *M. adductor mandibulae externus superficialis* in crocodylians and birds (Hofer, 1950; Poglayen-Neuwall, 1953b), and terminally ramifies as a sensory nerve across the rostral edge of the external acoustic meatus. Among lepidosaurs, the caudal nerve follows a relatively consistent path between *M. adductor mandibulae externus* and *M. adductor mandibulae posterior* muscle groups. In crocodylians, the nerve variably passes laterally through *M. adductor mandibulae posterior* near the caudal border of *M. adductor mandibulae externus profundus* and *M. adductor mandibulae externus medialis* (Figs. 8, 12). The nerve subsequently pierces the caudodorsal portion of *M. adductor mandibulae externus superficialis* and enters the overlying dermis near the dorsolateral surface of the quadratojugal. Among birds, the nerve maintains a constant position rostral to *M. adductor mandibulae posterior* and caudal to *M. adductor mandibulae externus superficialis* (e.g., *M. adductor mandibulae externus articularis externus*) and typically runs with the superficial temporal artery, a lateral branch of the temporo-orbital artery.

Temporo-orbital artery. The most topologically informative vascular structures in the adductor

chamber are the temporo-orbital artery [temporal artery of Oelrich (1956) and Haas (1973); external ophthalmic artery of Baumel (1993)] and the ophthalmic rete, which are both rostral continuations of the stapedial artery. The temporo-orbital artery (Sedlmayr, 2002) plesiomorphically shares the same path as the maxillary nerve (Figs. 6A, 7, 9, 12). In crocodylians, the rostradorsal shifting of the otic region led the temporo-orbital artery to enter the dorsotemporal fossa at a point dorsal to *M. adductor mandibulae externus profundus* rather than ventromedial to it (Figs. 8, 12). Despite this shift, the vessel maintains a position between *M. adductor mandibulae externus profundus* and *M. pseudotemporalis superficialis*. In all birds investigated, except Galloanserae, the temporo-orbital artery runs between the muscles of *M. adductor mandibulae internus* and *externus*. However, in Galloanserae, the temporo-orbital artery departs from the maxillary nerve and passes between *M. adductor mandibulae externus profundus pars coronoides* medially and *pars zygomaticus* laterally (Fig. 12D). Despite these changes, the temporo-orbital artery still reunites with the maxillary nerve on the rostradorsal margins of these muscles.

Occipital and superficial temporal arteries. In crocodylians, the occipital artery branches from the external carotid artery (Sedlmayr, 2002) outside of the adductor chamber and the skull in general, yet maintains a position dorsomedial to *M. depressor mandibulae*. On the other hand, the artery originates from several different regions in birds. In ducks, the occipital artery branches from the internal carotid artery caudal to the middle ear cavity, whereas in chickens, the artery arises from the external carotid artery outside of the middle ear cavity (Baumel, 1993). However, in flamingos (Holliday et al., 2006), gulls (Midtgård, 1984), and cormorants, the artery branches off the stapedial artery at the rostral portion of the middle ear cavity. The occipital artery then passes lateral to *M. pseudotemporalis superficialis* caudodorsally into a bony canal or the dorsal tympanic recess. In the latter case, the artery is often coupled with *M. pseudotemporalis superficialis pars absconditum* (Fig. 9). Despite this variation in origin, the vessel typically exits the skull between the caudal margin of *M. adductor mandibulae externus superficialis* and the rostradorsal edge of *M. depressor mandibulae*, dorsal to the external acoustic meatus and deep to *M. splenius capitus*.

