Structure of the Posthepatic Septum and Its Influence on Visceral Topology in the Tegu Lizard, *Tupinambis merianae* (Teiidae: Reptilia)

Wilfried Klein,[1] **Augusto S. Abe,**[2] **Denis V. Andrade,**[2] **and Steven F. Perry**[1]

[1]*Institut für Zoologie, Universität Bonn, 53115 Bonn, Germany*
[2]*Departamento de Zoologia, Universidade Estadual Paulista – Rio Claro, 13506-900 Rio Claro, SP, Brazil*

ABSTRACT The posthepatic septum (PHS) divides the body cavity of *Tupinambis merianae* into two parts: the cranial one containing the lungs and liver and the caudal one containing the remaining viscera. The PHS is composed of layers of collagenous fibers and bundles of smooth muscle, neither of which show systematic orientation, as well as isolated blood vessels, lymphatic vessels, and nerves. Striated muscle of the abdominal wall does not invade the PHS. The contractions of the smooth muscles may stabilize the pleurohepatic cavity under conditions of elevated aerobic needs rather than supporting breathing on a breath-by-breath basis. Surgical removal of the PHS changes the anatomical arrangement of the viscera significantly, with stomach and intestine invading the former pleurohepatic cavity and reducing the space for the lungs. Thus, the PHS is essential to maintain the visceral topography in *Tupinambis*. J. Morphol. 258:151–157, 2003.
© 2003 Wiley-Liss, Inc.

KEY WORDS: *Tupinambis*; lizard; posthepatic septum; functional morphology; histology; x-ray; electron microscopy

All amniotes are aspiration breathers. In addition to movements of the ribs, the activity of accessory ventilatory structures, such as the mammalian diaphragm, is well known to aid in breathing. In non-mammalian groups, however, accessory breathing apparatus may also be present (Perry, 1983). Teiioids, to which the tegu lizard *Tupinambis* belongs, show a unique mode of dividing the body cavity: a posthepatic septum (PHS) separates a pleurohepatic cavity for the single-chambered lungs and the liver from a peritoneal cavity for the other viscera (Duncker, 1978; Klein et al., 2000). The gross morphology of this PHS is well known (Butler, 1889; Broman, 1904; Hochstetter, 1906; Goodrich, 1930; Duncker, 1978; Klein et al., 2000). Briefly, the PHS is made up in part of the hepatic ligament and the ventral mesenteries and the degree of the attachment to the body wall differs within the Teiioidea, being greatest in *Tupinambis* and *Crocodilurus* (Klein et al., 2000). Hochstetter (1906) studied its histology, finding flat bundles of what he called "smooth muscle" in *Tupinambis* and *Ameiva*. These muscles are concentrated in the caudal part of the ventral hepatic ligament, from which point they enter the ventral mesentery, making the central part of the PHS thicker and less translucent than the more dorsal part (Hochstetter, 1906). This kind of visceral organization is unique among lizards and the tegu may provide insight into the constraints in the evolution of the highly derived respiratory system of mammals.

A high negative pressure is necessary to inflate the extremely stiff mammalian lung properly (West, 2000). This pressure can only be generated in a completely closed pleural cavity and with the help of a mechanism that increases the efficiency of rib breathing. Therefore, it appears that the mammalian lung as we know it can only have evolved together with an evolving diaphragm. During ontogeny, the diaphragm contains two large openings near the spinal column between the pleural and peritoneal cavities. If one or both of the holes remain open after birth, the resulting diaphragmatic hernia is life-threatening or lethal because the lungs cannot be inflated and the intestine is pulled into the pleural space (Langmann, 1980). If ontogeny recapitulates phylogeny, the diaphragm must have been perforated in the evolutionary history of mammals. However, it remains questionable what role such a perforated membrane could play in the respiratory system of an animal.

Tegu lizards provide the ideal organism for testing the hypothesis that a partial diaphragm free of skeletal muscle is better for inflating a stiff lung than no diaphragm at all. Tegus have the least compliant (flexible) lungs of any lizard (Perry and Duncker,

1978, 1980). This low compliance results in increased work in breathing, which, in turn, means that the metabolic cost of taking a breath is potentially high. Thus, as active predators (Köhler and Langerwerf, 2002) tegus are under selective pressure to evolve a highly efficient breathing mechanism.

The function of the PHS in teiioid lizards remains unclear. As seen in birds and testudines (George and Shah, 1954; Duncker, 1978), striated muscle from the innermost abdominal muscles can invade a septum and thereby play an active role in the respiratory mechanics of the breathing system. The respiratory role may be of minor importance, as in the case of mm. costoseptales in birds (Duncker, 1978), or it could be of major importance, as in the diaphragm of mammals. If striated muscle invades the PHS in the tegu, it could facilitate ventilation by varying the tension of the PHS and thereby regulating the volume of the pleurohepatic cavity, especially under stress (e.g., locomotion). It is therefore necessary to confirm the histological structure of the PHS in *Tupinambis merianae* using modern light and electron microscopic techniques, especially regarding its insertion on the body wall and the identity of the "smooth" muscle.

