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Postparietal and Prehatching Ontogeny of the Supraoccipital in *Alligator mississippiensis* (Archosauria, Crocodylia)

Jozef Klembara*

Comenius University, Faculty of Natural Sciences, Department of Ecology, Bratislava, Slovak Republic

ABSTRACT The first record of the postparietal bone of *Alligator mississippiensis*, documented by transverse histological sections, is presented. It is the first evidence of the presence of this bone within Recent reptiles. The postparietal is present in a specimen with a head length of 32.3 mm. The bone is a small dermal plate lying ventrally and posteriorly to the posterior margin of the parietal and dorsally to the trabecular bone, forming a dorsal surface of the supraoccipital portion of the neural endocranium. The trabecular bone develops perichondrally from the dorsal surface of the tectal cartilaginous bridge spanning between the dorsal portions of the otic capsules and occipital pilae. The bridge probably represents the fused tectum synoticum posterior plus tectum posterius. Later in ontogeny, the bridge ossifies endochondrally. The endochondrally ossifying bridge together with its perichondrally ossifying trabecular bone form the future supraoccipital. The trabecular bone is the integral part of the cranial endoskeleton and ontogenetically distinct from the dermal postparietal bone. J. Morphol. 249:147–153, 2001.

KEY WORDS: Crocodylia; *Alligator mississippiensis*; ontogeny; postparietal; supraoccipital; homology

Although there is no general agreement on what bone in osteolepiform ancestors of tetrapods (extrascapular medial or the bone[s] lying immediately to it) is homologous with the postparietal in tetrapods (reviewed by Jarvik, 1996), there is general agreement that the postparietal bones (sometimes fused into an unpaired bone) of early tetrapods lie at the posterior margin of the dermal skull roof and may descend as flanges onto the posterior surface of the neurocranium (Romer and Parsons, 1977). In the evolutionary line leading to mammals, the postparietals gradually obtain the position at the posterodorsal margin of the occiput. The postparietal bone is synonymously also termed the dermal supraoccipital (or dermo-supraoccipital) or interparietal (Romer, 1976; Romer and Parsons, 1977).

Within Recent tetrapods, bones that are homologized with the postparietal bones of the extinct tetrapods develop ontogenically dorsally to the posteriormost cranial tecta, tectum synoticum, and tectum posterius, and have been occasionally recorded as independent bones in various ontogenetic stages in anurans and mammals. During ontogeny, these independent bones may fuse with the frontoparietals in anurans (Roček, 1981; Smirnov, 1992); in mammals they fuse with the dorsal margin of the enchondrally ossifying supraoccipital cartilage to form together the occipital bone (Romer and Parsons, 1977; Jarvik, 1996). However, they may also persist as independent bones in adult anurans (Smirnov, 1977) as well as in mammals (Wegner, 1960).

Since the earliest investigations of the skull anatomy of vertebrates in the nineteenth century, only two articles record the possible presence of the postparietal bone in Recent reptiles. Both records were made on crocodylians: in *Alligator mississippiensis* (described as dermo-supraoccipital by Mook, 1921) and in two species of *Crocodylus: C. palustris* and *C. porosus* (described as interparietal by Deraniyagala, 1939). Mook's dermo-supraoccipital was identified in dried skulls and Deraniyagala's interparietal in dried skulls and cleared embryos.

The postparietal was not recorded in the two cleared embryos of *Crocodylus niloticus* studied by Iordansky (1973). Rieppel (1993) studied the process of ossification of the supraoccipital of *Alligator mississippiensis* on cleared and stained embryos, but did not find a separate dermal postparietal ossification in his material. All hatchling and embryonic specimens of *A. mississippiensis* studied by Brochu (1999) lacked the postparietal bone.