In crocodylians, the superficial temporal artery enters a canal in the postorbital at the rostrolateral corner of the dorsotemporal fenestra and exits rostral to the external acoustic meatus, dorsal to *M. adductor mandibulae externus superficialis*. In birds, the superficial temporal artery [temporal artery of Sedlmayr (2002)] consistently runs between *M. adductor mandibulae externus superficialis* and *M. adductor mandibulae posterior*. The vessel branches off the temporo-orbital artery, passes later-

ally, caudal to the squamosal attachments of *M. adductor mandibulae externus superficialis* and ramifies across the lateral surface of the head rostral to the external acoustic meatus. The most likely lepidosaurian homolog of the superficial temporal artery is the auricular artery (Oelrich, 1956), which, although branching off of the mandibular artery rather than the temporo-orbital artery, also passes between *M. adductor mandibulae externus superficialis* and *M. adductor mandibulae posterior* to ramify across the rostral border of the external auditory meatus.

The topological relationships between the caudal nerve and superficial temporal artery suggest that the quadrate belly of the avian *M. adductor mandibulae externus superficialis* (i.e., *M. adductor mandibulae externus articularis internus*; Zusi and Livezey, 2000) is more topologically similar to *M. adductor mandibulae posterior*, and may simply be a laterally displaced belly of this deeper muscle. Indeed, these two muscles have continuous attachments across both the lateral surface of the quadrate and the dorsolateral surface of the lower jaw. Alternatively, the space constraints developed by a small *M. adductor mandibulae externus superficialis* belly on the quadrate may be responsible for a dorsal shift in the path of the caudal nerve.

DISCUSSION

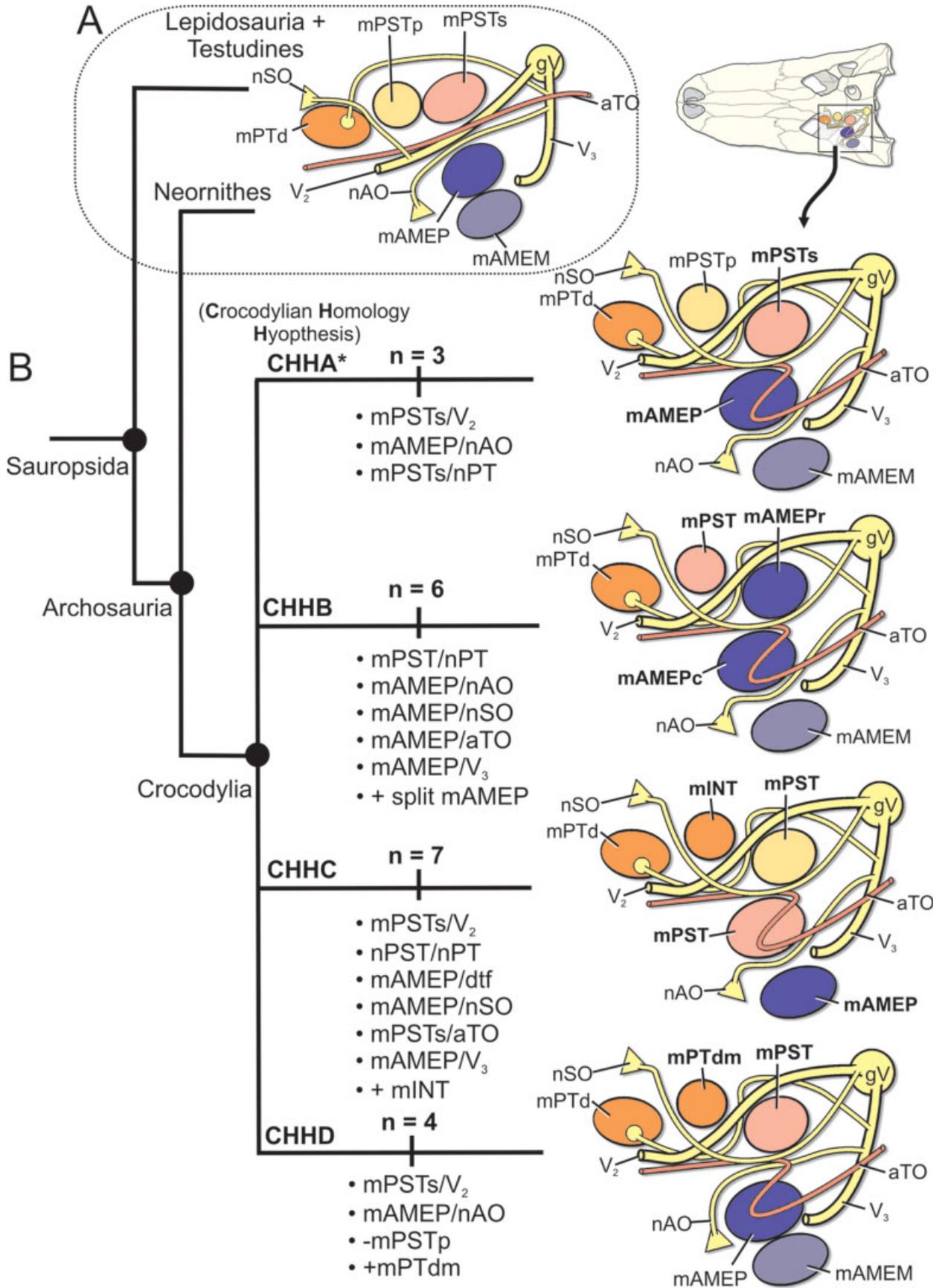
The Apomorphic Adductor Chamber of Crocodylians

