

Anatomy of the Fully Formed Chondrocranium of *Emydura subglobosa* (Chelidae): A Pleurodiran Turtle

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ABSTRACT The chondrocranium is a cartilaginous structure that forms around and protects the brain and sensory organs of the head. Through ontogeny, this skeletal structure may become more elaborate, remodeled and reabsorbed, and/or ossified. Though considerable attention has been given to the formation of the chondrocranium and a great amount of data has been gathered on the development of this structure among many craniates, the anatomy of this structure in turtles often is neglected. We describe the mature chondrocranium of the pleurodiran turtle, *Emydura subglobosa* (Chelidae) based on hatchling specimens. Though formation and ossification of bony elements has been studied previously in this species, a detailed description of the chondrocranium of this pleurodiran turtle has not been presented. Anatomy of the chondrocranium was described for *E. subglobosa* by examination of cleared and double-stained specimens. The orbitotemporal region of *E. subglobosa* is dramatically different from that of other described turtles (e.g., *Apalone spinifera*, *Pelodiscus sinensis*, *Chelydra serpentina*, *Macrochelys temminckii*, *Trachemys scripta*, *Chrysemys picta*, and *Eretmochelys imbricata*) in that a prominent taenia marginalis spans the space between the planum suprasetale and otic capsules, and the pila antotica (which becomes modified and ossified through ontogeny to form the processus clinoides) is greatly reduced and essentially absent in hatchling specimens. The morphology seen in *E. subglobosa* is similar to that of *Caretta caretta*, particularly as it relates to the taenia marginalis. Variation in the orbitotemporal region is briefly discussed in the context of the taenia marginalis, taenia medialis, pila metoptica, and pila antotica. *J. Morphol.* 274:1–10, 2013. © 2012 Wiley Periodicals, Inc.

KEY WORDS: *Emydura subglobosa*; chondrocranium; Chelidae; Pleurodira; anatomy

INTRODUCTION

Extant turtles typically are placed into one of two monophyletic clades, Pleurodira and Cryptodira (Gaffney and Meylan, 1988; Sterli, 2010); however, there is some discussion that Cryptodira is rendered paraphyletic relative to Pleurodira (Sterli, 2010). Turtles of these clades can be distinguished primarily by the mechanism of head retraction, by which pleurodires (side-neck turtles) pull their neck and head sideward under the anterior edge of the shell, whereas cryptodires retract their neck and head directly, and often completely,

inside their shell in a posteriorly-directed S-curve (Romer, 1956). The entire chondrocranium of cryptodiran turtles has been described in considerable detail (e.g., Shaner, 1926: *Chrysemys picta*; de Beer, 1937: *C. picta* and several other species; Belairs and Kamal, 1981: *Chelydra serpentina*; Sheil, 2003: *Apalone spinifera*; Sheil, 2005: *Macrochelys temminckii*; Sheil and Greenbaum, 2005: *C. serpentina*; Tulenko and Sheil, 2006: *Trachemys scripta*); however, although several structural regions of the chondrocranium of pleurodiran turtles have been described in some detail (e.g., Gaffney, 1979; Werneburg et al., 2009), only two detailed descriptions of the entire chondrocranium of a pleurodiran turtle have been published (Bona and Alcalde, 2009: *Phrynops hilarii*; Vieira et al., 2010; *Podocnemis expansa*).

Here, the chondrocranium of hatchling *Emydura subglobosa*, the Red-bellied Short-necked Turtle (Krefft, 1876), is described. This is a common, carnivorous species that lives in freshwater environments of northern Australia and Papua New Guinea (Legler and Georges, 1993). It has been proposed that *E. subglobosa* is an ideal pleurodiran species for evolutionary studies because it is easily kept in captivity and has simple breeding requirements (Nicol, 1993; Tzika and Milinkovitch, 2008). Although embryogenesis and ossification of the bony skeleton of this species has been described (Werneburg et al., 2009; Werneburg, 2011), the detailed anatomy of the entire chondrocranium has not been presented for this species.

MATERIALS AND METHODS

Two hatchling specimens of *E. subglobosa* (JCU 110 and JCU 111) were examined; these were specimens acquired for the John Carroll University teaching collection prior to 1990. The

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specimens were cleared and double-stained with Alcian Blue and Alizarin Red stains to visualize cartilage and bone, respectively, following the protocols of Wassersug (1976) and Taylor and Van Dyke (1985). Most membrane bones of the skull and the lower jaw were removed to better examine the details of the chondrocranium in isolation. A Leica MZ12.5 stereo dissection microscope equipped with a camera lucida was used to observe and illustrate the specimens. Illustrations were made of the dorsal and lateral views of the chondrocranium, as well as a detailed illustration of the orbitotemporal region. It was not possible to illustrate the ventral view of the chondrocranium, as most of the floor of the chondrocranium had already ossified and become fused to neighboring and investing bones, and removal of remaining portions of the pterygoid and parasphenoid would have led to the destruction of the ventral portion of the chondrocranium. Details of skeletal anatomy and terminology were referenced from Gaffney (1979; for the anatomy of the bony elements), Bellairs and Kamal (1981; for the anatomy of the chondrocranium and terminology of anatomical spaces), and Sheil and Greenbaum (2005; for anatomy of the chondrocranium and contact with bony skeleton).

RESULTS

The chondrocranium consists of the nasal, orbitotemporal, and occipital regions, and the well-formed chondrocranium of hatchlings is slightly longer than wide, and four times longer than high. In dorsal view (Fig. 1), the maximal width of the nasal capsule (nc) is approximately one-third the posterior width of the skull. The nasal region accounts for one-fourth the length of the chondrocranium and the nasal capsules are robust and the snout is somewhat tubular. The orbitotemporal region is approximately as long as the otic region, and the interorbital septum (is) is a high, thin structure, whereas the planum supraseptale (ps) is narrow and not as prominent; the planum supra-septale does not extend laterally beyond the level of the lateral margins of the otic capsule (oc). In dorsal and lateral view (Figs. 1–3), the taenia marginalis (tma) is prominent and attaches to the otic capsule. The occipital region is compressed antero-posteriorly and is occupied primarily by the exoccipital (ex), basioccipital (bo), and ventral portion of the supraoccipital; these elements form the margin of the foramen magnum.