The aim of this article is to describe prehatching ontogeny of the supraoccipital of *Alligator mississippiensis* and the first discovery of a completely inde-

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*Correspondence to: Jozef Klembara, Comenius University, Faculty of Natural Sciences, Department of Ecology, Mlynská dolina, 842 15 Bratislava, Slovak Republic. E-mail: klembara@fns.uniba.sk

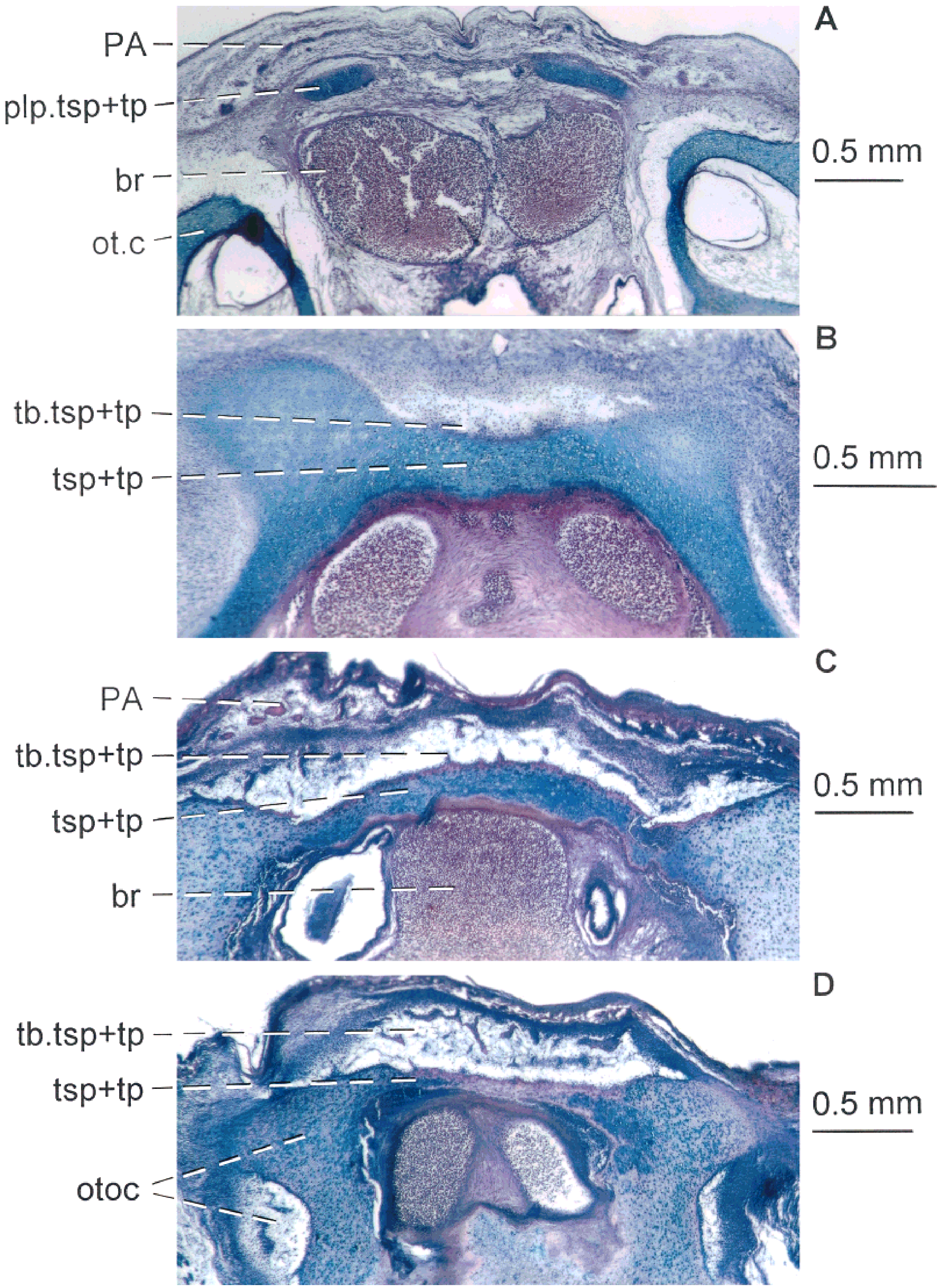
A
PA
plp.tsp+tp
br
ot.c
0.5 mm
B
tb.tsp+tp
tsp+tp
0.5 mm
C
PA
tb.tsp+tp
tsp+tp
br
0.5 mm
D
tb.tsp+tp
tsp+tp
otoc
0.5 mm