Another possible function of the PHS may be simply to prevent the viscera from shifting cranially along the pressure gradient during inspiration. Except for the presence of a PHS, teiid lizards show no marked difference in the anatomical arrangement of their viscera compared with several other lizard families, such as, e.g., scincids, iguanids, or lacertids (Broman, 1904; Becker, 1993). Therefore, it is possible that the PHS in teiids has no significant effect on the general visceral topology because in its absence the remaining suspensory ligaments (mesos) would be sufficient to keep the viscera in place. To test this hypothesis, we removed the septum in some tegu lizards and compared X-ray images of their viscera with those from intact tegus.

MATERIALS AND METHODS

All specimens of *Tupinambis merianae* used in this study were captive-bred at the Universidade Estadual Paulista in Rio Claro, SP, Brazil. These tegus were fed every third day and fresh water was available ad libitum. Details about housing and breeding of tegus in Rio Claro, SP, were described previously (Lopes and Abe, 1999).

Histology

Five specimens of *Tupinambis merianae* (M_B: 1254.2 $\pm$ 170.9 g; SVL: 329.4 $\pm$ 18.2 mm) were killed by an intraperitoneal injection of pentobarbitone (50 mg kg^{-1}, Sagatal™, Bayer, Germany). The lungs were filled intratracheally with 2.5% glutardialdehyde in 0.1 Sörensen-phosphate buffer (pH 7.4; 300 mOsm l^{-1}) up to three-quarters of maximum lung volume (previously determined on pressure-volume diagrams). Subsequently, the same fixative was injected into the closed pleurohepatic and peritoneal cavities through a reservoir of fixative placed 20 cm above the animal, allowing complete perfusion of the entire body cavity. Lungs and viscera were left in situ overnight in the refrigerator, removed the

next day, and stored in the same buffer but with 1.0% glutardialdehyde. To remove the PHS completely without any damage, the part of the body wall attached to the PHS was removed intact.

Part of the body wall together with the PHS was trimmed and samples were taken from the free PHS and dorsally, laterally, ventrally, dorso- and ventrolaterally from the transition body wall–PHS. Samples were dehydrated, embedded in paraffin, and orientated such that the PHS was cut transversely. From every embedded part of the PHS three samples were cut into slices of 5–7 μm using a Leitz™ 1400 microtome and stained with AZAN after the method of Heidenhain (Romeis, 1968).

Electron Microscopy

Electron microscopy was carried out on a total of six samples from the ventral and lateral transition body wall–PHS and from the free PHS. These samples were postfixed with 2% OsO$_4$ for 2 h, washed in cacodylate buffer, embedded in Epon 812, and ultrathin sections (80–100 nm) were prepared using an Ultracut (Reichert-Jung) ultramicrotome. The ultrathin sections were contrasted with uranyl acetate and lead citrate using standard techniques before electron microscopic evaluation with a Zeiss™ EM 109.

Surgery

To rupture the PHS, four tegus were anesthetized with CO$_2$. When the animal no longer displayed any reaction to handling or pinching with a forceps, it was fixed with a rubber band in a supine position on an operation table and a constant low CO$_2$-flow was provided to the nostrils. The belly was disinfected with tincture of iodine before surgery. First, one incision (1.5–2.5 cm, depending on the size of the tegu) was made with scissors on the ventrolateral body wall caudal to the last long rib. The fat-body, stomach, and intestine were retracted and the PHS was ruptured with forceps in a stepwise fashion beginning at the lateral part and moving to the dorsal midline and ventrally, approaching the abdominal vein as closely as possible. The caudal part of the hepatic ligament was resected. The same surgery was carried out on the other side. The incisions were sutured and disinfected with tincture of iodine. Tegus were then released and allowed to recover.

After experimentation, animals were killed and visual inspection verified the persistence of the septal lesion.

X-Ray Images

X-ray images were taken from four tegus with intact PHS (M_B: 1221.7 $\pm$ 193.7 g; SVL: 300.0 $\pm$ 15.4 mm) and four tegus living without a PHS for 11 months (M_B: 911.3 $\pm$ 142.4 g; SVL: 281.5 $\pm$ 16.1 mm). X-ray imaging was carried out at the Departamento "Clinica e Cirurgia Veterinária" at UNESP in Jaboticabal, SP, Brazil. The main part of the procedure was carried out in the early morning, when temperatures were still low and the animals generally remained quiescent. Nevertheless, they were physically restrained. An X-ray apparatus (TUR, Dresden, D 800-3) at 35 Kv, 4 mAs, and 200 mA was used and pictures of each tegu were taken on Kodak™ film (T-MAT G/RA) in a dorsoventral as well as lateral–right direction. Two tegus of each group were fed the evening before the experiment with minced meat ad libitum, whereas the other two of each group were fasted for 4 days. In one of the fasting animals of each group 15 ml of barium sulfate (100% Bariogel™) were injected into the stomach through the esophagus. X-ray photographs were made immediately and 60, 120, and 240 min after injection.