Lepidosaurs best approximate the plesiomorphic sauropsid condition for the topological relationships of adductor chamber constituents (Fig. 12A), and these patterns are fundamentally similar in turtles, as well. Divergences from these patterns—for example, a nerve running medial rather than lateral to a muscle—likely reflect apomorphic shifts in adductor chamber construction. Parsimony (Patterson, 1982) suggests that the best-supported hypothesis of muscle homology is that which exhibits the fewest number of derived character state changes in topology. For example, the adductor chambers of palaeognaths are more or less topologically similar to the plesiomorphic lepidosaur condition (Fig. 12C) despite the obvious morphological differences between these clades. Among neognaths, several neurovascular structures exhibit variation in their topological positions to muscles (Fig. 12D). In Galloanserae, both the rictal nerve and the temporo-orbital artery deviate laterally, running through *M. adductor mandibulae externus profundus* rather than medial to it. In some Psittaciformes (e.g., *Ara ararauna*), the rictal nerve passes through *M. pseudotemporalis superficialis* rather than lateral to it. Because neither neurovascular structure completely shifts its intermuscular course, it is difficult to regard the positional arrangement as a full character transition. None-

theless, the adductor chambers of turtles, lepidosaurs, and neornithines are remarkably similar and conservative, particularly compared to the patterns found in crocodylians (Figs. 12, 13).