Nasal Capsule

The nasal capsule is well chondrified, one-third the entire length of the entire chondrocranium, and directed ventrally only slightly relative to the primary axis of the chondrocranium. Laterally, the nasal capsule has a relatively broad zona annularis (za) that bears a short ectochoanal cartilage (ec) that extends posteriorly to the level of the sphenethmoid commissure (sc). The ectochoanal cartilage is confluent with the planum antorbitale (pla) and, as seen in dorsal view (Fig. 1), does not extend laterally beyond the lateral margin of the zona annularis. In lateral view (Fig. 3), the sphenethmoid commissure is narrow, curves slightly

anterolaterally, and connects the anterior portion of the planum supraseptale and the posteromedial portion of the nasal capsule that forms the dorsal margins of the orbitonasal fissure (onf; Fig. 3). A small, parasagittal fenestra olfactoria (fo) is present in the dorsal surface of the nasal capsule, and is enclosed dorsally by the sphenethmoid commissure (Figs. 1 and 2). The fenestra narina (fn) is relatively large, conspicuous and open ventrally. The rostrum of the nasal capsule is open dorsally and laterally, and the nasal capsule bears a conspicuous flap of cartilage at its anterolateral margin (Figs. 1 and 3), as a result of having a deep vertical incision near the posterior margin of the capsule. As seen in lateral view (Fig. 3), the margins of the fenestra narina are open dorsally and a deep gap interrupts the zona annularis. Posterior to each fenestra narina, the floor of the nasal capsule bears a broad, shallow, longitudinal channel that extends the length of the floor of the nasal capsule. Details of the internal anatomy of the nasal capsules were not studied.

Orbitotemporal Region

The orbitotemporal region is composed of a narrow, thin planum supraseptale and a conspicuous interorbital septum. The planum supraseptale is slightly concave ventrolaterally and convex dorso-medially, and it extends dorsolaterally over the orbit and is perforated by a single foramen near the posterodorsal margin, near the base of the taenia marginalis (Fig. 2); this foramen is for the trochlear nerve (4). In lateral view (Fig. 3), the dorsal margin of the planum supraseptale is irregular, convex, and extends dorsally beyond the level of the dorsal margin of the nasal and otic regions. In dorsal view (Fig. 1), the planum supraseptale extends between the level of the ectochoanal cartilage and otic capsule. Posteroventrally, each planum supraseptale is pierced by a relatively large, irregular foramen for the optic nerve (2), which is separated only narrowly from the foramen for the ophthalmic artery (foa) by the pila metoptica (pm). The taenia marginalis is a thin but prominent structure that extends from the posterior margin of the planum supraseptale and connects to the dorsolateral margin of the otic capsule (Figs. 1–3). In dorsal view (Fig. 2), a relatively short, triangular, cartilaginous pila antotica (pa) is present; these structures are the remnants of the lateral margins of the postorbital cartilage, which has been modified developmentally; each pila antotica extends dorsolaterally from the remnants of the crista sellaris (i.e., ventral portion of posterior orbital cartilage), which ossifies to form the dorsum sellae (ds). A relatively short, triangular, cartilaginous taenia medialis (tm) is present at the posterior margin of the planum supraseptale (Fig. 2). The interorbital septum is relatively long, thin,