Figure 1

pendent postparietal dermal ossification recorded on transverse histological sections of an embryo of *A. mississippiensis*. A cartilaginous bridge, spanned between the posteriormost dorsal portions of the otic capsules and the occipital pilae, which ossifies as the supraoccipital, is variously called the tectum synoticum (Rieppel, 1993) or tectum posterius (Shiino, 1914). It probably represents the tectum synoticum posterior plus tectum posterius (tsp+tp) (de Beer, 1937; Klembara, 1991).

Rieppel (1993) calls the bone that develops from the dorsal surface of the tsp+tp during the early ontogeny of *Alligator mississippiensis* the trabecular bone (of dermal appearance). With growth, this bone fills the space between the endochondral supraoccipital ossification (ossifying in the tsp+tp) and the posterior margins of the parietals. For this portion of the future supraoccipital, which Rieppel (1993) calls the trabecular bone (of dermal appearance), I also use the term trabecular bone. It designates the trabecular architecture of the bone developing perichondrally from the dorsal surface of the tsp+tp. It is designated the tb.tsp+tp here.

MATERIALS AND METHODS

For this study, the following transversely sectioned ontogenetic stages of *Alligator mississippiensis* arranged according to the head lengths were used (FS — stages after Fergusson [1985]): Stage 5 (FS 21) — 17.9 mm; Stage 6B (FS 23) — 22.3 mm; Stage 7A (FS 24) — 23.8 mm; Stage 8A (FS 25) — 25.4 mm; Stage 9B (FS 27) — 32.3 mm; Stage 10A (FS 27) — 33.1 mm; Stage 11A (hatchling) — 36.5 mm. The thickness of histological sections of Stages 5, 6B, 7A, 8A, and 9B is 12 μm and of Stages 10A and 11A is 15 μm. The histological sections were stained with Alcian blue, erythrosin, and Mayers's hematoxylin. The specimens are from Florida, Dade County, Everglades National Park (collector: Dr. J.A. Kushlan), USA. Histological sections were examined and photographed using a WILD M8 stereomicroscope.

RESULTS

The following description of the ontogeny of the supraoccipital of *Alligator mississippiensis* starts at Stage 7, in which the perichondrally ossifying tb.tsp+tp first appears. It is followed by a description of the progressive growth of the tb.tsp+tp up to Stage 11A, at which stage the boundary between the endochondral ossification of the tsp+tp is almost indistinguishable from the tb.tsp+tp. The presence of the dermal postparietal bone in the Stage 9B is related to the ontogenetic status of the tb.tsp+tp. The latter structure conveys the impression of being a dermal ossification and it has been considered by some previous authors (see Discussion) to be a separate postparietal dermal ossification.

Stage 7A

In Stage 7A the anterior margin of the tsp+tp extends into a pair of plate-like processes (plp.tsp+tp, Fig. 1A) that are not connected by their lateral margins with the otic capsules and that are not connected together in the mesial plane. The dorsal surface of the posterior portion of the tsp+tp, in the depression bilaterally flanked by the cartilaginous elevations of the posteriormost portions of the otoccipital region of the endocranium, starts to ossify perichondrally. The perichondral cells form a distinct lining from which several clusters of cells spread slightly dorsally. They represent the initial phase of the formation of the future bony trabeculae (tb.tsp+tp, Fig. 1B).

