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A Study on Biliary Ductal System and Bile Fistula in the American Alligator, *Alligator mississippiensis*

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ABSTRACT The anomalous arrangement of bile ducts in the Crocodylia has not been fully appreciated. A clear understanding of biliary anatomy is necessary in order to create complete bile drainage in these reptiles. The object of this study was to clarify the anatomy of the bile ductal system and to establish total bile fistulas in the American alligator, *Alligator mississippiensis.* Bile duct anatomy was studied in 104 juvenile alligators, and bile fistulas were constructed in seven alligators. In 93 out of 104 (89%) of the juveniles dissected there was an interconnection between the right and left hepatic duct before the right hepatic duct emptied into the gallbladder. The left hepatic duct then entered the duodenum independently of the cystic duct which drained the gallbladder directly into the duodenum. In 8% of the animals, the left hepatic duct did not enter the duodenum but joined with the right duct, forming a common hepatic duct that emptied into the gallbladder. In 3% of the cases, the right hepatic duct emptied into the gallbladder, while the left duct had no communication with the right hepatic duct and drained separately into the duodenum. This arrangement of bile ducts is similar to that seen in birds and reflects the common ancestry of crocodiles and birds. In other reptiles, the biliary system shows much more variability and is different from the alligator. In five of seven alligators in which total biliary diversion was attempted, the biliary catheter remained in place and stayed patent from 2–7 weeks. Bile flow was extremely low (1.5–2.5 ml/24 h) when compared to that of mammals (80–100 ml/24 h). This study demonstrates the variable nature of the biliary ductal system in *Alligator mississippiensis* and suggest a method for constructing an effective total bile fistula in these animals. *J. Exp. Zool. 279:554–561, 1997.* © 1997 Wiley-Liss, Inc.

In our earlier studies on bile acid metabolism in the American alligator (*Alligator mississippiensis*), we reported that 3α, 7α, 12α-trihydroxy-5β-cholestanoic acid (THCA), 3α, 7α-dihydroxy-5β-cholestanoic acid (DHCA), and 3α, 7α, 12α-trihydroxy-5α-cholestanoic acid were the principal components of bile in the species (Tint et al., ’80, ’81). In order to determine if these bile acids are normally produced exclusively in the liver and are not the result of secondary metabolism, we attempted to establish a total bile fistula in the alligator. However, it was found difficult to maintain a functioning fistula and to obtain adequate bile flow. This led us to examine in detail the anatomy of the extra hepatic bile ducts in these animals.

Anatomical variation in the bile ducts of vertebrates has been noted for more than a century (Weidersheim and Parker, 1897), and gastrointestinal surgeons are well aware of the potential variation in the human gallbladder and bile ducts (Hatfield and Wise, ’76 Hicken et al., ’49; Linder et al., ’76). We are not aware of any studies that have actually quantified the variation seen in a nonhuman species. The brief description of the alligator gallbladder and ductal system by Chiasson (’62) gave no indication of any variation in the anatomy and is in fact incorrect. The earlier descriptions, however, appear to be more accurate. Rathke (1866) described the biliary anatomy in *Crocodylus rhombifer, Alligator lucius = A. mississippiensis, A. cynocephalus = Caiman latirostris,* and *A. Palpebrosus = Paleosuchus*

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plapebrosus, and Taguchi ('20) pointed out some variation in the ductal anatomy in his description of the gallbladder and the biliary ductal system from a total of five specimens that included *Alligator sinensis, Crocodylus porosus,* and *Crocodylus vulgaris* = *C. niloticus*. Wettstein ('54) also described the biliary system of *Crocodylus*. Wu and Chen ('94) mentioned individual variation in the branches of the bile ducts of four specimens of *Alligator sinensis*. We had the opportunity to examine in detail the anatomy of the biliary ductal system of 104 American alligators and were able to clarify some of the confusion in the literature. Our experience with preparing a total, competent, and long-lasting bile fistula in alligators, described here, should aid investigations of bile salt metabolism in this species.

MATERIALS AND METHODS

Biliary anatomy

Viscera from 104 juvenile alligators (90–150 cm total length) were collected from commercial alligator farms in southwestern Louisiana. The liver, gallbladder, extra hepatic ducts, stomach, and duodenum were collected en bloc for our study. Blunt dissection exposed the gallbladder and the various bile ducts, and measurements were made. A drawing of the gallbladder and biliary duct of each individual was made. To confirm the identity of the structures, histologic examinations were carried out using 10% formalin-fixed tissue from five animals. In addition, radiopaque contrast (3–8 ml) was injected into these gallbladders to visualize the biliary drainage pattern radiographically.