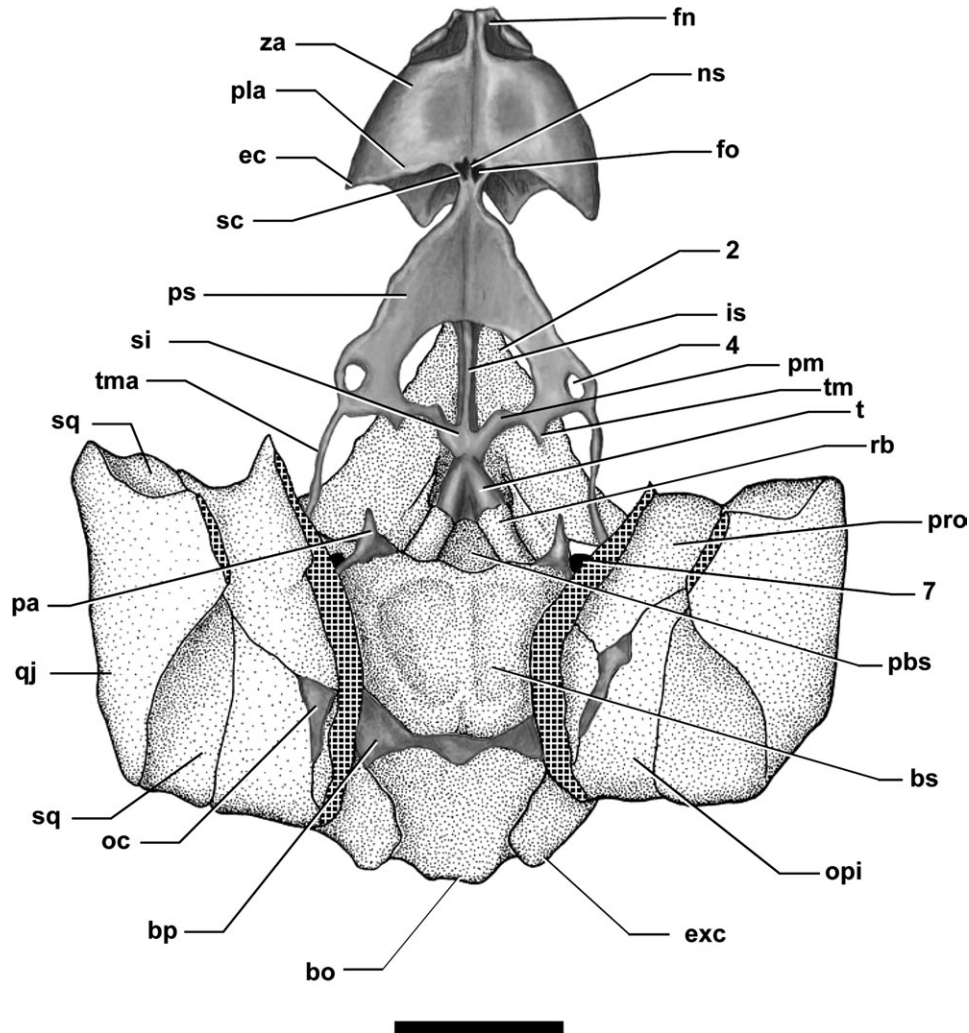


Fig. 1. Dorsal view of mature chondrocranium of a hatchling *E. subglobosa*, showing the maximum extent of chondrocranial development, prior to major modification of cartilages via absorption or endochondral ossification. Dermal bones of the skull table and maxillary arcade have been removed to allow unhindered view of chondrocranium. Gray denotes cartilage; stippling denotes bone; hatched lines denote cut bones. 2, foramen for optic nerve, cranial nerve 2; 4, foramen for cranial nerve 4; 7, foramen for facial nerve, cranial nerve 7; bo, basioccipital; bp, basal plate; bs, basisphenoid; ec, ectochoanal cartilage; exc, exoccipital; fn, fenestra narina; fo, fenestra olfactoria; is, interorbital septum; ns, nasal septum; oc, otic capsule; opi, opisthotic; pa, pila antotica; pbs, parabasisphenoid; pla, planum antorbitale; pm, pila metoptica; pro, prootic; ps, planum suprasedale; qj, quadratojugal; rb, rostrum basisphenoidale; sc, sphenethmoid commissure; si, subiculum infundibuli; sq, squamosal; t, trabeculae; tm, taenia medialis; tma, taenia marginalis; za, zona annularis. Scale bar = 5 mm.

and five times as high anteriorly (at the level of the planum antorbitale) as posteriorly (at the level of the foramen for the ophthalmic artery). At this point in development, the pituitary fenestra (not illustrated) has been closed ventrally by the parabasisphenoid (pbs) from below (Fig. 2), forming a conspicuous fossa, the sella turcica (stu). The anterior and posterior margins of the sella turcica are formed by the ossified portions of the trabeculum (t) (forming the rostrum basisphenoidale) and dorsum sellae, respectively. The basicranial fenestra of an early embryonic stage is not visible, but rather this region in the floor of the cavum cranii is indicated by a shallow depression on the dorsal

surface of the planum basale of the basioccipital. Additionally, the posterior half of each trabeculum is well ossified but cartilage remains where the two trabeculae meet and fuse below and posterior to the subiculum infundibuli (si). The crista sellaris (i.e., ventral portion of posterior orbital cartilage) is completely replaced by bone and forms the osseous dorsum sellae at the posterior margin of the sella turcica (Fig. 3). In dorsal view (Fig. 2), the foramen for the oculomotor nerve (3) is located posterior of the planum suprasedale, between the trabecula and taenia marginalis. The foramen for the trigeminal nerve (5) is posterior of the foramen for the oculomotor nerve, between the pila antotica

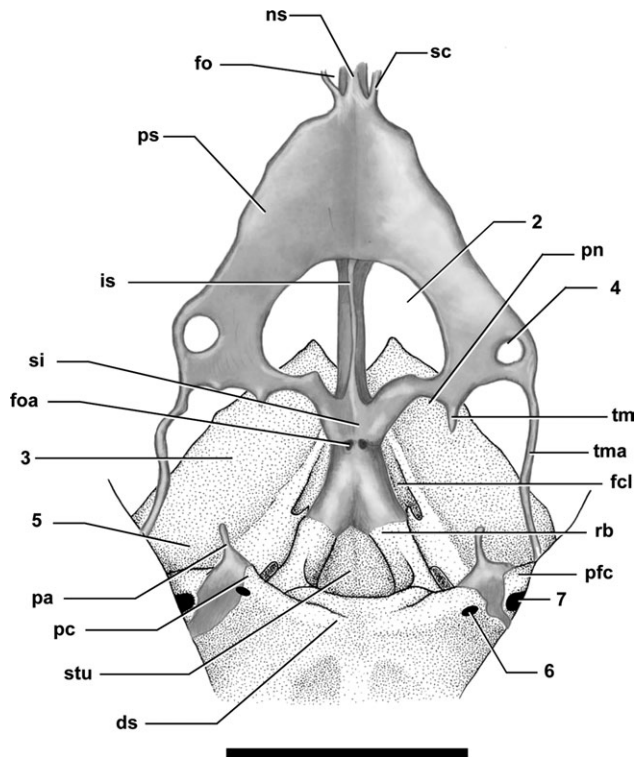


Fig. 2. Dorsal view of the orbitotemporal region of the mature chondrocranium of a hatchling *E. subglobosa*, showing the maximum extent of chondrocranial development, prior to major modification of cartilages via absorption or endochondral ossification. Note the greatly reduced pila antotica and presence of the thin taenia marginalis, which connects the planum suprasetale and otic capsule. Gray denotes cartilage; stippling denotes bone. 2, foramen for optic nerve, cranial nerve 2; 3, foramen for oculomotor nerve, cranial nerve 3; 4, foramen for cranial nerve 4; 5, foramen for trigeminal nerve, cranial nerve 5; 6, foramen for abducens nerve, cranial nerve 6; 7, foramen for facial nerve, cranial nerve 7; ds, dorsum sellae; fcl, foramen caroticum laterale; fo, fenestra olfactoria; foa, foramen for ophthalmic artery; is, interorbital septum; ns, nasal septum; pa, pila antotica; pc, processus clinoideus; pfc, prefacial commissure; pn, prootic notch; ps, planum suprasetale; rb, rostrum basisphenoidale (= ossified portions of trabeculae); sc, sphenethmoid commissure; si, subiculum infundibuli; stu, sella turcica; tm, taenia medialis; tma, taenia marginalis. Scale bar = 5 mm.