Stage 8A

In Stage 8A, as in Stage 7A, the anterior margin of the tsp+tp bears two plp.tsp+tp. Immediately posteriorly, the tsp+tp is not covered with the trabecular bone. The bony lining and very short trabeculae cover the posteriormost section of the anterior third and the whole middle third of the length of the tsp+tp (tb.tsp+tp, Fig. 1C). It may be noted that in its posterior section the layer of the tb.tsp+tp is dorsoventrally thicker than the underlying cartilaginous tsp+tp (Fig. 1D). Some of the bony trabeculae spread slightly dorsally from the bony lining of the tsp+tp; however, most of them are situated more dorsally in the tissue and with no connection with the bony lining. The posterior section of the posterior third of the tsp+tp is not covered by trabecular bone. The cartilage of the tsp+tp shows no trace of resorption.

Stage 9B

In Stage 9B both of the anterior plate-like processes protruding from the anterior margin of the cartilaginous bridge (plp.tsp+tp) are still present, as in the two preceding stages. The tsp+tp is partially resorbed in this stage, most intensively in the middle section of its length, below the tb.tsp+tp (Fig. 2A–C). The tb.tsp+tp is well developed and it is thicker than the partially resorbed underlying

Fig. 1. *Alligator mississippiensis*. Transverse sections through the supraoccipital portion of the otoccipital region of the neurocranium of Stage 7A (**A,B**) and Stage 8A (**C,D**) in anterior to posterior sequence, respectively, showing the relative positions of the structures of the future supraoccipital. br, brain; ot.c, otic capsule; otoc, endochondrally ossifying posterolateral portion of the otoccipital region of the neural endocranium; PA, parietal; plp.tsp+tp, plate-like processes of the tectum synoticum posterior plus tectum posterius; tb.tsp+tp, trabecular bone developing from the tectum synoticum posterior plus tectum posterius; tsp+tp, tectum synoticum posterior plus tectum posterius.

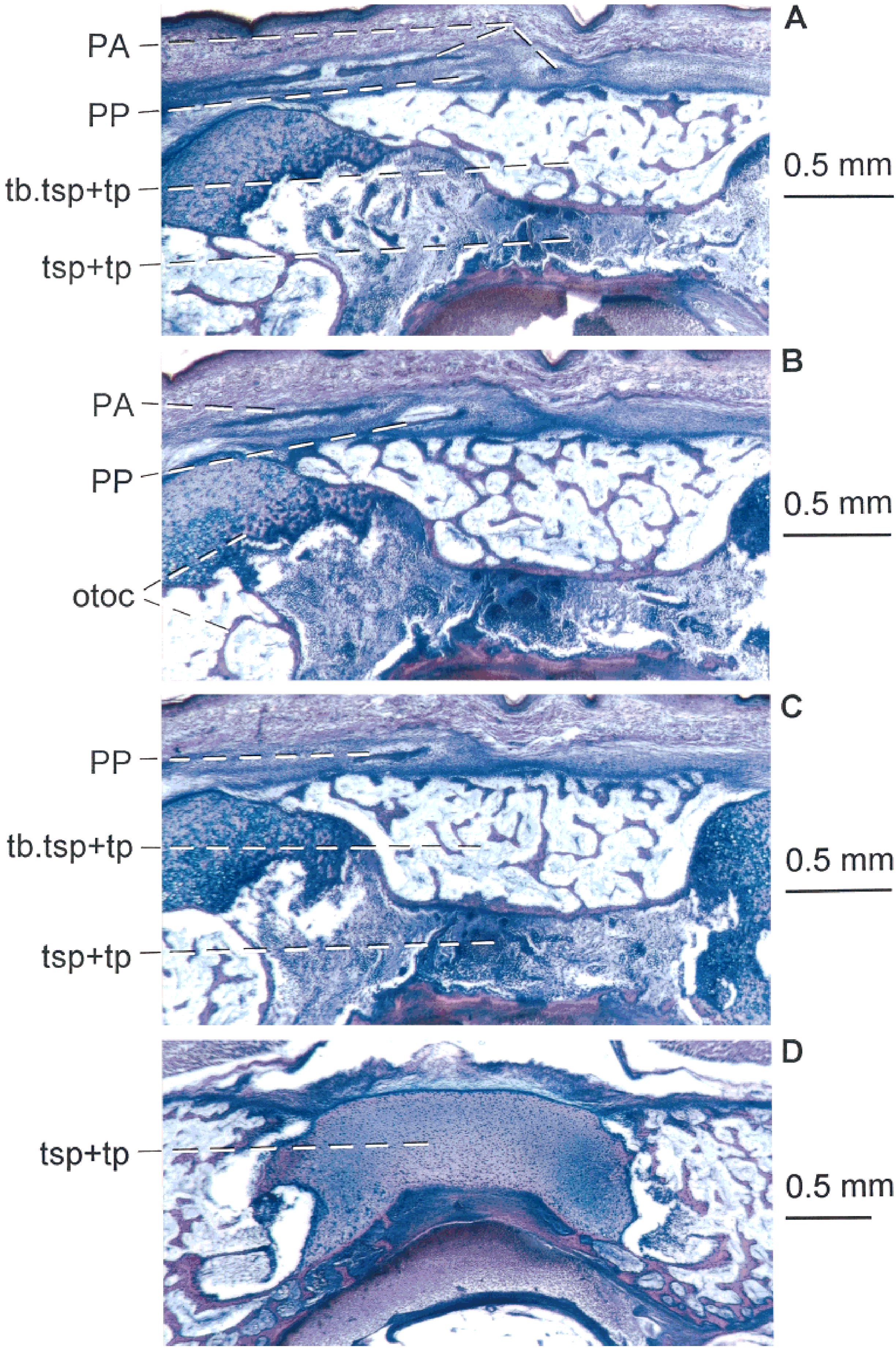
A
PA
PP
tb.tsp+tp
tsp+tp
0.5 mm
B
PA
PP
otoc
0.5 mm
C
PP
tb.tsp+tp
tsp+tp
0.5 mm
D
tsp+tp
0.5 mm