The muscles of the crocodylian dorsotemporal fossa (i.e., *M. pseudotemporalis superficialis* vs. *M. adductor mandibulae externus profundus*) have the most variable interpretations of homology (Lakjer, 1926; Iordansky, 1964; Haas, 1973; Busbey, 1989; Fig. 13). Sauropsid dorsotemporal musculature is typically dominated by two muscles: (1) a rostral belly that attaches to the front of the neurocranium (e.g., prootic, laterosphenoid) and (2) a caudal belly that attaches to the parietal and squamosal (and abuts *M. adductor mandibulae externus medialis*), typically occupying much of the caudal part of the dorsotemporal fossa (Figs. 4, 12, 13). This study subjected alternative crocodylian homology hypotheses to a topological similarity test to determine the number of steps from the plesiomorphic condition that each hypothesis would require (Fig. 13). The crocodylian homology hypothesis with the fewest character state changes from the plesiomorphic condition (Fig. 13A) is “crocodylian homology hypothesis A” (CHHA; Fig. 13). This hypothesis identifies the rostral belly of the dorsotemporal region as *M. pseudotemporalis superficialis* and the caudal belly as *M. adductor mandibulae externus profundus* (Fig. 13B), requiring only three changes in neuromuscular topology: positional switches between *M. pseudotemporalis superficialis* and the maxillary nerve, the rictal nerve and *M. adductor mandibulae externus profundus*, and the pterygoid nerve and *M. pseudotemporalis superficialis*. On the contrary, the most common previous interpretation of homology—“crocodylian homology hypothesis B”: both bellies are *M. adductor mandibulae externus profundus* (Lakjer, 1926; Iordansky, 1964; Busbey, 1989)—requires changes in six character suites (i.e., the mandibular, pterygoid, rictal, and supra-orbital nerves and temporo-orbital artery) and the formation of two separate *M. adductor mandibulae externus profundus* bellies (pars rostralis and pars caudalis). Two alternative homology hypotheses (crocodylian homology hypotheses C and D) also result in more steps than crocodylian homology hypotheses A. Hypothesis C interprets the muscles in the dorsotemporal fossa and on the laterosphenoid to be *M. pseudotemporalis* (e.g., Schumacher, 1973) and *M. adductor mandibulae externus profundus* to attach to the quadrate (i.e., homologous to *M. adductor mandibulae externus medialis* in other hypotheses). While this scenario supports the rictal nerve-*M. adductor mandibulae externus profundus* criterion, other relevant criteria fail (i.e., maxillary, mandibular, and pterygoid nerves, temporo-orbital artery etc.), and a neomorphic muscle, *M. intermedius* (Iordansky, 1964), is required.

Crocodylian homology hypothesis D, a novel hypothesis proposed here, has only one extra step



compared to homology hypothesis A. This hypothesis suggests that the small slip of muscle on the laterosphenoid lateral bridge is a small, neomorphic belly of *M. pterygoideus dorsalis* (*M. pterygoideus dorsalis minimus*) instead of *M. pseudotemporalis profundus*, which in turn is considered to be eliminated. Except for this switch in terminology, which presumes a nonhomology between the two muscles, Crocodylian homology hypothesis D has the same character-state changes as Crocodylian homology hypothesis A, thus supporting the positional interpretation of *M. pseudotemporalis superficialis* and *M. adductor mandibulae externus profundus* in crocodylian homology hypothesis A. Despite the failure of the *M. pseudotemporalis superficialis*–maxillary nerve character suite (i.e., the failure of the trigeminal topology) in both homology hypotheses A and D, *M. pseudotemporalis superficialis* still maintains a position medial to the mandibular nerve, both within the temporal region, and in the medial mandibular fossa via its connection with *M. intramandibularis*. Moreover, although previous hypotheses relied on the maxillary nerve as the primary criterion (e.g., *M. pseudotemporalis superficialis* lies medial to the maxillary nerve), the *M. pseudotemporalis superficialis*–maxillary nerve criterion would require the muscle on the laterosphenoid to be *M. adductor mandibulae externus profundus*, in turn breaking the *M. adductor mandibulae externus profundus*–mandibular nerve criterion that the paradigm assumes. Thus, not only do particular characters in crocodylians (e.g., rictal nerve, maxillary nerve) depart from the plesiomorphic condition, it is impossible to homologize crocodylian jaw muscles with those of other reptiles without violating the assumptions of the trigeminal topological paradigm.

The adductor chamber of crocodylians has diverged from the classic trigeminal topology most likely because of the suturing of the palate to the braincase—specifically, the characteristic evolution and eventual elimination of the epipterygoid in early eusuchians (see below and Holliday, 2006). Previous studies have also recognized the fallibility of the trigeminal paradigm, noting its susceptibility to developmental and phylogenetic perturbations. Haas (2001) recognized that not all amphibians fit the common topological pattern. Presley (1993) described how the route of the maxillary division shifts due to development of new bony elements (e.g., the alispher-

noid of mammals). Rieppel (1988) illustrated perhaps the most extreme violation of the paradigm in the amphisbaenian *Trogonophis* in which the maxillary division of the trigeminal nerve actually passes medial to the epipterygoid, within the cavum epiptericum. Therefore, it may not be so surprising that such an apomorphic reptilian group as crocodylians also violates this paradigm.