Bile fistula

Bile fistula were established in three female and four male alligators weighing 4.1–5.9 kg (total length 104–114 cm). Nembutal (pentobarbital sodium, 50 mg/ml; Abbott Laboratories, North Chicago, IL) was given intraperitoneally at a dose of 20–30 mg/kg. Induction of anesthesia followed in about 1–2 h. Alligators were taped to an operating table prior to surgery. A midline incision of about 8 cm was made just below the rib cage, and the gallbladder was mobilized from the mesoduodenum and the cystic duct, dissected, and ligated. Cholecystostomy was made by insertion of silicone tubing (0.040 in. ID x 0.085 in. OD; Dow Corning, Midland, MI) into the gallbladder and fixed with a purse-string suture. The tubing was exteriorized through a dorsal subcutaneous channel to an area near the hind legs of the animal. The exteriorized tubing was fixed by tape and inserted into an 18 oz plastic bag (Whirl-Pak sterile sampling bag; Fisher Scientific, Springfield, NJ) which was also secured by tape for bile collection and volume measurements. We used this method to construct bile fistula in the first three alligators before we had completed our survey in biliary ductal anatomy. After we were fully aware that in most but not a few alligators the left hepatic duct had direct connection with the duodenum, we modified the method mentioned above. After ligation of the cystic duct, the left hepatic duct was dissected in mesoduodenum, double-ligated, and transected between the ligations. The procedure followed for cholecystostomy and externalization of the bile drainage tubing was the same as mentioned above. This modified method was employed in four alligators. Alligators were maintained in dry tanks for 5–7 days postoperatively and then placed in environmental chambers at 29°C and maintained on a dry pelleted diet as previously described (Joanen and McNease, '87).

Assay for bile acids

Bile samples were stored at –20°C until assayed. Bile acids were processed for analysis as previously described (Tint et al., '80, '81, '86, '90). One milliliter of bile was deproteinized and the bile acids deconjugated and then methylated. Finally, trimethylsilyl ether derivatives of the bile acids were prepared and quantitated by gas chromatography.

RESULTS

Gross anatomy

The gallbladder of the alligator is an oblong, thin-walled sac situated just under the right lobe of the liver. In the juvenile alligators we studied, gallbladder size was 42 x 13 mm (Table 1). In 93/104 (89%) of the alligators studied, bile flows from

TABLE 1. Measurements of alligator gallbladder and bile ducts

Gallbladder length × width	Cystic duct (width mm)[1]		Hepatic duct (width mm)[1] Left		Hepatic duct (width mm)[1] Right	
42 ± 5 × 13 ± 2	1.5 (4)	2.0 (96)	1.0 (64)	1.5 (36)	1.0 (11)	1.5 (89)

[1]The percentage of animals with the measurements (mm) indicated from a total of 53 specimens is given in parentheses.

the liver by way of a short right hepatic duct and a longer left hepatic duct. The right duct drains directly into the gallbladder. The left hepatic duct splits into two branches, one of which is connected to the right hepatic duct and one of which drains directly into the duodenum (Figs. 1, 2). Both the right and left hepatic ducts show numerous proximal anastomotic branches. Morphological variations in these communications and the relative positions of the right and left hepatic ducts are not unusual. This arrangement of bile ducts comprises the predominant pattern present in the majority of alligators. Less commonly, in 8/104 or about 8% of the specimens, the left hepatic duct does not enter the duodenum but joins with the right duct just prior to entry into the gallbladder (Fig. 3A). The least common pattern, seen in only 3/104 or less than 3% of the alligators, is a total separation of the right and left hepatic ducts. The right hepatic duct drains into the gallbladder, while the left hepatic duct drains independently into the duodenum (Fig. 3B). There is no interconnection between the two hepatic ducts in this pattern. Measurements of gallbladder size and of the diameter of the ducts is given in Table 1.

Histologic findings

Histologic findings confirmed that the putative sections of cystic and hepatic ducts are biliary ducts and not blood vessels.