and taenia marginalis, and represents the prootic notch (pn). In dorsal view, (Fig. 2), the foramen caroticum laterale (fcl) lies beneath the trabeculum, and each canalis caroticus lateralis (not illustrated) travels parallel to the trabeculum and are open dorsally, anterior and medial to the base of the processus clinoideus (pc; Fig. 2). The foramen for abducens nerve (6) is ovoid and pierces the lateral margins of the ossified portions of the dorsum sellae, at the base of the processus clinoideus. The rostrum basisphenoidale (rb) represents the anterior elongation of the basisphenoid (bs) (the ossified portion of the parabasisphenoid), which is anterior to the dorsum sellae (Fig. 1).

Otic Capsule

The otic capsule is large and conspicuous, longer than high and, as seen in dorsal view (Fig. 1), four times longer than wide. The anterior half of the otic capsule has ossified to form the prootic (pro), and posteriorly to form the opisthotic (opi) (Fig. 1). Only small remnants of cartilages of the otic capsule are visible externally in hatchlings. The anteromedial wall of each otic capsule is pierced by at least one foramen—a nearly circular foramen for facial nerve (7). Laterally, the otic capsule meets a relatively large, semilunate quadrate cartilage (qc) that is largely replaced by bone (to form the quadrate bone) and is invested by the squamosal (sq) and quadratojugal (qj). The ventral margins of the quadrate bone (q) and remaining portions of quadrate cartilage (qc) are deeply concave and form the margin of the cavum tympani (ct), which occupies about one-third of the lateral margin of the quadrate cartilage and is deeply conical (Fig. 3). Each quadrate bone (q) (i.e., the ossified portion of the quadrate cartilage) is two times longer than wide, and twice as long as high (though much of it is invested by the squamosal and quadratojugal and is not visible in Figs. 1 and 3). The quadrate cartilage (qc) has begun to ossify in its anterior portion, but remains cartilaginous posteriorly at the area articularis of the quadrate cartilage. The tectum synoticum, which forms a bridge over the hind brain between the otic capsule, could not be studied due to its removal during the dissection of the specimens to view the structures that lie beneath it, but significant portions of this structure were replaced by the supraoccipital.

Basal Plate

The basal plate (pb) forms the posteriormost portion of the floor of the braincase and is nearly as long as wide and is well ossified, although a small portion of it remains cartilage. The floor of the cavum cranii is formed by the osseous portion of the basisphenoid and is large; as seen in dorsal view (Figs. 1 and 2), this depression is wider anteriorly and narrows posteriorly. The basisoccipital is narrowly separated from the parabasisphenoid by the dorsum sellae (ossified portion of crista sellaris). Nearly circular foramina for the facial nerve (7) pierce each side of the anterior margin of the basal plate; the anterior margin of each foramen is formed by the prefacial commissure (pfc; Fig. 2). Additionally, foramina for abducens nerve (6) pierce the base of the dorsum sellae (i.e., cartilaginous remnants of the pila metoptica).

DISCUSSION

A thorough summary of the general reptile chondrocranium was presented by Bellairs and Kamal