Figure 2

tsp+tp. There is no trace of separation between the tb.tsp+tp and the endochondrally ossifying tsp+tp. The posteriormost section of the tsp+tp remains cartilaginous and no tb.tsp+tp is formed here (Fig. 2D).

The bone interpreted here as the postparietal is present in Stage 9B on the left side of the head only (Fig. 2A–C). It is a small dermal plate lying immediately dorsally to the tb.tsp+tp and posteroventrally to the posterior margin of the parietal. No part of the postparietal is fused to the tb.tsp+tp or to the parietal.

Stages 10A and 11A

In Stages 10A and 11A, the tsp+tp is substantially resorbed in some portions, but it is mostly ossified through its length. The trabecular architecture of this endochondral ossification is basically identical to that of the tb.tsp+tp. In both stages no independent postparietal has been recorded. It would be impossible to recognize, once it had fused with the tb.tsp+tp or with the parietal during ontogeny.

DISCUSSION

The postparietal in Stage 9B is a very small bone relative to the size of the parietal or the supraoccipital portion of the endocranium. It is present only on one side of the head. It may be that the right–left asymmetry in the development of this bone is only intraspecific variation. The position of the postparietal on one side clearly indicates that this bone is not a median, unpaired element in *Alligator mississippiensis*, at least in the stage of its early ontogeny. The postparietal appears late in ontogeny; all other exocranial bones are already well developed.

The postparietal of *Alligator mississippiensis*, as identified in Stage 9B, casts doubts on the correctness of the identification of the dermo-supraoccipital of Mook (1921) and of the interparietal of Deraniyagala (1939) as an independent dermal bone of the posterior skull table. In addition, the identification of the postparietal in Stage 9B and its topology clarify relationship of the postparietal to the individual ontogenetic components of the supraoccipital.