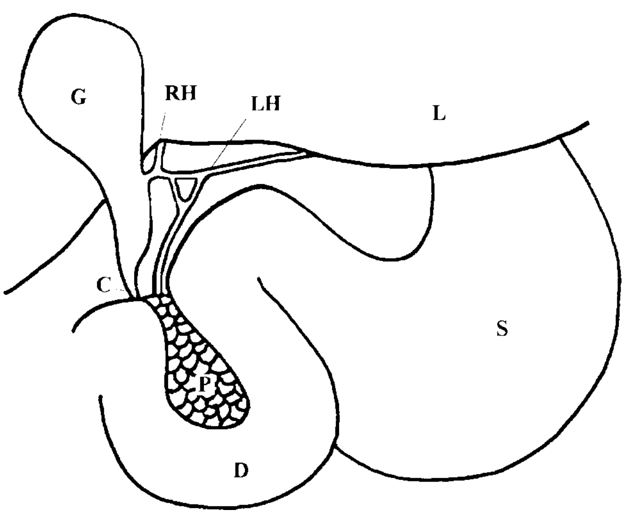

Fig. 1. The biliary system of the alligator seen in 89% of the specimens examined (pattern 1) showing an interconnection between the right and left hepatic ducts. The right hepatic duct drains into the gallbladder, which connects with the duodenum via the cystic duct. The left hepatic duct goes down through the pancreas and joins the duodenum directly. C, cystic duct; D, duodenum; G, gallbladder; L, liver; LH, left hepatic duct; P, pancreas; RH, right hepatic duct; S, stomach.

Radiologic findings

Radiopaque contrast injected into the gallbladder filled the right and left hepatic ducts in a retrograde manner (Fig. 4). The pattern confirmed a direct communication between the right hepatic duct and gallbladder, interconnection between right and left hepatic ducts, and flow from the left hepatic duct into the duodenum. Outflow from the gall bladder to the duodenum via the cystic duct was observed. The radiologic outline of the gallbladder and biliary system confirmed the predominant anatomic pattern seen in Figure 1.

Bile fistula

Bile fistulas were constructed is seven alligators. The animals recovered without incident and were able to eat their regular food and return to aquatic conditions 1 week after surgery. Two of the seven fistulas failed either because of kinking in the fistula tubing or because little bile flowed out of the fistula. In the remaining five animals, the external fistula remained in place and patent from 2–7 weeks. In these five animals, bile output averaged 1.5–2.5 ml/24 h (Table 2). In the longest bile fistula experiment (alligator 7), bile flow decreased from 4.3 ± 0.6 ml/24 h during the first 3 weeks to 2.5 ± 3.1 ml/24 h during the last 4 weeks. Table 3 shows the change in biliary outputs of the major bile acids in alligator 5 after 14 days with an intact fistula. The total biliary bile acid output decreased from 545 µg/h in the first 24 h to 78 µg/h after 14 days. During this period the ratio of THCA to DHCA declined from 8.1 to 1.3:1. After 14 days with a functioning bile fistula, these two bile acids composed 95% of the total biliary bile acid.

DISCUSSION

The standard description of the extrahepatic ducts in the alligator depicts a long hepatic duct from the left lobe of the liver draining into the gallbladder, a shorter duct from the right hepatic lobe emptying into the gallbladder, and a third duct from the right lobe of the liver joining the cystic duct to form the common bile duct (Chiasson, '62). Our findings are at variance with this description. First, the main drainage from the gallbladder to the duodenum is through the cystic duct and not a common bile duct. The latter structure was not found in our dissections. A common bile duct probably does not occur in the Crocodylia (Rathke, 1866; Taguchi, '20; Wettstein, '54; Wu and Chen, '94). Second, the left hepatic duct usu-

Fig. 2. A photograph of dissected alligator viscus showing similar biliary ductal system to pattern 1.

ally empties directly into the duodenum (see Figs. 1, 3) and in only 8/104, or about 8% (see Fig. 2), indirectly into the gallbladder. Third, the right hepatic duct invariably drains into the gallbladder. It does not join the cystic duct, not does it enter the duodenum. Wu and Chen ('94) describe a pattern essentially similar to Figure 1 in the bile ducts of four Chinese alligators (*Alligator sinensis*), and similar patterns for *Crocodylus vulgaris* = *C. niloticus* were described by Taguchi ('20).