RESULTS
Effects of Surgery

Postmortem control, which was carried out 4–11 months after surgery, revealed no regrowth of mes-
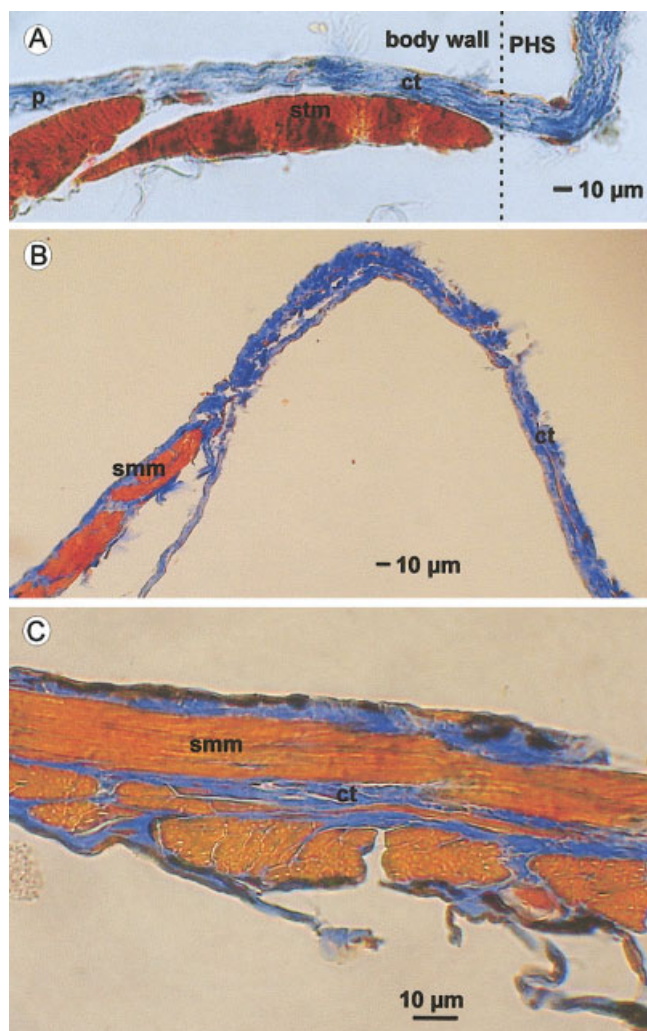
Fig. 1. The histological structure of the PHS in *Tupinambis merianae*. LM. **A:** Transition PHS–pleuroperitoneal membrane. **B,C:** Free PHS. ct, connective tissue; p, peritoneum; smm, smooth muscle; stm, striated muscle. AZAN staining.

enteries and ligaments. Also, no newly formed attachments were detected. During destruction of the PHS, it retracted to its origin on the liver and stomach. Although these residues were still detectable during postmortem control, the lesions had not closed.

Histology and Electron Microscopy

The peritoneum forms the innermost layer in the body cavity, being attached to the body wall muscles. The transition from the parietal pleuroperitoneal membrane (PPM) to the free PHS is continuous, without any borderline. Both PPM and lateral parts of the PHS consist mostly of collagenous fibers, but also contain pigment cells and isolated bundles of smooth muscle (Fig. 1A). There is no qualitative difference between the samples from the ventral, lateral, or dorsal body wall. Striated muscle does not invade the PHS or the PPM. Towards its insertion

on liver and stomach, the free PHS is thickened due to abundant smooth muscle (Fig. 1B). Layers of longitudinal fibers alternate with transversely orientated ones (Fig. 1C). Electron microscopy clearly demonstrates the difference between the striated muscle of the body wall and the smooth muscle in the PHS (Fig. 2A–D). Also, the mixed orientation of connective tissue fibers and smooth muscle fibers can be seen (Fig. 2A,B). No striated muscle was detected in the PHS.

X-Ray Images

The X-ray images demonstrate the division of the body cavity into two parts. The PHS is located at the level of the last long ribs. It is transversely orientated in the body cavity and clearly delineates the boundary between the pleurohepatic and the peritoneal cavities (Fig. 3A). The lungs occupy most of the pleurohepatic space, the liver taking up the ventrocaudal part. This pattern is also visible in the recently fed tegus. Here the ventral part of the PHS is displaced cranially due to the filling of the stomach and intestine, but the craniocaudal expansion of the lungs remains unchanged (Fig. 3B).

In tegus without PHS, no distinct pleurohepatic cavity is perceptible and the space for the lungs is greatly reduced (Fig. 3C). This can be seen more easily in the fed tegus, where the lungs are displaced to the most cranial and dorsal parts of the body cavity by the stomach and intestine (Fig. 3D).

Injection of barium sulfate reveals that in tegus with intact PHS, the stomach and the intestine are located in the mid-caudal region of the body cavity. The stomach lies on the left side of the body cavity, reaching caudally nearly to the pelvic region and turning cranially to form the letter J. The intestine lies medially to the stomach, which the transport of barium sulfate reveals to occupy the middle of the body cavity (Fig. 4A–D). Tegus without PHS, on the other hand, show a complete disorganization of the viscera, in which the entire stomach is turned such that the morphological caudal end lies in the cranial part of the former pleurohepatic cavity (Fig. 4E–H). Additionally, the intestine is also displaced cranially to the level of the shoulder girdle next to the heart.