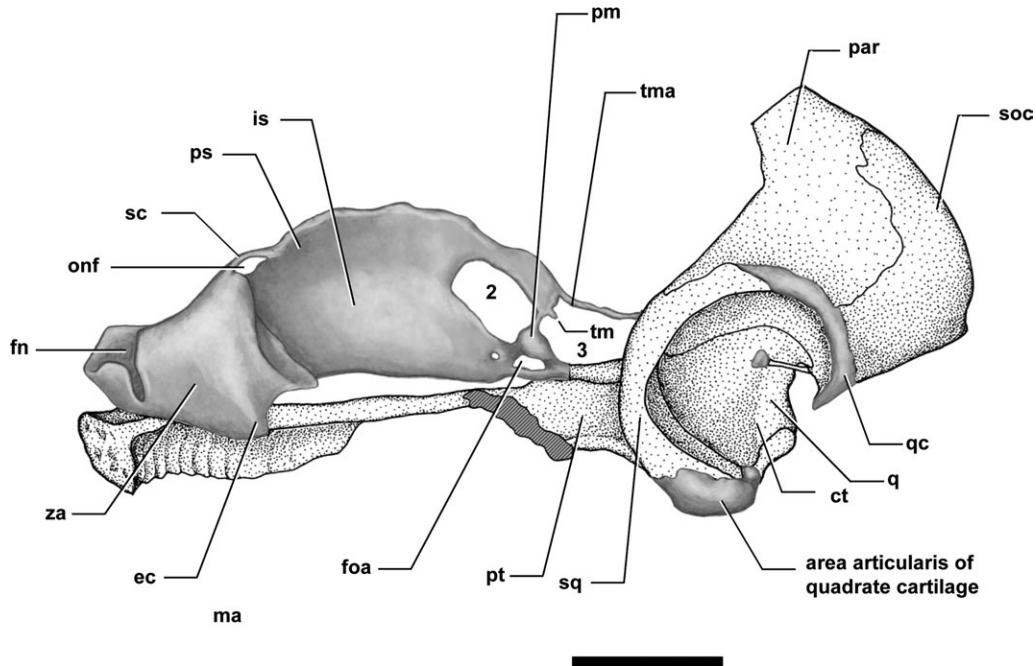


Fig. 3. Left lateral view of the mature chondrocranium of a hatchling *E. subglobosa*, showing the maximum extent of chondrocranial development, prior to major modification of cartilages via absorption or endochondral ossification. Dermal bones of the skull table and maxillary arcade have been removed to allow unhindered view of chondrocranium, particularly in the nasal and orbitotemporal regions. Gray denotes cartilage; stippling denotes bone; hatched lines denote cut bones. 2, foramen for optic nerve, cranial nerve 2; 3, foramen for oculomotor nerve, cranial nerve 3; ct, cavum tympani; ec, ectochoanal cartilage; fn, fenestra narina; foa, foramen for ophthalmic artery; is, interorbital septum; ma, maxilla; onf, orbitonasal fissure; par, parietal; pm, pila metoptica; ps, planum suprasedale; pt, pterygoid; q, quadrate bone; qc, quadrate cartilage; sc, sphenethmoid commissure; soc, supraoccipital; sq, squamosal; tm, taenia medialis; tma, taenia marginalis; za, zona annularis. Scale bar = 5 mm. Note, quadratojugal has been removed from this figure to improve the view of the taenia marginalis.

(1981), in which the identification of structures and spaces were explicitly defined by reference to neighboring cartilages, vessels, and nerves. In the orbitotemporal region, four primary anatomical spaces [fenestra epiotica (fep), fenestra prootica (fpr), foramen for cranial nerve 2 (2), and foramen for cranial nerve 3 (3)] were defined and bordered by five conspicuous structures [taenia marginalis (tma), taenia medialis (tm), pila accessoria (pacc), pila metoptica (pm), and pila antotica (pa); Fig. 4]. The taenia marginalis (tma) and taenia medialis (tm) were described, respectively, as outer and inner bars of cartilage that extend from the posterior margin of the planum suprasedale (ps; Bellairs and Kamal, 1981:20–21). The taenia marginalis is a long, slender bar that extends completely through the orbitotemporal region to contact the dorsolateral margin of the otic capsule, and forms the lateral and dorsal margins of the fenestra epiotica (fep); additionally, this structure contacts the ventral surface of the frontals and parietals in the orbit. The taenia medialis spans from the planum suprasedale to the dorsal margin of the pila metoptica (pm), forming the dorsal margin of the foramen for cranial nerve 2, at which point it is connected laterally to the taenia marginalis via the pila accessoria (pacc). Additionally, the taenia medialis extends posteriorly to contact the pila

antotica, which together form the dorsal and posterior margins of the foramen for cranial nerve 3.

Considerable work to describe chondrocranial diversity has been published for snakes and lizards (summarized in Bellairs and Kamal, 1981), but relatively little has been done with turtles. What has been published for Testudines suggests that this clade underwent some restructuring of the orbitotemporal cartilages and anatomical spaces and major changes involved the taenia marginalis and taenia medialis. For *Emys orbicularis* (Cryptodira: Emydidae), Bellairs and Kamal (1981:210) state that, "...the taenia marginalis is represented only by a short projection from the back of the planum suprasedale, and the pila antotica is not connected with the planum. Thus, there is a gap between the anterior and posterior orbital cartilage systems which corresponds with the fenestra metoptica..." Though there is no mention of early development of this region, all illustrations of the chondrocranium in *E. orbicularis* (Bellairs and Kamal, 1981:fig. 73) and *C. picta* (Bellairs and Kamal, 1981:fig. 72) are consistent with this written description, and at most show the taenia marginalis (tma) merely as a tiny, triangular projection from the posterolateral margin of the planum suprasedale. In a single figure of the adult chondrocranium of *Dermochelys coriacea*, Bellairs and