The Crocodylia are more closely related to birds than to either the Chelonia or the Squamata (Gautier et al., '88), and the biliary ductal system reflects this close affinity. In birds, as in the Crocodylia, the left hepatic duct (hepato-enteric duct) enters the duodenum independently of the cystic duct, and there is no common bile duct (Crompton and Nesheim, '72; McLelland, '79). We are not aware of any studies on the anatomical variation of the biliary system in birds.

Among the other reptiles, the ductal anatomy is clearly different from that of birds and crocodiles. In the squamates, the biliary system has not been described in any detail, but there appears to be considerable variation among species, some with separate cystic and hepatic ducts that enter the duodenum through the pancreas and some with a single cystic duct that passes through the pancreas (Guibé, '70; Moscona, '80). A common bile duct has been described in the snakes, *Natrix piscator* (Sabnis, '67) and Typhlops (Robb, '60). In the lizard, *Sceloperus occidentalis*, the hepatic duct and the cystic duct enter the duodenum separately (Ells, '54). In a detailed study on the biliary ductal system of the European pond turtle, *Emys orbicularis*, Dornesco and Zaharia ('67) describe a cystic duct from the gallbladder to the duodenum and single hepatic duct that splits into two branches, one of which enters the gallbladder and the other of which enters the duodenum. However, in turtles *Chrysemys punctata* and *Kinosternon* there is but a single cystic duct entering the duodenum (Guibé, '70).

Our study is the first in which the variation in a large series of dissections of a nonhuman species has been quantified. In a review of the variations encountered in the human biliary ductal system, Lindner et al. ('76) discuss anomalies in