DISCUSSION
Effects of Surgery

The present study was part of a larger one in which 26 tegus underwent surgery: 13 tegus were sham-operated and in 13 the PHS was ruptured as described above. Since all animals recovered from surgery, the surgical procedure itself was considered satisfactory. In one of the operated tegus (~1 year old), the PHS was absent, possibly due to an ontogenetic defect. This tegu did not differ in behavior or size from the ones of the same clutch but the viscera were disorganized, as seen in the tegus in which the PHS had been surgically removed. The high survival
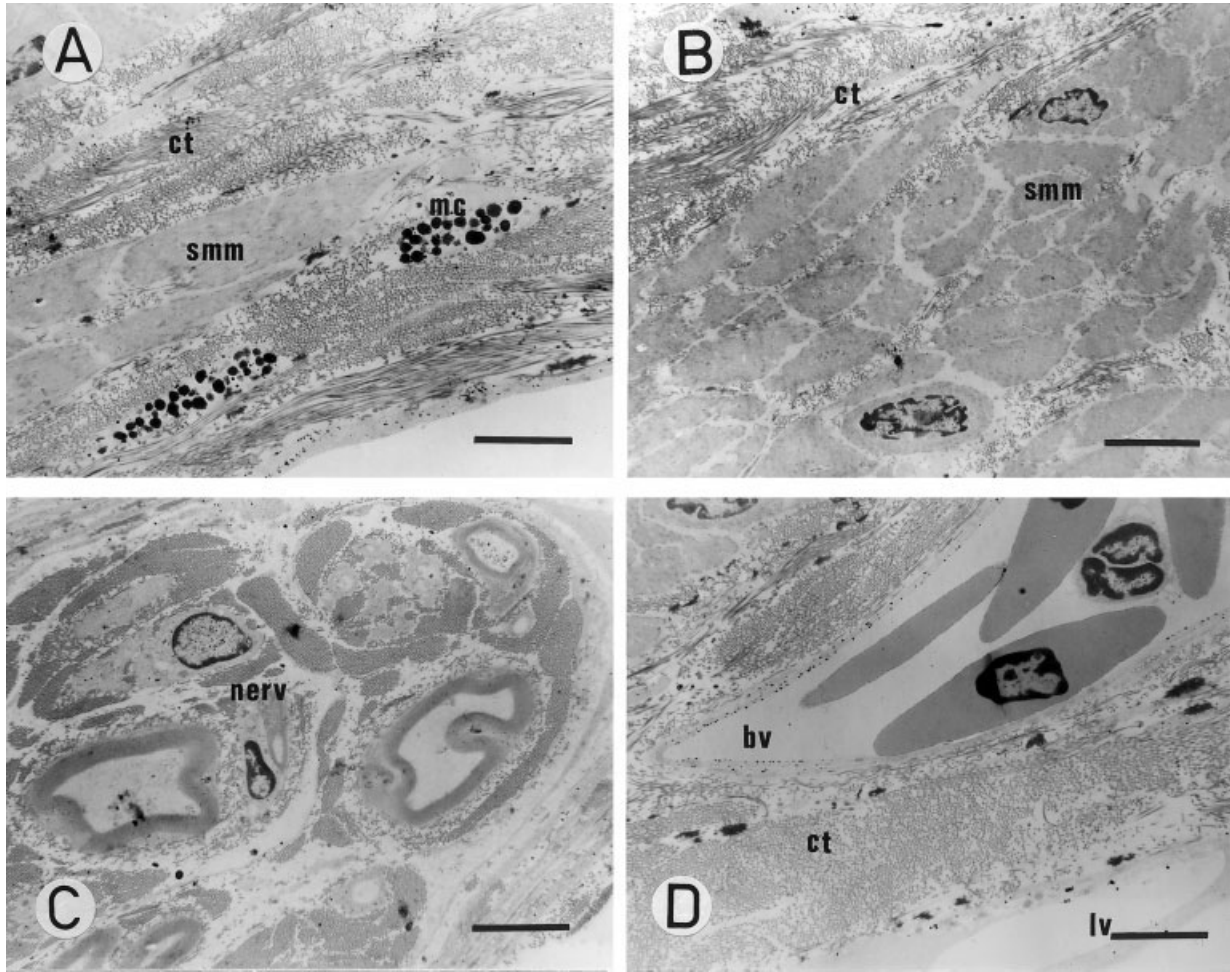
Fig. 2.   The PHS of *Tupinambis merianae*. TEM. **A,B:** PHS containing connective tissue and smooth muscle. **C:** Nerve in the PHS. **D:** Blood vessel and lymphatic vessel in the PHS. Scale bar = 3 μm. bv, blood vessel; ct, connective tissue; lv, lymphatic vessel; mc, mast cell; smm; smooth muscle.

rate among the septum-removed animals suggests that the PHS is not necessary for survival under laboratory conditions, but this conclusion is not necessarily applicable to free-living tegus. By analogy, mammals (including man) in which the diaphragm is paralyzed by transsection of the phrenic nerve can survive, but their aerobic capacities are severely limited (Katagiri et al., 1994).