Topology, Development, and Dermatomes: The Need for Additional Nerves

The inability to rely on the main trigeminal divisions requires the use of additional topological criteria, such as secondary nervous structures (e.g., pterygoid, caudal, and rictal nerves) that were found to be almost as consistent as the ophthalmic, maxillary, and mandibular nerves. Indeed, certain structures exhibited static patterns among all clades, including the paths of the caudal and mandibular nerves lateral (rostral) to *M. adductor mandibulae posterior*, and some of the contents of the cavum epiptericum (e.g., *M. protractor pterygoideus*, ophthalmic nerve, and the motor branch to *M. constrictor internus dorsalis*; Holliday, 2006). The relationships between the caudal and mandibular nerves and *M. adductor mandibulae posterior* are consistent among the sauropsid groups investigated despite the muscle's developmental origin from either *M. adductor mandibulae internus* or *externus rudiments* (Rieppel, 1987, 1990). The caudolateralmost soft-tissue structure in the adductor chamber is *M. adductor mandibulae posterior*, which may simply occupy the periphery of the topologically informative structures. This periphery construct holds true for the medialmost structures as well (e.g., *M. pterygoideus dorsalis*, *M. protractor pterygoideus*, pterygoid nerve, and the motor branch to *M. constrictor internus dorsalis*), which also exhibit relatively little variation in topological patterns compared to those in the temporal region.

Although adult trigeminal topologies may be similar, differing ontogenetic trajectories of the character complexes may cloud the assessment of homology (Rieppel, 1988). Overall, however, conservative developmental mechanisms are responsible for the consistent patterns found in the sauropsid adductor chamber. Predominantly sensory and some motor rami of the trigeminal nerve proved informative as boundaries of the adductor chamber and as criteria

Fig. 13. Parsimony analysis of muscle homology hypotheses within the dorsotemporal fossa of crocodylians [i.e., Crocodylian Homology Hypotheses (CHH) A–D]. **A:** Plesiomorphic condition common to lepidosaurs, turtles, and birds. Color codes are the same as in Figure 12. **B:** Four separate hypotheses of muscle homology listing the number of topological and muscular character state changes ($n = x$) away from the plesiomorphic condition. CHHA is the most parsimonious homology hypothesis. See Figure 4 for muscle attachments. aTO, temporo-orbital artery; dtf, dorsotemporal fossa; gV, trigeminal ganglion; mAMEM, musculus (M) adductor mandibulae externus medialis; mAMEP, M. adductor mandibulae externus profundus; mAMEPc, caudal belly of mAMEP; mAMEPr, rostral belly of mAMEP; mINT, M. intermedium; mPTd, M. pterygoideus dorsalis; mPTdm, M. pterygoideus dorsalis pars minimus; nPT, pterygoid ramus of the mandibular nerve; nSO, supraorbital branch of the maxillary nerve; V₁, ophthalmic nerve; V₂, maxillary nerve; V₃, mandibular nerve.

for muscle homology. In general, the major sensory components (e.g., mandibular, supraorbital, and frontal nerves) project to their target dermal fields via chemoattractant signals from the integument prior to the development of significant muscular organization (Covell and Noden, 1989; Kuratani and Tanaka, 1990; Scott, 1992), motor rami and innervation (Vogel, 1992; Song and Boord, 1993), and muscular attachment (Edgeworth, 1935; de Beer, 1937; McClearn and Noden, 1988).