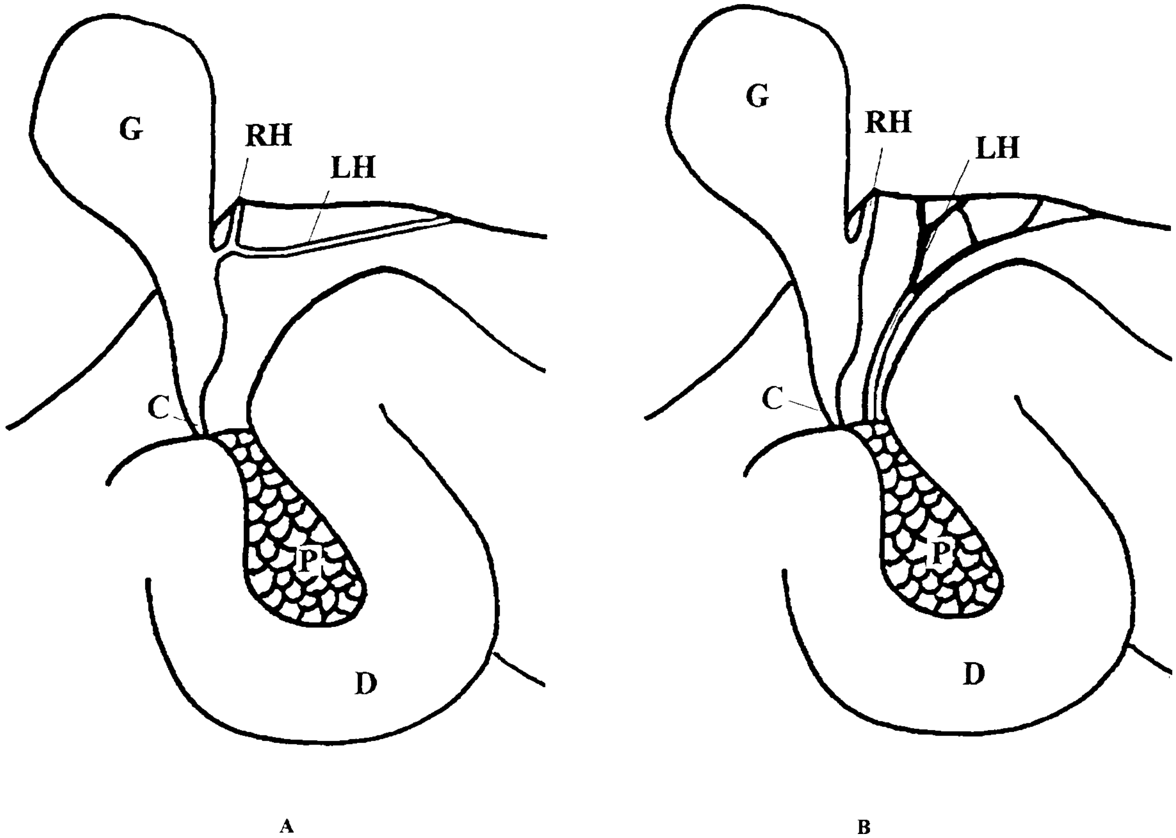

Fig. 3. **A:** The bile duct system seen in 8% of the alligators (pattern 2). This pattern is similar to pattern 1 except that the left hepatic duct does not enter the duodenum but drains into the gallbladder. Abbreviations as in Fig. 1. **B:** The bile duct system seen in 3% of the alligators (pattern 3). The right (via cystic duct) and left hepatic ducts have no interconnection with each other and empty independently into the duodenum. Abbreviations as in Fig. 1.

the site of entry of the common bile duct into the duodenum but do not discuss variations in the anatomy of the left and right hepatic ducts. They reported anomalies ranging from 5.6 to 23% in a very large sample. The difference in drainage patterns we observed in the alligator accounts for some of the difficulties we encountered in preparing a total biliary diversion. Our study suggested for the first time that it is possible to prepare biliary fistulas in alligators that remain competent for a considerable period of time. As mentioned above, in most alligators (92%), there are two paths of bile flow into the duodenum: 1) a cystic duct from the gallbladder which collects all of the bile drained from the right hepatic duct and some bile (in 89% of the alligators) through a connection with the left hepatic duct and 2) a left hepatic duct (or hepato-enteric duct). To obtain a total diversion of bile, either both the cystic and left hepatic ducts are cannulated (suitable in 92% of cases) or both ducts are isolated and ligated and bile is drained through a cholecystostomy (suitable for all cases). The first method for total bile diversion is ideal. However, it is also far more than difficult to perform because the cannulation has to be carried out inside a very deep and narrow rib cage. This method was not used in this study. The second method for total bile fistula is more practical, although some problems still remain. Preliminarily, in this study, we only ligated the cystic duct and drained the bile through cholecystostomy so that it probably did not represent total biliary diversion. Then we attempted to apply the second method in four alligators. We were certain that in two of the four animals the left hepatic duct was successfully ligated, while in another two the ligated "duct" was not confidently identified. In one successful case (alligator 7), this method produced the best result among all seven alligators in which surgery for biliary fistula was performed. The fistula lasted 48 days with a bile output averaging 2 ml/day. However, the same procedure employed on another alligator (alligator 11) proved unsuccessful, and very little bile came out

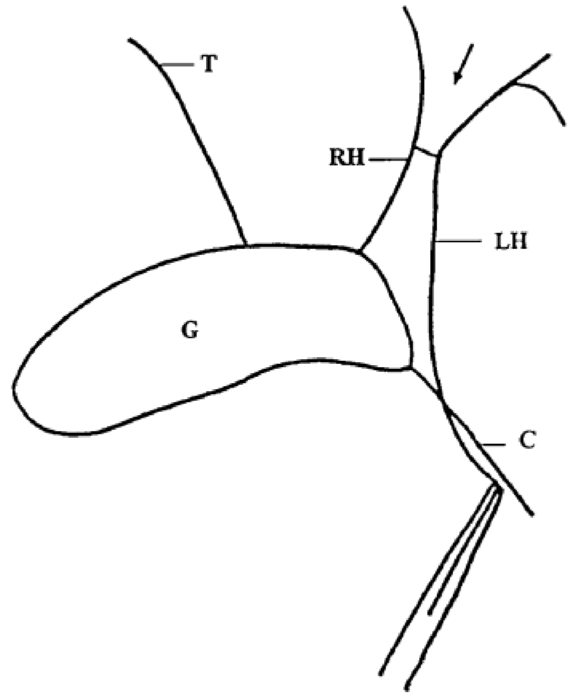

Fig. 4. **A:** A radiograph of the biliary tree of an alligator. After radiopaque contrast has been injected through the gallbladder, the dye fills the right and left hepatic ducts. **B:** An illustration mirroring the X-ray picture in A. The arrow points to the interconnection between the right (RH) and left (LH) hepatic ducts. T, the tubing through which the radiopaque contrast is injected into the gallbladder. The dye in the right hepatic duct drains into the gallbladder (G) and flows into the duodenum via the cystic duct (C). The left hepatic duct and its distal end (clamped in this picture) directly joins the duodenum.

of the fistula after its establishment. Two possibilities might account for the failure: 1) alligator 11 may have been an individual (pattern 3) in which the left hepatic duct had no communication with the right hepatic duct, or 2) the silicone tubing that drained the bile through cholecystomoy was positioned such that the tip of the drainage tubing was blocked by the wall of the gallbladder.