Histology and Electron Microscopy

Histological examination showed no striated muscle from the abdominal wall invading the PHS. The PHS was continuous with the PPM, which forms the innermost layer of the coelomic cavity. The collagenous fibers as well as the bundles of smooth muscle showed no regular orientation: longitudinal and transverse sections occurred simultaneously in a single section. This observation is in agreement with Hochstetter's (1906) description of densely packed flat bundles of smooth muscles in the PHS of *Tupinambis*. He also found bundles of smooth muscles

concentrated in the medial part of the PHS, as demonstrated by our results.

To produce respiratory movements with the PHS, the smooth muscle fibers should ideally be orientated as those found in the mammalian diaphragm, i.e., originating at the body wall and converging toward the center of the PHS. The smooth muscles of the PHS, however, did not approach the body wall, but were concentrated in the central parts of the PHS. Therefore, contraction of the smooth muscle does not affect the volume of the pleurohepatic cavity by moving the liver caudally, but could increase the tone of the PHS. Also, contraction of smooth muscle in general is slow and of long duration compared with that of striated muscles. Thus, the PHS appears not to be involved in respiratory activities on a breath-by-breath basis. However, the PHS could support breathing under conditions of elevated aerobic demand, such as locomotion, when contraction of smooth muscle fibers would stiffen the PHS and maintain a large pleurohepatic space. Indeed, teiids are characterized as actively foraging lizards
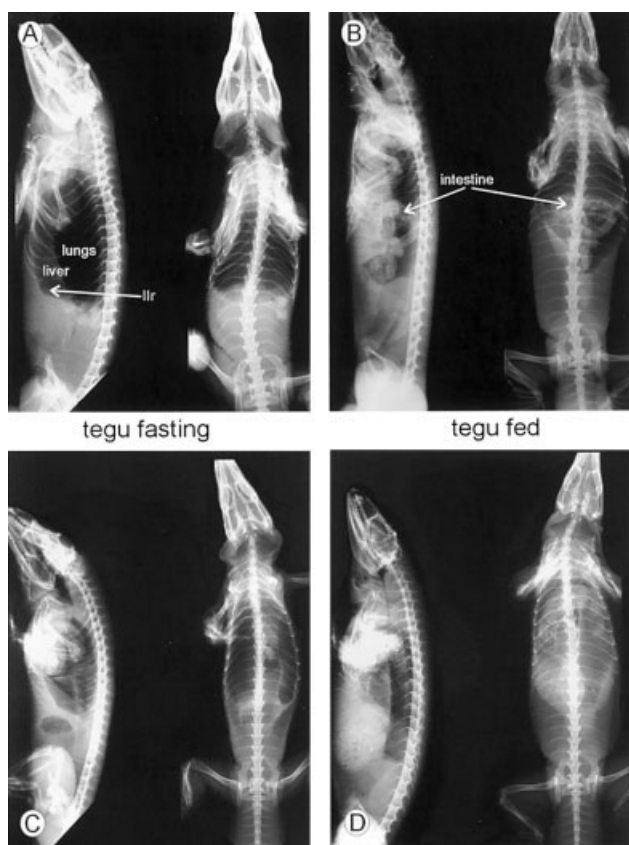
Fig. 3. X-ray images of *Tupinambis merianae* with PHS (**A,B**) and without PHS (**C,D**). The left part of each picture shows an image in lateral–right direction and the right part in dorsoventral direction. The tegus on the left side fasted for 4 days and the ones on the right were fed the evening before the experiment. Note the clear pleurohepatic cavity in the tegus with intact PHS and the reduced lung volume in the tegus without PHS. llr, last long rib.

(Magnusson et al., 1985; Garland, 1993). During resting states the smooth muscles may be relaxed, allowing partial collapse of the lungs. During exercise, the changes in volume produced by movements of the ribs may, as a result, be greater when the smooth muscle in the PHS contracts and consequently result in greater tidal volumes.

Recently, Pickering and Jones (2002) proposed a nonrespiratory origin of the mammalian diaphragm by describing an external sphincter muscle on the esophagus of *Xenopus laevis*. They propose that this muscle prevents reflux of stomach content into the esophagus and considered it homologous to the crural part of the mammalian diaphragm. As the mammalian diaphragm is composed of costal, sternal, and crural parts (Sobotta and Becher, 1975), an originally nonrespiratory role of at least one of these parts cannot be ruled out. Furthermore, a nonrespiratory function of one of the diaphragm parts suggests a stepwise evolution of the mammalian diaphragm, starting with a muscle-free membrane, that successively has been invaded by striated muscles, resulting in the present role as the main inspiratory motor in mammals. The hypothesis of

Pickering and Jones (2002) supports the idea that the PHS of teiids can be seen as an analogous structure to the mammalian diaphragm, as it probably changed its primary role of fixing the viscera in the body cavity to a more respiratory function in the larger teiids, such as *Tupinambis*.