These data suggest that the target integumentary regions of the supraorbital, rictal, and caudal nerves—the orbitotemporal boundary, the corner of the mouth, and the ototemporal boundary, respectively—are developmentally conserved dermatomes (Fig. 14). In addition, the two motor rami (motor branch to the *M. constrictor internus dorsalis* and pterygoid nerve) also maintain consistent somatotopic relationships between their nuclei and their muscular targets, *M. constrictor internus dorsalis* and *M. adductor mandibulae internus*, respectively (Barnikol, 1951; Song and Boord, 1993; Figs. 7–9, 12). However, other rami, such as the main motor branch to *M. adductor mandibulae externus* (Poglayen-Neuwall, 1953a,b), project via intramuscular rather than intermuscular routes, and offer little resolution of muscle homology. Additional motor rami hitchhike along the large sensory branches (e.g., caudal and rictal nerves) and innervate muscles along their intermuscular paths (Fig. 12D). Thus, many muscle groups receive dual innervation from anatomically different nerves (Barnikol, 1951; Poglayen-Neuwall, 1953a,b). For example, motor rami to the sauropsid *M. adductor mandibulae externus superficialis* typically travel along one or two main rami as well as the caudal and rictal nerves. Motor rami to *M. adductor mandibulae posterior* originate from the pterygoid and caudal nerves, and individually from the mandibular nerve. Therefore, not only the main trigeminal divisions but also sensory and some motor branches all contribute as valid topological criteria for testing muscle homology.

Homology and the Requirement of Multiple Testing Criteria

The atomistic breakdown of organisms into smaller subunits is necessary for comparisons of identifiably similar parts, and in many cases, there is little disagreement as to the commonality of shared features among different taxa (Rieppel and Kearney, 2002; Hall, 2003). For example, the homology of the adductor chamber as a whole among sauropsids and even within Amniota is unquestioned. The space is consistently surrounded by other homologous parts including the orbital, otic, encephalic, pharyngeal, and integumentary components of the head. However, the division of the adductor chamber itself into smaller parts and the testing of homology of these components becomes increas-