An important consideration in the performance of surgery on alligators is the dosage of anesthetic. Nembutal is generally recommended at a dose of approximately 10–30 mg/kg to induce anesthesia in reptiles (Bennett, '91). Some authors have advised that a dose of 7–9 mg/kg be given intramuscularly (Brisbin, '66) or 7–9 mg/kg intraperitoneally (Jones, '77). Our experience suggests that a larger dose of Nembutal is re-

TABLE 2. Bile fistula in alligators: Bile flow and duration

Animal	Bile flow (ml/24 h)	Duration (days)
A-5	1.7 ± 0.6	22
A-6	2.2 ± 0.8	18
A-7	2.5 ± 1.0	48
A-8	1.8 ± 1.0	14
A-9	1.5 ± 0.7	16

TABLE 3. Biliary bile acid output in an alligator[1]

Time	THCA	DHCA	CA (μg/h)	CDCA	DCA
First day	378.2	46.5	64.9	35.4	20.1
10 days	57.0	42.8	4.9	2.4	0.8
14 days	41.7	32.2	3.2	0.3	0.1

[1]Time indicates days after fistula was constructed. THCA, 3α,7α,12α-trihydroxy-5β-cholestanoic acid; DHCA, 3α,7α-dihydroxy-5β-cholestanoic acid; CA, cholic acid; CDCA, chenodeoxycholic acid; DCA, deoxycholic acid.

quired for abdominal surgery. We recommend that animals with body weights of around 5–7 kg be given an initial dose of 100 mg Nembutal (approximately 20 mg/kg) intraperitoneally. After 1–2 h of observation, another dose of 50 mg may be given if the animals are still not immobilized. With our regimen of larger doses, the alligators take at least a full day to recover, and in some instances up to 48 h, but without any apparent aftereffects. This is in contrast to the shorter recovery period of 2–3 h reported by Brisbin ('66) for animals receiving the usual recommended doses of Nembutal. However, for surgery of the biliary ductal system, the deeper anesthesia is necessary.

A surprising finding in this study was that even in the most successful fistulas bile flow did not exceed 4.3 ml for the first 24 h and averaged only 2.4 ml/24 h after 4 weeks. This is in marked contrast to studies in the rabbit in which initial bile flow averaged 207 ml/24 h and 82 ml/24 h after 5 days (Xu et al., '92) and the nutria (*Myocastor coypus*) in which a bile flow of approximately 104 ml/24 h was recorded (Tint, '86). As this is the first attempt at a bile fistula in a reptile, we do not know at present if such a low rate of bile secretion is normal. It is possible that part of the bile flowed into the duodenum via the left hepatic duct in those animals without ligating this duct. However, in the most successful case (alligator 7) with a ligated left hepatic duct, bile flow rate was higher than others but not significantly. It is most possible that low bile output reflects the very slow metablism in alligators. In the domestic fowl, a bile rate of 12–24 ml/24 h was estimated (Lind, '67). Gallbladder volume in fasted snakes is twice that of fed snakes, indicating a rapid emptying following a meal, but secretion rates have not been measured (Secor et al., '94, '95). The alligators with bile fistulas resumed feeding 1 week after surgery, but there was no obvious change in bile flow at this time.

The total biliary bile acid output in bile fistula alligators decreased from 545 µg/h to 76 µg/h in 2 weeks. The first 24 h bile acid output could be regarded as biliary bile acid flux in the alligator. The bile acid output was very low (545 µg/h) compared with our previous data from New Zealand white rabbits (32,900 µg/h), almost 100-fold lower (Xu et al., '92). This low bile acid output may reflect a slower metabolic rate in alligators (Coulson and Hernandez, '83) or may be the result of a complete shutdown of the digestive system, as is seen in fasted snakes (Secor et al., '94, '95). The bile acid output reached a plateau (77 µg/h) after 14 days. This may be the maximum hepatic bile acid synthesis rate in alligators. The composition of the bile collected through a fistula in alligators suggests the THCA and DHCA are the normal major bile acids in the alligators, as previously reported by Haslewood ('78) and Tint et al. ('80). However, in humans these bile acids are potentially hepatotoxic intermediates for the primary bile acid, cholic acid. In an autosomal recessive disease, Zellweger syndrome, oxidation and cleavage of the side chain of bile acid precursors are deficient, and bile acid intermediates such as THCA and DHCA accumulate and become the major portion of the bile acid pool (Hanson et al., '79; Mathis et al., '80). These two bile acids form the bulk of the bile in the alligator. How the alligator is able to tolerate high levels of these potentially hepatoxic bile acids is not known.