X-Ray Images

The results of visceral topology obtained by the X-ray images are in accordance with earlier descriptions of tegu morphology (Broman, 1904; Hochstetter, 1906; Duncker, 1978; Klein et al., 2000), in which the lungs are located dorsocranially in the body cavity, the stomach, on the left side, and the remaining viscera, in the medial and caudal part. The pathological reorganization of the viscera following removal of the PHS is consistent with the hypothesis that the ventral and dorsal mesopneumonium and dorsal and ventral mesenteries, common to all lizards, are not sufficient for fixing the viscera to maintain a given space for the lungs in tegus.

In this case, how do other lizards, which also possess single-chambered lungs like the tegu but lack PHS, maintain their visceral organization? Tegus are very large and actively foraging lizards that can reach a body weight of more than 5 kg (Abe, 1987), whereas most lizards are much smaller (Zug, 1993). In small lizards, changes in the morphology of mesos or organs may improve adhesive forces leading to "structural tightness" of the viscera in general (Gans, 1970). This, together with multiple branching of the ventral hepatic ligament, as reported for lacertid, iguanid, and scincid lizards, as well as for *Ameiva* and *Tupinambis* (Broman, 1904; Hochstetter, 1906; Klein et al., 2000) may be sufficient to fix the liver to the ventral body wall. The liver itself may also be broad and dome-shaped and act as a mechanical barrier for the intestine in non-teiioid lizards.

With increasing body size the forces acting on the lungs and viscera or those produced by lungs and viscera themselves may concomitantly increase the need for additional structures to keep the viscera or lungs in place. This may be of increasing importance during locomotion, where breathing is impaired according to a mechanical constraint, as suggested by Carrier (1987, 1990). Therefore, the PHS may be of significance in actively foraging tegus in order to maintain a large pleural space. Other large lizards such as *Iguana iguana*, which can be even larger than tegus, do not need a PHS-like structure, as they do not breathe during intense locomotion but sustain exercise mainly anaerobically (Wang et al., 1997; Farmer and Hicks, 2000). Additionally, the single-chambered lungs of tegus are the least compliant ones of all lizards (Perry and Duncker, 1978), and therefore the pressures produced during inspiration may be relatively great compared with those of other lizards. Without any additional structure to
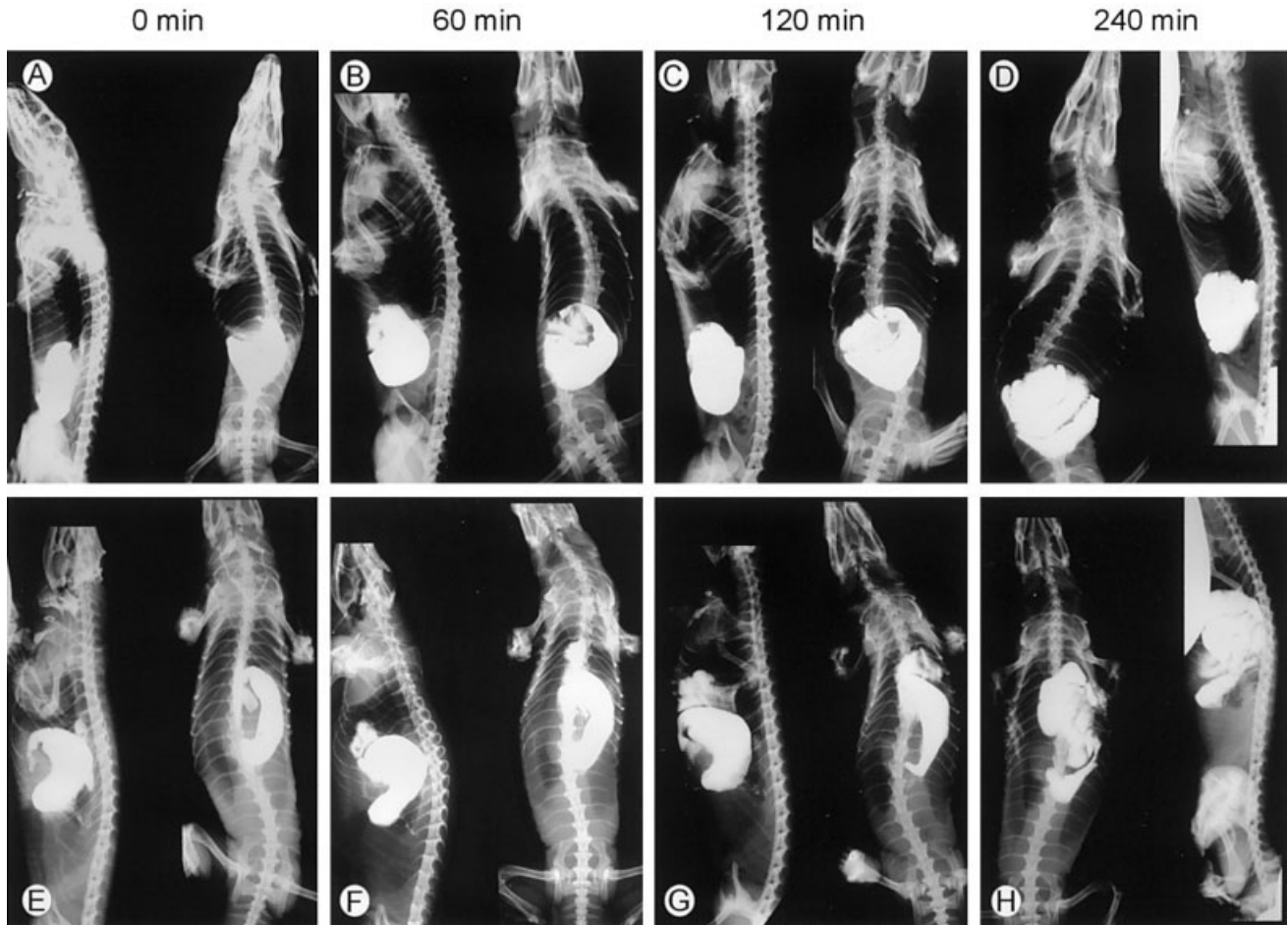
Fig. 4.   X-ray images of *Tupinambis merianae* with intact PHS (**A–D**) and with removed PHS (**E–H**) immediately, 60, 120, and 240 min after injection of barium sulfate into the stomach. The left part of each picture shows an image made in lateral–right direction and the right part taken in dorsoventral direction. Note the clear localization of stomach and intestine caudal to the PHS in the intact tegu (**A–D**) and the lack of this organization in the tegu without PHS (**E–H**).