Fig. 2. *Alligator mississippiensis* (S 9B). Transverse sections through the supraoccipital portion of the otoccipital region of the neurocranium in anterior (**A**) to posterior (**D**) sequence to show the relationship of the postparietal bone to the structures of the future supraoccipital. otoc, endochondrally ossifying posterolateral portion of the otoccipital region of the neural endocranium; PA, parietal; tb.tsp+tp, trabecular bone developing from the tectum synoticum posterior plus tectum posterius; PP, postparietal; tsp+tp, tectum synoticum posterior plus tectum posterius.

Dermo-supraoccipital of *Alligator mississippiensis* of Mook (1921)

Mook (1921) described a postparietal bone in two juvenile skulls of *Alligator mississippiensis*: 1) in the first skull (skull length, 35.3 mm), the postparietal lies posterior to the parietal and anterior to the supraoccipital and the postparietal is united with both bones by means of sutures; 2) in the second skull (skull length, 39.5 mm), the postparietal–parietal suture is obscure and the postparietal appears to be partially fused with the parietal.

The head length of the specimen examined here is slightly shorter than the skull length of the first skull of Mook (1921), in which the postparietal has been identified as a separate bone. However, because in specimens Stage 10A and S 11A no postparietal is present, the identification of the dermo-supraoccipital in larger specimens of *A. mississippiensis* by Mook (1921) seems doubtful. Further, in his specimens the dermo-supraoccipital is a relatively large bone, much larger than the postparietal as preserved in Stage 9B. The outline of the dermo-supraoccipital of Mook (1921) corresponds well with the outline of the portion of the supraoccipital ontogenetically formed by its trabecular bone component (tb.tsp+tp).

Interparietal of *Crocodylus* of Deraniyagala (1939)

Deraniyagala (1939) did not describe the process of fusion of the postparietal with the parietal or supraoccipital during ontogeny of *Crocodylus palustris* and *C. porosus*.

The interparietal of both species of *Crocodylus* of Deraniyagala (1939) has the same position and outline as the dermo-supraoccipital in *Alligator mississippiensis* of Mook (1921). The postparietal was not recorded in two embryos (skull lengths, 29.4 and 35.6 mm) of *C. niloticus* by Iordansky (1973) and it is absent in this genus in adult specimens (Iordansky, 1973; personal observation). Rieppel (1993) expressed doubts on the correctness of the identification of the dermo-supraoccipital of Deraniyagala (1939) and concluded that his illustrations suggest that his dermo-supraoccipital is nothing but the supraoccipital ossifying in the synotic tectum. However, Rieppel (1993), studying the process of the ossification of the otoccipital neurocranial structures of *A. mississippiensis*, did not exclude the possibility of the identification of this element as a dermo-supraoccipital. However, the skull length of the embryo of *C. palustris* with the interparietal (Deraniyagala, 1939: fig. 126) corresponds to about Stage 5 *A. mississippiensis*, and the tb.tsp+tp is not formed in embryos smaller than Stage 7A, while the cartilaginous bridge starts to ossify endochondrally even later. In this instance, knowledge of the sequence of ossification of the neurocranial structures in the skull of *Crocodylus* is needed. Nevertheless, as in the case of the dermo-supraoccipital of Mook (1921), the outline of the interparietals of Deraniyagala's (1939) *Crocodylus* specimens corresponds very well to the outline of the trabecular bone portion of the supraoccipital (tb.tsp+tp) in *A. mississippiensis*.

Ossification of the Supraoccipital in *Alligator mississippiensis*

Rieppel (1993) found that in his 53-day-old specimen of *Alligator mississippiensis* the trabecular bone (of dermal appearance) covered the entire endochondral supraoccipital ossification and filled the space between the endochondral supraoccipital ossification and the posterior margins of the parietals. He found no separation between the trabecular bone (of dermal appearance) and the underlying endochondral bone in the area of the supraoccipital. Rieppel (1993) concluded that additional histological investigations are required to clarify the relation between the endochondral and dermal ossifications in the area of the supraoccipital in *A. mississippiensis*.