After 14 days of bile diversion in the alligator, it was noted that the C_{24} bile acids (cholic, denodeoxycholic, and deoxycholic acids) declined to almost zero, while dihydroxy C_{27} bile acid remained unchanged (Table 2). This result is difficult to explain without further research. It is possible that alligators lack the enzyme system necessary to metabolize these intermediate products to C_{24} bile acids, as suggested by Haslewood ('78). When bile was drained completely, the reduction of THCA, in addition to the already deficient enzyme system for cleavage of the side chain of these precursors, may have been the cause for the near disappearance of C_{24} bile acids. The buildup of these C_{27} bile acids in an alligator with a bile fistula suggests that this may be an ideal animal model to study this defect in bile acid metabolism as seen in patients with Zellweger syndrome.

In summary, the biliary anatomy of the alligator appears to differ significantly from that described by Chiasson ('62). Our study provides a thorough description of the morphology and potential variations of the bile ductal system in *Alligator mississippiensis*. These findings should provide a firm basis for further research on the biliary metabolism in alligators, which can be a valuable model for some diseases states in humans.

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LITERATURE CITED

Bennett, R.A. (1991) A review of anaesthesia and chemical restraint in reptiles. J. Zoo. Wildl. Med., *22*:282–303.

Brisbin, I.L. (1966) Reactions of the American alligator to several immobilizing drugs. Copeia, 1966:129–130.

Chiasson, R.B. (1962) Laboratory Anatomy of the Alligator. W.C. Brown Publisher, Dubuque, IA.

Coulson, R.A, and T. Hernandez (1983) Alligator metabolism, studies on chemical reactions in vivo. Comp Biochem. Physiol. [B], *74*:1–182.

Crompton, D.W.T., and M.C. Nesheim (1972) A note on the biliary system of the domestic duck and a method for collecting bile. J. Exp. Biol., *56*:545–550.

Dornesco, G.T., and C. Zaharia (1967) Les canaux évacuateur de la bile et du suc pancréatique chez *Emys orbicularis* L. Anat. Anz., *120*:298–317.

Ells, H.A. (1954) The gross and microscopic anatomy of the liver and gall bladder of the lizard, *Sceloperus occidentalis biseriatus* (Hallowell). Anat. Rec., *119*:213–229.

Gautier, J., A.G. Kluge, and T. Rowe (1988) Amniote phylogeny and the importance of fossils. Cladistics, *4*:105–205.

Guibé, J. (1970) L'appareil digestif. In: Traité de Zoologie, Tome XIV: Reptiles, Fasc. II. P.P. Grassé, ed. Masson et Cie, Paris, pp. 521–548.

Hanson, R.F., P. Szczepanik, G.C. Williams, G. Grabowski, and H.L. Sharp (1979) Defects of bile acid synthesis in Zellweger's syndrome. Science, *203*:1107–1108.

Haslewood, G.A.D. (1978) The Biological Importance of Bile Salts. North-Holland Publishing Co., Oxford.

Hatfield, P.M., and R.E. Wise (1976) Anatomic variation in the gallbladder and bile ducts. In: Roentgenology of the Gallbladder an Biliary Tract. B. Felson, ed. Grune and Stratton, New York, pp. 15–22.

Hicken, N.F., Q.B. Coray, and B. Franz (1949) Anatomic variations of the extrahepatic biliary system as seen by cholangiographic studies. Surg. Gynecol. Obstet., *82:577*–584.

Joanen, T., and L. McNease (1987) Alligator farming in Louisiana, USA. In: Wildlife Management: Crocodiles and Alligators. G.J.W. Webb, S.C. Manolis, and P.J. Whitehead, eds. Surrey Beatty and Sons, Pty., Chipping Norton, New South Wales, Australia, pp. 329–340.