stabilize the space for the lungs, the remaining viscera would be sucked into the pleural space, as demonstrated here for tegus with removed PHS, thereby reducing the effectiveness of the aspiration mechanism.

Among mammals, the length of the alimentary canal has been shown to differ between herbivores, omnivores, and carnivores, being shortest in the last group (Jacobshagen, 1937). The tegu, a mainly carnivorous species (Köhler and Langerwerf, 2000), may consume up to 20% of its own body weight at one time (WK, pers. obs.), and in such cases the esophagus and stomach need to be very distensible. This flexibility of the stomach may also have an effect on the mesenteries, which must fix the stomach but still allow for its distension.

In reptiles with highly heterogeneous lungs, the entire lung is attached to the body wall (snakes), or in part to the body wall and to a postpulmonary septum (testudines and monitor lizards) (Duncker, 1978). Such attachment prevents the densely partitioned respiratory regions from collapsing and thus mechanically stabilizes the heterogeneous lungs

(Perry and Duncker, 1980). Single-chambered lungs, on the other hand, are fixed in an undivided pleuroperitoneal cavity only by mesopneumonia. The left ventral mesopneumonium is reduced in nearly all lizard groups, at least in its caudal part, or it inserts on the lateral body wall (Broman, 1904). The right ventral mesopneumonium, however, is complete in numerous groups of lizards and inserts on the ventral mesentery or on the dorsal surface of the liver, but may also be reduced as seen in scincids (WK, pers. obs.). Teiids are among the few lizards with single-chambered lungs that completely lack both ventral mesopneumonia and, therefore, the role of reserving space for the lungs may be accomplished by the PHS.

This study shows that the posthepatic septum in *Tupinambis* is essential for the proper anatomical arrangement of their viscera and to maintain a given space for the lungs. Because striated muscle inserting in the PHS is lacking, a breath-by-breath support of breathing is unlikely. However, an increase in septal tone could help preserve the expiratory reserve volume and increase the efficiency of

costal breathing, thus allowing tegus to compensate for the high work of breathing necessary to ventilate their stiff lungs. In mammals, a similar selective pressure to ventilate their low compliant lungs may have occurred and the development of the lung–diaphragm complex can only be explained by evolution of both systems together. There are two theoretical explanations for the origin of the mammalian diaphragm: 1) that the lung inserts itself between the body wall and the innermost layer of body wall musculature, thus forming a primarily muscular diaphragm (Gräper, 1928); and 2) that a primarily muscle-free septum is invaded secondarily by slips of body wall muscle (Broman, 1911). Although the latter hypothesis is supported by embryological studies (Corliss, 1976), there is no direct evidence that a muscle-free diaphragm would actually work in an adult mammal. Some mammals (e.g., dogs) can live with a paralyzed diaphragm, which therefore acts like a muscle-free septum. In cats and rabbits, on the other hand, a paralyzed diaphragm leads to a substantially decreased performance or to death (Katagiri et al., 1994).

The fact that the mammalian diaphragm and the PHS are not homologous structures, but have comparable function, supports the hypothesis of the membranous origin of the mammalian diaphragm by demonstrating that a perforated membrane without striated muscle can aid respiration in a species with stiff lungs. One can postulate convergent evolution of membranous structures with similar functions based exclusively on selective pressure acting on a similar complex of interdependent mechanisms in teiid lizards and in the ancestors of mammals.

ACKNOWLEDGMENTS

LITERATURE CITED

Abe AS. 1987. Ventilação, trocas gasosas, tensão de gases e pH do sangue no teiú, *Tupinambis teguixin*: efeitos da temperatura (Reptilia Teiidae). Thesis, UNESP-Rio Claro, SP, Brazil.

Becker HO. 1993. Vergleichende Untersuchungen am respiratorischen Apparat anguimorpher Eidechsen: Eine stammesgeschichtliche Deutung. Dissertation. Rheinische Friedrich-Wilhelms-Universität Bonn.