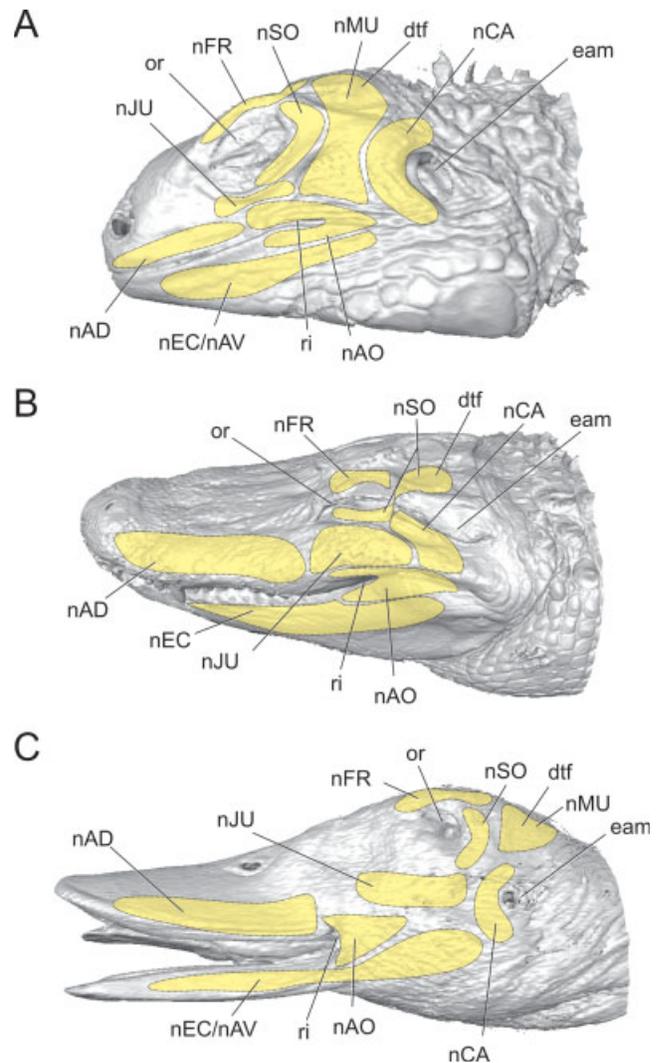


Fig. 14. Postulated dermatome loci of topologically informative sensory nerves. **A:** Lepidosauria (*Iguana iguana*). **B:** Crocodylia (*Alligator mississippiensis*). **C:** Neornithes (*Anas platyrhynchos*). dtf, dorsotemporal fossa; eam, external acoustic meatus; nAD, dorsal alveolar branch of the maxillary nerve; nAO, ramus to the corner of the mouth (anguli oris) of the mandibular nerve; nAV, ventral alveolar branch of the mandibular nerve; nCA, caudal ramus of the mandibular nerve; nEC, external cutaneous branch of the mandibular nerve; nFR, frontal ramus of the ophthalmic nerve; nJU, jugal branch of the maxillary nerve; nMU, muscular branches of the mandibular nerve; nSO, supraorbital branch of the maxillary nerve; or, orbit; ri, rictus.

ingly nebulous. The greater morphological complexity and taxonomic variability of these subunits require not only more rigorous homology tests but also multiple tests using a range of criteria. Occasional failure of any single test should not necessarily falsify a hypothesis of homology, but merely only drive investigations into further similarity testing and probing the mechanisms underlying these differences.

Obviously, not all putative homologies are robust under all criteria, nor would they necessarily be

under a different criteria set. For example, the position of *M. adductor mandibulae externus medialis* is often the means to establish the homology of other muscles (Lakjer, 1926; Haas, 1973). However, *M. adductor mandibulae externus* underwent significant reorganization during the evolution of birds and crocodylians, greatly modifying the adductor chamber compared to that of lepidosaurs. In lepidosaurs, the *M. adductor mandibulae externus* complex is partitioned by the Bodenaponeurosis, the parasagittally situated aponeurosis that attaches to the coronoid process, and reliably differentiates *M. adductor mandibulae externus profundus* and *M. adductor mandibulae externus medialis* (Lakjer, 1926; Haas, 1973; but see Rieppel, 1990). However, the Bodenaponeurosis may be an autapomorphy of Lepidosauria rather than a shared feature of Sauropsida, and, if its homolog is still present at all, it has been greatly modified in both crocodylians and birds.

In crocodylians, the mandibular adductor tendon (Iordansky, 1964; Schumacher, 1973) is the best candidate for a homolog of the Bodenaponeurosis. However, it has undergone significant folding associated with the suturing of the quadrate to the braincase, and forms more of a shared aponeurosis (for all bellies of *M. adductor mandibulae externus* and posterior) rather than the anchor for two (*M. adductor mandibulae externus profundus*, *M. adductor mandibulae externus medialis*; Fig. 5B–D). Moreover, *M. adductor mandibulae externus medialis* (Iordansky, 1964; Schumacher, 1973; Busbey, 1989) is a relatively nebulous muscle belly that has few to no fascial boundaries separating it from *M. adductor mandibulae externus profundus*, *M. adductor mandibulae externus superficialis*, *M. pseudotemporalis superficialis*, and *M. adductor mandibulae posterior*, particularly near its mandibular attachment (Fig. 8). In ratites, *M. adductor mandibulae externus* has an internal aponeurosis that partially separates a deep belly (*M. adductor mandibulae externus profundus*) from a more lateral one (*M. adductor mandibulae externus medialis*) (Webb, 1957; Elzanowski, 1987; Fig. 6C,D), but the two bellies are generally indistinguishable suggesting that, if present, the Bodenaponeurosis is greatly reduced.