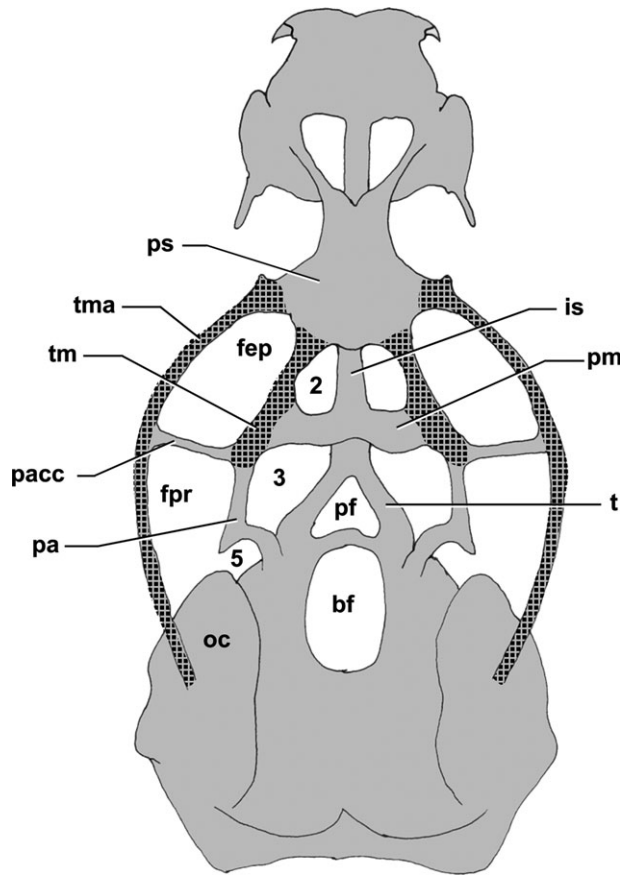


Fig. 4. The generalized condition of the reptile chondrocranium showing major anatomical spaces in the orbitotemporal region [modified from Bellairs and Kamal (1981:fig. 2)]. The margins of the foramen for cranial nerve 2 is formed by the interorbital septum (is), taenia medialis, and pila metoptica; the foramen for cranial nerve 3 is formed by the trabeculae (t), pila metoptica, pila antotica, and taenia medialis; the fenestra epiotica (which does not transmit nerves or vessels) is formed by the taenia marginalis, taenia medialis, and pila accessoria; and the fenestra prootica (which accommodates the passage of cranial nerves 5 and 7) is formed by the otic capsule, pila antotica, taenia marginalis, and pila accessoria. Hatch marks indicate either the taenia marginalis or taenia medialis. 2, foramen for cranial nerve 2; 3, foramen for cranial nerve 3; 5, foramen for cranial nerve 5; bf, basicranial fenestra; fep, foramen epiotica; fpr, fenestra prootica; is, interorbital septum; oc, otic capsule; pa, pila antotica; pacc, pila accessoria; pf, pituitary fenestra; pm, pila metoptica; ps, planum suprasedptale; t, trabeculum; tm, taenia medialis; tma, taenia marginalis.

Kamal (1981:fig. 79) imply a possible connection between the planum suprasedptale and the otic capsule via the taenia marginalis (tma); however, it is unclear whether or not a physical connection truly exists. Additionally, in their summary of chondrocranial anatomy among turtles, Bellairs and Kamal (1981:226) also stated that, "The planum suprasedptale is well developed and its fenestrations are less extensive than those of lizards. However, the taenia marginalis of some forms is incomplete (Fig. 73) so that there is a gap between the back of the planum suprasedptale and the pila antotica and otic

capsule [thereby leaving the fenestra prootica (fpr) open dorsally]." No mention was made of other taxa that retain or develop a connection between the planum suprasedptale and otic capsule via the taenia marginalis.

The anatomy of the orbitotemporal region of *Caretta caretta* (Cryptodira) was described in detail by Kuratani (1987, 1989, 1999). Of particular interest is his treatment and discussion of the taenia marginalis. Kuratani (1987:fig. 1a,b; "tm") labeled a structure as the taenia marginalis in a simplified reconstruction of the chondrocranium with associated extracranial structures. In subsequent illustrations (Kuratani, 1987:figs. 1–6), this structure appears as a rod or band of cartilage that spans the orbital region and forms the dorsal margin of the foramen for cranial nerve 2, and is confluent with the posterior margin of the planum suprasedptale and dorsal margin of the pila metoptica. Additionally, through these figures, it was inferred that this structure extends posteriorly to contact the dorsal margin of the pila antotica and eventually contacts the otic capsule. By Stage II (Kuratani, 1987:fig. 3), it was inferred (by means of dotted lines posterior to the foramen for cranial nerve 2) that a band of cartilage connects the structure labeled as the taenia marginalis and the otic capsule (but not illustrated contacting the otic capsule). The written description of the taenia

Fig. 5. Left lateral view of the chondrocranium in amniotes, showing possible evolutionary changes in formation of the orbitotemporal region in reptiles, particularly the taenia marginalis, taenia medialis, and pila antotica. Crocodylians, lizards, and tuatara exhibit a generalized anatomy of the mature chondrocranium in which the foramina for optic (2), oculomotor (3), and trigeminal (5) nerves are separated by the pila metoptica and pila antotica, and a conspicuous taenia marginalis spans the space between the planum suprasedptale and otic capsules, and a taenia medialis connects the planum suprasedptale with the pila metoptica and pila antotica. Cryptodiran and pleurodiran turtles exhibit different morphologies, in which the taenia marginalis is either present (the pleurodire *Emydura*, and the cryptodire *Caretta*) or absent/reduced (the cryptodire *Emys*), and the pila antotica is either present and large as in other reptiles (cryptodires) or absent/reduced (pleurodires). Among reptiles, the most dramatic modifications of the orbitotemporal region are observed among snakes (with highly kinetic skulls) and turtles (with akinetic skulls). Bird (*Anas*; de Beer, 1937:plate 96); Crocodylian (*Crocodylus*; Bellairs and Kamal, 1981:fig. 81); Snake (*Natrix*; Rieppel, 1993:fig. 7.4e); Lizard (*Acanthodactylus*; Rieppel, 1993:fig. 7.4d); Tuatara (*Sphenodon*; de Beer, 1937:plate 88); Cryptodires (*E. orbicularis*; de Beer, 1937:plate 92, from Kunkel, 1912); Pleurodires (*E. subglobosa*); Protherian Mammals (*Ornitorhynchus*; de Beer, 1937:plate 105). Gray denotes pila antotica; black fill denotes taenia marginalis. Abbreviations: 2, foramen for optic nerve, cranial nerve 2 (= fpo, foramen pseudopticum, sensu de Beer, 1937:plate 105, for *Ornitorhynchus*; = fo, optic foramen, sensu de Beer, 1937:plate 105, for *Ornitorhynchus*); 3, foramen for oculomotor nerve, cranial nerve 3 (= no, notch for oculomotor nerve, sensu de Beer, 1937:plate 96, for *Anas*); 5, foramen for trigeminal nerve, cranial nerve 5; fep, foramen epiphaniale; foa, foramen for ophthalmic artery; fs, fenestra septalis; nc, nasal capsule; oc, otic capsule; tm, taenia medialis; tma, taenia marginalis.

marginalis is not explicit and lacks detail to infer the sequence of events associated with connection of the planum suprasetale, pila metoptica, pila antotica, and otic capsules. Kuratani (1989) also provided a comprehensive review of orbitotemporal

anatomy for *C. caretta* through development, and offered some discussion of the homology of specific cartilages, as well as a comparison with those of a placental mammal (*Oryctolagus*, the European Rabbit). Illustrations (Kuratani, 1989:figs. 1a, 3, 4,