Broman I. 1904. Die Entwicklungsgeschichte der Bursa omentalis und ähnlicher Rezessbildungen bei den Wirbeltieren. Entwicklungsgeschichtliche Monographien.

Broman I. 1911. Über die Entwicklung des membranösen Pericardiums und des Zwerchfells bei den Wirbeltieren. Ergeb Anat Entwickl-Gesch 20:1–42.

Butler GW. 1889. On the subdivision of the body-cavity in lizards, crocodiles and birds. Proc Zool Soc 31:452–474.

Carrier DR. 1987. The evolution of locomotor stamina in tetrapods: circumventing a mechanical constraint. Paleobiology 13: 326–341.

Carrier DR. 1990. Activity of the hypaxial muscles during walking in the lizard *Iguana iguana*. J Exp Biol 152:453–470.

Corliss CE. 1976. Patten's human embryology. New York: McGraw-Hill.

Duncker H-R. 1978. Funktionsmorphologie des Atemapparates und Coelomgliederung bei Reptilien, Vögeln und Säugern. Verh Dtsch Zool Ges 72:99–132.

Farmer CG, Hicks JW. 2000. Circulatory impairment induced by exercise in the lizard *Iguana iguana*. J Exp Biol 203:2691–2697.

Gans C. 1970. Strategy and sequence in the evolution of the external gas exchangers of ectothermal vertebrates. Forma et functio 3:61–104.

Garland TJ. 1993. Locomotor performance and activity metabolism of *Cnemidophorus tigris* in relation to natural behaviors. In: Wright JW, Vitt LJ, editors. Biology of whiptail lizards of the genus *Cnemidophorus*. Norman: Oklahoma Museum of Natural History. p 163–210.

George JC, Shah RV. 1954. The occurrence of a striated outer muscular sheath in the lungs of *Lissemys punctata granosa* Schoepff. J Anim Morphol Physiol 1:13–16.

Goodrich ES. 1930. Studies on the structure and development of vertebrates. New York: Macmillan.

Gräper L. 1928. Zwerchfell, Lunge und Pleurahöhlen in der Tierreihe. Anat Anz Erg Hefte 66:71–77.

Hochstetter F. 1906. Über die Entwicklung der Scheidewandbildungen in der Leibeshöhle der Krokodile. Voeltzkows Reise in Ostafrika. Wissenschaftliche Ergebnisse 4:141–205.

Jacobshagen E. 1937. IV. Mittel- und Enddarm. In: Bolk L, Göppert E, Kallius E, Lubosch W, editors. 3. Bd. Darmsystem, Atmungssystem, Coelom. Berlin: Urban und Schwarzenberg p 563–724.

Katagiri M, Young RN, Platt RS, Kieser TM, Easton PA. 1994. Respiratory muscle compensation for unilateral or bilateral hemidiaphragm paralysis in awake canines. J Appl Phys 77: 1972–1982.

Klein W, Böhme W, Perry SF. 2000. The mesopneumonia and the post-hepatic septum of the Teiioidea (Reptilia: Squamata). Acta Zool (Stockh) 81:109–119.

Köhler G, Langerwerf B. 2000. Tejus — Lebensweise Pflege Zucht. Offenbach: Herpeton.

Langmann J. 1980. Medizinische Embryologie, 6th ed. Stuttgart: Georg Thieme.

Lopes HR, Abe AS 1999. Biologia reprodutiva e comportamento do teiu, *Tupinambis merianae*, em cativeiro (Reptilia, Teiidae). In: Fang TG, Montenegro OL, Bodmer RE. editors. Manejo y Conservación de Fauna Silvestre en América Latina. La Paz, Bolivia: Instituto de Ecología. p 259–272.

Magnusson WE, de Paiva LJ, da Rocha RM, Franke CR, Kasper LA, Lima AP. 1985. The correlation of foraging mode in a community of Brazilian lizards. Herpetologica 41:324–332.

Perry SF. 1983. Reptilian lungs. Functional anatomy and evolution. Adv Anat Embryol Cell Biol 79:1–81.

Perry SF, Duncker H-R. 1978. Lung architecture, volume and static mechanics in five species of lizards. Resp Phys 34:61–81.

Perry SF, Duncker H-R. 1980. Interrelationship of static mechanical factors and anatomical structure in lung evolution. J Comp Physiol B 138:321–334.

Pickering M, Jones JFX. 2002. The evolution of the diaphragm. Abstr Comp Biochem Physiol A 132:S25.

Romeis B. 1968. Mikroskopische Technik. München: R. Oldenbourg.

Sobotta J, Becher H. 1975. Atlas of human anatomy, vol. 2. Visceral organs. München: Urban & Schwarzenberg.

Wang T, Carrier DR, Hicks JW. 1997. Ventilation and gas exchange in lizards during treadmill exercise. J Exp Biol 200: 2629–2639.

West JB. 2000. Respiratory physiology — the essentials, 6th ed. Baltimore: Lippincott Williams & Wilkins.

Zug GR. 1993. Herpetology. San Diego: Academic Press.