Jones, D.M. (1977) The sedation and anesthesia of birds and reptiles. Vet. Rec., *101*:340–342.

Lind, G.W., R.R. Gronwall, and C.E. Cornelius (1967) Bile pigments in the chicken. Res. Vet. Sci., *8*:280–282.

Lindner, H.H., V.A. Pena, and R.A. Ruggeri (1976) A clinical and anatomical study of anomalous terminations of the common bile duct into the duodenum. Ann. Surg., *184*:626–632.

Mathis, R.K., J.B. Watkins, P. Szczepanik-van Leeuween, and I.T. Lott (1980) Liver in the cerebro-hepato-renal syndrome: Defective bile acid synthesis and abnormal mitochondria. Gastroenterology, *79*:1311–1317.

McLelland, J. (1979) Digestive system. In: Form and Function in Birds. A.S. King and J. McLelland, eds. Academic Press, London, Vol. 1, pp. 69–181.

Moscona, A.A. (1980) Anatomy of the pancreas and Langerhans islets in snakes and lizards. Anat. Rec., *227*:232–244.

Rathke, C. (1866) Untersuchungen über die Entwickelung und den Körperbau der Krocodile. F. Vieweg und Sohn, Braunschweig.

Robb, J. (1960) The internal anatomy of *Typhlops* Schneider (Repilia). Aust. J. Zool., *8*:181–216.

Sabnis, J.H. (1967) Anatomy and histology of the liver and gall bladder in *Natrix piscator piscator* (Schneider), REPTILIA: OPHIDIA. Rev. Roum. Biol. Zool., *12*:233–237.

Secor, S.M., and J. Diamond (1994) Rapid upregulation of snake intestine in response to feeding: A new model of intestinal adaptation. Am. J. Physiol., *266*:G695–G705.

Secor, S.M., E.D. Stein, and J. Diamond (1995) Adaptive response to feeding in Burmese pythons: Pay before pumping. J. Exp. Biol., *198*:1313–1325.

Taguchi, H. (1920) Beiträge zur Kenntnis über die feinere der Eingeweideorgane der Krokodile. Mittelunger aus der Medizinischen Fakultat der Kaiserlichen Universitat zu Tokyo, *25*:119–188.

Tint, G.S., B. Dayal, A.K. Batta, S. Shefer, T. Joanen, L. McNease, and G. Salen (1980) Biliary bile acids, bile alcohols and sterols of *Alligator mississipiensis*. J. Lipid Res., *21*:110–117.

Tint, G.S., B. Dayal, A.K. Batta, S. Shefer, T. Joanen, L. McNease, and G. Salen (1981) The fecal bile acids and sterols of *Alligator mississippiensis*. Gastroenterology, *80*:114–119.

Tint, G.S., J. Bullock, A.K. Batta, S. Shefer, and G. Salen (1986) Ursodeoxycholic acid, 7-ketolithocholic acid, and chenodeoxycholic acid are primary bile acids of the nutria (*Myocastor coypus*). Gastroenterology, *90*:702–709.

Tint, G.S., G. Xu, A.K. Batta, S. Shefer, W. Nieman, and G. Salen (1990) Ursodeoxycholic acid, chenodeoxycholic acid and 7-ketolithocholic acid are the primary bile acids of the guinea pig. J. Lipid Res., *31*:1301–1306.

Weidersheim, R., and W.N. Parker (1897) Elements of the Comparative Anatomy of Vertebrates. Macmillan and Co. Ltd., London.

Wettstein, O.V. (1954) Crocodilia (2). In: Handbuch der Zoologie. W. Kükenthal and T. Krumment, eds. DeGruyter, Berlin, Vol. 7(1,4), pp. 321–421.

Wu, X.B., and B.H. Chen (1994) Histology of the digestive system of Chinese alligator. 1. The liver, gall bladder and pancreas. In: The Chinese Alligator. B.H. Chen, C.H. Hua, and B.H. Li, eds. An Hui Scientific Technology Publishing House, He Fei, P.R. China, pp. 54–59.

Xu G., G. Salen, A.K. Batta, S. Shefer, L.B. Nguyen, W. Niemann, T.S. Chen, R. Arora-Mirchandani, G.C. Ness, and G.S. Tint (1992) Glycocholic acid and glycodeoxycholic acid but not glycoursocholic acid inhibit bile acid synthesis in the rabbit. Gastroenterology, *102*:1717–1723.