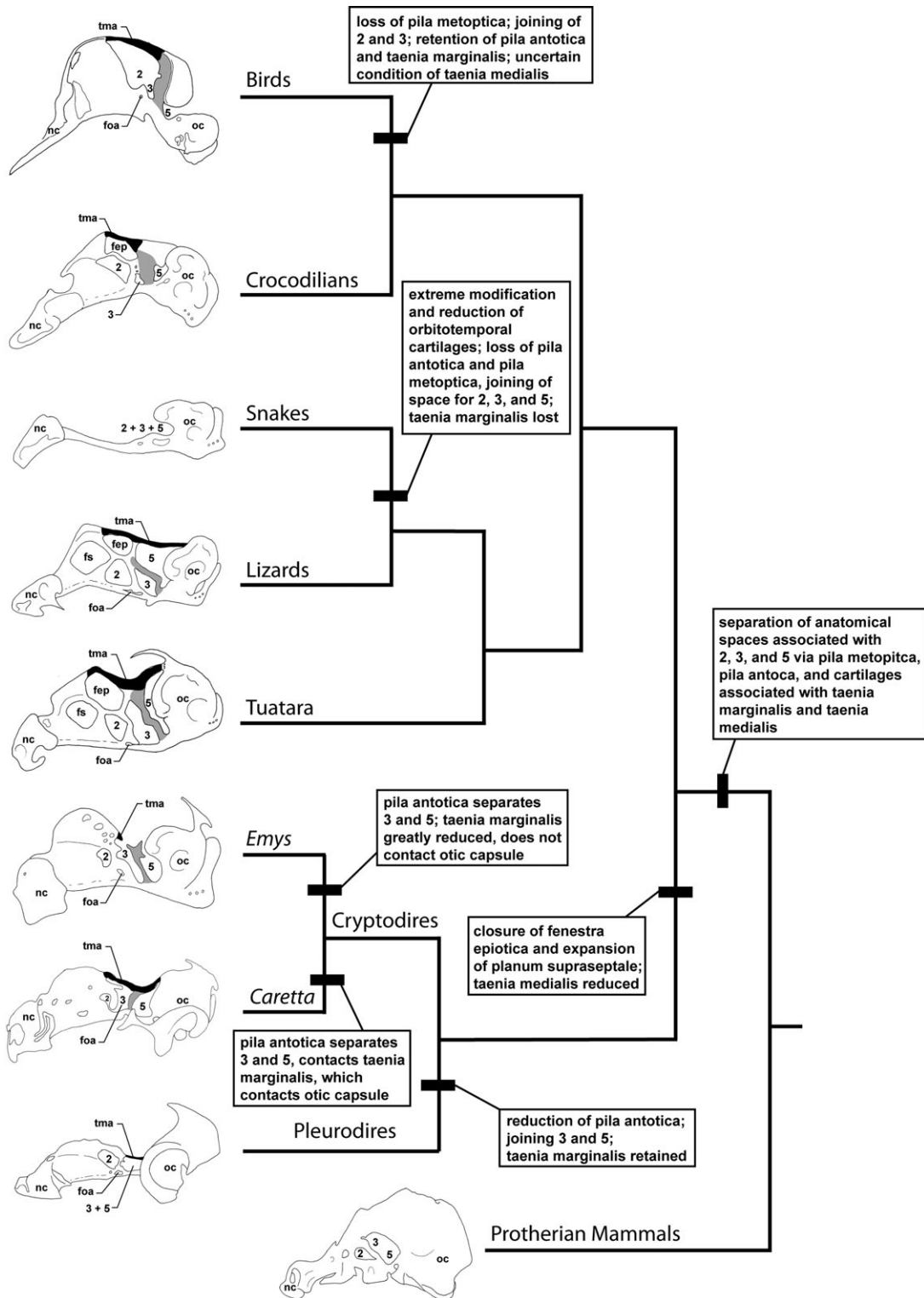


Fig. 5.

and 6) clearly show a band or rod of cartilage forming the dorsal margin of the foramen for cranial nerve 2, but none of these structures were explicitly labeled as the taenia marginalis. Though cartilage does span over the foramen for cranial nerve 2, contact between the dorsal margin of the pila metoptica and the otic capsule is not illustrated until Stages B and E (Kuratani, 1989:figs. 1a and 4b, respectively); interestingly, connection is not indicated between these structures in a younger Stage-D specimen (Kuratani, 1989:fig. 4a), suggesting some variation in the relative timing of this contact, or that this connection may be made and later lost. Throughout his written discussion of the homology of cartilages, there is no mention of the taenia marginalis. A more recent discussion of the cartilages in the orbitotemporal region in *C. caretta* is presented by Kuratani (1999). Kuratani (1999:807) states that by Stage III, "...the dorsal end of this process [the planum suprasedale] and that of the orbital cartilage are connected by a strip of cartilage, the taenia marginalis," thereby explicitly naming the band of cartilage that forms the dorsal margin of the foramen for cranial nerve 2 as the taenia marginalis. The only written mention of the taenia marginalis contacting the otic capsule appears in his description of a Stage-VII specimen (Kuratani, 1999:813), in which, "...the taenia marginalis is connected to the dorsal edge of the auditory capsule (Fig. 10a)." Illustrations throughout the paper are consistent with his written description.

We suggest that there has been some confusion concerning the identity of the taenia marginalis and taenia medialis, primarily because of the presumed derived morphology observed in turtles. Bellairs and Kamal (1981:20) identify the taenia medialis (abbreviated "tm" in their figures) as the inner bar of cartilage that passes from the planum suprasedale and pila metoptica (thereby forming dorsal margin of the foramen for cranial nerve 2), and joining the pila metoptica and antotica (Fig. 4). However, Kuratani (1987:188, 192, 195, 198; 1999:807) names this structure the taenia marginalis and uses the same abbreviation (tm) in all figures.