The process of ossification of the supraoccipital described here differs slightly from that observed and described by Rieppel (1993) in cleared and stained embryos. The tb.tsp+tp does not start to develop on the anterior margin of the tsp+tp, as observed by Rieppel (1993), but rather about in the middle section of the tsp+tp length. Later, it spreads anteriorwards and posteriorwards. In Stage 8A (FS 25), the tb.tsp+tp is still absent dorsal to the anterior portion of the tsp+tp. Rieppel (1993) stated that in his 53-day-old specimen (FS 25) the parietals meet in the loosely defined suture in the dorsal midline of the skull, and the trabecular bone (of dermal appearance) covers the entire supraoccipital endochondral ossification (unfortunately, he did not report the cranial length of this specimen). In Stage 9B (FS 27) described here, the parietals are already fused in their posterior sections; hence, this specimen is of larger size than that of 53 days of Rieppel (1993). However, in Stage 9B the posterior section of the tsp+tp is not covered by the tb.tsp+tp (Fig. 2D). The postparietal as described here is a small, completely independent dermal plate lying dorsal to the tb.tsp+tp. Therefore, the tb.tsp+tp of the future supraoccipital on one side and the dermal postparietal bone on the other are two different structures. The tb.tsp+tp is a bone that develops from the perichondral lining of the tsp+tp, although it does possess a dermal appearance as stated by Rieppel (1993).

Homology of the Postparietal

Within extinct tetrapods, the postparietal is present in many early amphibian tetrapods (e.g., anthracosaurs, temnospondyls), in many early amniotes belonging to anapsids (e.g., captorhinomorphs, millerosaurs, pareiasaurs), early diapsids and archosaurs, and synapsids; it may be either a paired or an unpaired element (Carroll, 1988).

The postparietal as recorded in specimen Stage 9B of *Alligator mississippiensis* is the only record of this bone within Recent reptiles. Within other groups of Recent tetrapods, the dermal bone that develops dorsal to the tectum synoticum and tectum posterius and almost completely or completely behind the (fronto)parietal(s) has been recorded in several Recent anurans and mammals, both in embryos and in adults.

In anurans, this dermal bone is unpaired or paired and it mostly participates in the formation of the posteromedian portion of the compound frontoparietal complex (Jarvik, 1967; Roček, 1981; Smirnov, 1992, 1995, 1997; see also Sewertzoff, 1891, and Luther, 1914). According to Jarvik (1967, 1980, 1996; see also Roček, 1981, 1988), this anuran median element is probably homologous with the median extrascapular (os iniacum in the sense of Bjerring, 1995) of osteolepiform fishes. According to Smirnov (1997), the bones lying on the tectum synoticum in *Bombina orientalis* exactly correspond in their topology to the postparietals of many labyrinthodont tetrapods, and they must be considered homologous (see also Smirnov, 1995, for *Pelobates fuscus*). In *Discosauriscus austriacus*, a Lower Permian seymouriamorph tetrapod, the postparietals are paired bones, but occasionally fuse together, forming one median postparietal (Klembara, 1993, 1995). According to Klembara (1994, 1996), the postparietals of *D. austriacus* are homologous with the median extrascapular, originally probably paired (Jarvik, 1980), of osteolepiforms.

In Recent mammals, the dermal bone that develops dorsal to the tectum synoticum plus tectum posterius is called the interparietal (reviewed by Wegner, 1960) and it generally develops as a paired element. Later in ontogenesis, both elements fuse into one median interparietal (Kadam, 1973; Köhncke, 1985; Timm, 1987). This may occasionally persist as an independent bone in adults, but normally it fuses with the dorsal portion of the enchondrally ossifying supraoccipital, and is thus included in a single occipital bone. However, in ruminants and some rodents the interparietal fuses with the parietal (Stadtmüller, 1936). According to Jarvik (1996), the interparietal of *Homo sapiens* is homologous with the medial extrascapular of the osteolepiform fish *Eusthenopteron foordi*.

It is highly probable that all these bones, paired or unpaired, having the same topology as the postparietal in Stage 9B of *Alligator mississippiensis*, are homologous structures.

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