Perhaps the best avian candidate for a Bodenaponeurosis homolog is the aponeurosis paracoronioidea (Weber, 1996; Zusi and Livezey, 2000) in Galloanserae. However, avian myologists (e.g., Hofer, 1950; Vanden Berge and Zweers, 1993; Weber, 1996; Zusi and Livezey, 2000) do not typically recognize *M. adductor mandibulae externus medialis* but rather apply a different nomenclature. Overall, the avian *M. adductor mandibulae externus pars ventralis* (pars medialis; Van Gennip, 1986; Vanden Berge and Zweers, 1993) may be most similar to the *M. adductor mandibulae externus medialis* of other sauropsids. Nonetheless, birds have partitioned their adductor musculature into so many functional

compartments that the identification of an unambiguous *M. adductor mandibulae externus medialis* is difficult if not impossible. Finally, even if the Bodenaponeurosis, or its possible crocodylian (mandibular adductor tendon) or avian (aponeurosis paracoronioidea) homologs, is a reliable homology criterion (Rieppel, 1990), this study failed to find any nonmuscular topological criteria (i.e., nerves, vessels) that separate *M. adductor mandibulae externus medialis* from *M. adductor mandibulae externus profundus* in crocodylians or birds, eliminating it from accurate comparisons among taxa.

Likewise, although the pterygoideus muscles maintain consistent bony attachments across sauropsids and particular neurovascular structures (e.g., pterygoid nerve and sphenopalatine artery) separate the pterygoideus muscles from other muscles, only musculoskeletal criteria distinguish *M. pterygoideus dorsalis* from *M. pterygoideus ventralis*. Therefore, although the identifications of *M. pterygoideus dorsalis* and *ventralis* are robust using various musculoskeletal and developmental criteria, they draw no support from neurovascular criteria. Therefore, hypotheses of homology of these muscles may not be as robust as those that are subject to all three testing criteria. Likewise, applicability of relatively few testing criteria led to the hesitant identification of the small muscle belly on the crocodylian laterosphenoid lateral bridge as *M. pseudotemporalis profundus*. The muscle shares positional qualities with *M. pterygoideus dorsalis* but, if the muscle is indeed *M. pseudotemporalis profundus*, it has an apomorphic position relative to ramus pterygoideus of the mandibular nerve (nPT; Figs. 12, 13). Thus, additional data (e.g., developmental data, motor innervation) are necessary to further test the homology of this muscle.

Muscles may share topological similarity but, due to evolutionary changes, may violate tests of attachment similarity or developmental connectivity. The adductor mandibulae posterior attaches within the medial mandibular fossa in all non-neognath diapsids. However, it attaches to the lateral or dorsal surface of the mandible in many neognaths, violating the musculoskeletal attachment position common to other sauropsids. Likewise, *M. adductor mandibulae posterior* may develop from either *M. adductor mandibulae internus* or *externus rudiments* (Rieppel, 1990) among non-avians despite its homologous position caudal to mandibular and caudal nerves among diapsids. Therefore, while neurological criteria support homology of *M. adductor mandibulae posterior* among diapsids, developmental and perhaps musculoskeletal criteria do not.

Finally, hypotheses of homology at an intramuscular level of similarity can be confounded by accessory structures. The formation of intertendons and fibrocartilaginous sesamoids in jaw muscles is relatively common in sauropsids (Hofer, 1950; Schumacher, 1973). These cartilaginous structures have

often been used as a musculoskeletal criterion to separate two different muscles, particularly *M. pseudotemporalis superficialis* from *M. intramandibularis* in turtles, crocodylians, and birds (Lakjer, 1926; Hofer, 1950; Iordansky, 1964; Schumacher, 1973; Vanden Berge and Zweers, 1993). Increases in compressional force on muscular tissues lead to increased formation of fibrocartilage, in turn forming a thickened tendon or sesamoid that acts as a functional entheses (Benjamin and McGonagle, 2001). It is thus more plausible that *M. intramandibularis* is merely the continuation of *M. pseudotemporalis superficialis* into the Meckelian (medial mandibular) fossa and therefore a single continuous muscle rather than two separate muscles that share a common sesamoid attachment. Thus, the components of larger homologous cephalic structures present a variety of interpretations of homology, each reliant on the relative power of several similarity testing criteria, each of which must be incorporated to adequately describe the morphology and evolution of jaw muscles, their intertwining neurovasculature, and the adductor chamber as a whole among amniotes.

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