In an illustration of the orbitotemporal region of a pleurodiran turtle (*Phrynops hilarii*), Bona and Alcalde (2009:fig. 1) labeled the taenia marginalis (abbreviated "tm") as the band of cartilage connecting the pila metoptica and pila antotica, thereby forming the dorsal margin of the foramen for the oculomotor nerve (their "focn"), which is the foramen for cranial nerve 3. We suggest that this structure is in fact the taenia medialis, because it occupies the position of this structure as described in Bellairs and Kamal (1981). Though Vieira et al. (2010) presented some aspects of development in the neurocranium of *Podocnemis expansa* (another pleurodiran turtle), no mention was made of the taenia marginalis or taenia medialis.

The taenia marginalis has been identified in several cryptodiran turtles, though, again some confusion exists in terms of labeling this structure. Sheil (2003: *A. spinifera*), Sheil (2005: *M. temminckii*), Sheil and Greenbaum (2005: *C. serpentina*), and Tulenko and Sheil (2007: *T. scripta*) identified the taenia marginalis based on relative position as a small, triangular dorsolateral process from the planum suprasedale, but incorrectly used the abbreviation "tm" for this structure (which should be limited to use for the taenia medialis). To avoid confusion with the taenia medialis, and to be consistent with terminology and abbreviations used in Bellairs and Kamal (1981), the taenia marginalis should have been abbreviated "tma."

Perhaps the simplest way to explain the differences between Testudines and the general reptile condition is to assume that within turtles the foramen epiotica (fep) is closed and the planum suprasedale expands to occupy this space; additionally, the pila antotica has lost contact with the pila metoptica and taenia medialis. If the foramen epiotica (which does not transmit nerves or vessels that could be used as a point of reference, and has no known function) were closed, it would be possible for the taenia medialis and pila accessoria to remain essentially intact (though not demarked by boundaries), and still roof the foramen for cranial nerve 2 while forming a bridge between the pila metoptica, taenia medialis, and taenia marginalis. Most turtles differ from the general reptile condition by lacking contact between the pila antotica and pila metoptica and the only exceptions to this seem to be in a Stage-19 *Phrynops hilarii* (Bona and Alcalde, 2009:fig. 1) and an adult *D. coriacea* (Bellairs and Kamal, 1981:fig. 79).

The most explicit description of the taenia marginalis in a cryptodiran turtle that is similar in form to that seen in the general reptile chondrocranium can be found in Kuratani (1999:813), in which he states that in *C. caretta*, "...the taenia marginalis is connected to the dorsal edge of the auditory capsule (Fig. 10a)"—this structure is clearly illustrated in his Figures 10 and 11. Additionally, earlier formation of the taenia marginalis can be seen in his Figures 6–9. *Emydura subglobosa* is the second species of turtle to present a well-developed taenia marginalis that connects the planum suprasedale and the otic capsule.

Superficially, much of the chondrocranium of *E. subglobosa* is congruent with that observed in other turtles. However, hatchling *E. subglobosa* have a thin, conspicuous taenia marginalis that extends from the posterior margin of the planum suprasedale to the otic capsule, similar to the condition seen in *C. caretta* (Kuratani, 1987, 1989, 1999). These are the only species of turtles in which this condition is reported. However, it has been reported in several other species of turtles

(e.g., *A. spinifera* [Sheil, 2003], *C. serpentina* [Sheil and Greenbaum, 2005], *Eretmochelys imbricata*, *M. temminckii* [Sheil, 2005], and *T. scripta* [Tulenko and Sheil, 2006]) as a tiny process that extends from the posterior margin of the planum suprasetale and does not contact the otic capsule; rather, in these species it extends only slightly into the space that otherwise accommodates the oculomotor nerve (3) (Figs. 1–3; Sheil and Greenbaum, 2005:fig. 1).

Among other reptilian sauropsids (Fig. 5), the taenia marginalis is known to form a thin, rod-like contact between the planum suprasetale and the otic capsule in crocodylians (*Crocodylus*), tuatara (*Sphenodon*), and squamates (e.g., *Acanthodactylus*; Rieppel, 1993:fig. 5). *C. caretta* and *E. subglobosa* represent examples of the two major clades of turtles (Cryptodira and Pleurodira, respectively), each of which also shows the generalized reptile condition of the taenia marginalis, such that it forms a bridge between the planum suprasetale and otic capsule; in all other species of turtles, the taenia marginalis is greatly reduced. It may be possible that this structure is present in all species of turtles, but is a transient bridge of cartilage that forms and disappears quickly during development. This explanation, although possible, may not be probable, as many embryos at many stages have been examined by authors from a diversity of cryptodiran turtles, yet it remains otherwise undocumented. Because this connection is present in lizards, tuatara, crocodylians, and some turtles (Fig. 5), perhaps it represents a transient characteristic for modern reptiles that disappears during development in some advanced species (i.e., those with many highly derived character states), such as snakes (with kinetic skulls; Lee et al. [1999]) and turtles (with akinetic skulls; Simonette, 1963; Bellairs and Kamal, 1981:227; Rieppel, 1993). This structure also may be visible in early embryos of *E. subglobosa*; however, a more extensive investigation that examines specimens at earlier developmental stages is required. It will be necessary to determine whether the taenia marginalis is truly transient or if it persists into adulthood. Additionally, to understand the condition of the taenia marginalis and the taenia medialis as they interact with the otic capsule, pila metoptica, and pila antotica, it will be necessary to conduct studies that document the developmental history of these embryonic structures among a greater diversity of turtles, with the primary focus of addressing this issue. To discuss the evolutionary and developmental history of these structures in a more comprehensive manner, it may be necessary consider the monophyly of Cryptodira and Pleurodira, as well as the evolutionary placement of turtles among other reptiles, and the implications that these changes make to our understanding of chondrocranial evolution.

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